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Deadwood enrichment in Fennoscandian spruce forests – New results from the EVO experiment

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ABSTRACT

In Fennoscandian forests, evidence on the effects of variable tree retention, prescribed burning and deadwood creation on deadwood quantity and quality is still scarce. We studied the effects of prescribed burning, tree retention and downed wood creation on the deadwood profile in managed boreal Norway spruce forest stands over a 16-year period. The stand scale treatments of the experiment included cuttings with a constant volume of dispersed retention trees (50 m^3 ha^{-1}, ca. 200 trees per ha), and three levels of downed deadwood creation (5, 30 and 60 m^3 ha^{-1}), in both upland and paludified biotopes of *Myrtillus* site type, with or without prescribed burning, with three replicates each.

After 16 years since the treatments, the diverse deadwood profiles with varying distribution by decay class were formed. The volume of deadwood varied from 9 to 107 m^3 ha^{-1} with a mean of 65 m^3 ha^{-1}. The index of deadwood diversity was positively influenced by prescribed burning and negatively influenced by deadwood creation. The volume of all deadwood and coarse woody debris (CWD), volume and number of logs, as well as dead to live volume ratio increased after prescribed burning and with the level of deadwood creation. The positive effect of deadwood creation on the total CWD volume was higher in the upland biotopes than in the paludified ones. The highest amounts of all deadwood, CWD and logs were recorded in the upland biotopes after prescribed burning without deadwood creation. Our findings highlight the impact of tree retention with prescribed burning and deadwood creation in diversifying deadwood profile and maintaining deadwood continuum for decades.

1. Introduction

Deadwood serves as habitat, shelter, and nutrient source for multiple organisms, which provide a wide range of ecosystem services, e.g., carbon and nutrient storage, decomposition, nutrient turnover, and pollination (Stokland et al., 2012; Löfroth et al., 2023). The biodiversity of species dependent on deadwood could be driven by either resource availability represented by deadwood amount or habitat heterogeneity characterized by deadwood diversity or both (Seibold et al., 2015; Sandström et al., 2019). Deadwood quantity and quality are regulated by various abiotic, biotic, and anthropogenic factors, interacting across landscapes and forest stands, as well as by natural disturbances and forest management practices (Shorohova and Kapitsa, 2015; Kapusta et al., 2020; Bujoczek and Bujoczek, 2022). Timber harvesting, fire suppression, and salvage logging reduce deadwood abundance and diversity (Siitonen, 2001; Löfroth et al., 2023). Natural disturbance dynamics have been largely eliminated, and the irregular occurrence of disturbance events has been replaced by a regular management regime of thinning, clearcutting and replanting (Schelhaas et al., 2003). Early successional forests with post-disturbance deadwood legacies have vanished (Kuuluvainen and Gauthier, 2018). In Fennoscandia, hundreds of species are threatened due to unavailability of deadwood (Kålås et al., 2010; ArtDataBanken, 2015; Hyvärinen et al., 2019). Thus, restoring a continuous supply of various amount and quality of diverse deadwood is vital to reverse the negative trends in biodiversity and forest ecosystem resilience (Löfroth et al., 2023).

In Finland, the number of fires and the area burned are currently small, having declined drastically during the twentieth century from 10 – 15 000 ha to less than a thousand hectares ha annually (Lindberg et al., 2020, 2021; Finnish Statistical Yearbook of Forestry 2022, 2023). Since

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1960s fire suppression, changes in forest structure and decrease of prescribed burning as a tool for enhancing forest regeneration have led to reduction in the diversity of fire related species and habitats (Hyvärinen et al., 2019) and negatively influenced the quantity and quality of deadwood (Similä and Junninen, 2012; Halme et al., 2013). In contrast to many countries, where prescribed burning is mainly used to reduce forest fuels to decrease fire hazard, in Finland it is currently used as a tool for ecological restoration and forest regeneration (Similä and Junninen, 2012; Lindberg et al., 2020).

The long-term viability of many species, including threatened ones, relies on rehabilitation of habitat availability and suitability within managed forest landscapes. Variable retention forestry, and habitat restoration through prescribed burning and artificial addition of coarse woody debris have been practiced in Fennoscandian forests to some extent during the past few decades. In the 1990s, several forest management experiments, and later, in the 2000s, ecological restoration experiments were established in Finland and in Sweden to compare the effects of various treatments on different species groups (Gustafsson et al., 2020, Koivula and Vanha-Majamaa, 2020). However, there is still little evidence on ecological effects of prescribed burning combined with variable retention felling with deadwood addition especially in the long term (Sandström et al., 2019; Koivula and Vanha-Majamaa, 2020).

Burning may decrease the amount of deadwood, particularly coarse woody debris (CWD) of advanced decay (Eriksson et al. 2013) and create variable patterns of new CWD depending on the rates of post-fire tree mortality (Sidoroff et al., 2007). Living tree retention alone generally supports a variety of living trees, CWD volumes and qualities over time with increasing of downed CWD and decreasing standing CWD (Jönsson et al., 2023). The effectiveness of deadwood creation is affected by pre-treatment deadwood amount, stand age, natural tree mortality and tree species composition (Doerfler et al., 2017). Moreover, both short- and long-term effects of burning and retained wood on the deadwood quantity and quality can be mediated by within-site biotope variability related to complex effects of variation in topography and site moisture on the deadwood profile. Burning may further affect within-site moisture variability, as the water-table level may rise following fire, thus potentially increasing topography-related paludification in surface depressions (Simard et al., 2007).

Our objective was to evaluate the effects of the following combined restoration treatments: live tree retention, deadwood creation and prescribed burning, on the deadwood amounts and diversity in managed mature southern boreal mesic Norway spruce (*Picea abies* (L.) H. Karst.) forest stands over the 16-year period. The restoration treatments aimed at rehabilitation of threatened habitats and species composition (Vanha-Majamaa et al., 2007). We estimated 1) total volumes of deadwood, volumes of coarse and fine woody debris (CWD and FWD, respectively), deadwood to live tree volume ratios, as well as diversity of living trees and CWD and 2) analyzed the deadwood distributions by size, tree species, decay class and position, before and 16 years after prescribed burning, dispersed retention and deadwood creation. The effects of within tree stand variation in site conditions were taken into account by characterizing upland and paludified biotopes separately within each stand.

We hypothesized that (1) both amount and diversity of deadwood increase after prescribed burning with the increased level of deadwood creation with more pronounced effects in the upland biotopes; (2) higher amounts of fuel in upland biotopes with higher level of deadwood creation lead to higher intensity of fire, and, consequently, increased fire-induced tree mortality; (3) snags and downed logs decomposing at different rates form a diverse deadwood profile.

2. Materials and methods

2.1. Study area and Evo restoration experiment

The study was performed in Finland, in the Evo-Vesijako area (61°N, 25°E), within the southern boreal zone (Ahti et al., 1968). The mean annual temperature in the study area is +3.1 °C with mean annual precipitation of 670 mm and the mean length of the growing period of 160 days. The bedrock consists of orogenic granitoids and is covered with a thick layer of till (Anon., 1995). The area has been influenced by slash-and-burn cultivation, grazing and small-scale gap and selective fellings until the end of the 19th century. After the Second World War the forests have been intensively managed according to general Finnish silvicultural guidelines, which include clear-cut harvesting, artificial regeneration and thinnings during the rotation period. Thus, the forest structure has become relatively even-aged, and the amount of deadwood has been reduced considerably.

The Evo restoration experiment was established in 2001 in mature Norway spruce dominated forest stands of the mesic site type (Vanha-Majamaa et al., 2007). The general aim has been to analyze the effects of restoration treatments on the biodiversity and ecosystem functioning.

The Norway spruce dominated stands had a mixture of birch (*Betula pendula* Roth., *B. pubescens* Ehrh.), European aspen (*Populus tremula* L.), and Scots pine (*Pinus sylvestris* L.). Altogether 24 stands were selected for the experiment. Each stand consisted of an upland and a paludified biotope. The upland biotopes belonged to the *Myrtillus* site type, but some stands also had characteristics of the *Oxalis-Myrtillus* site type (Cajander 1926). The vegetation and moisture conditions of the paludified biotopes varied considerably and consisted of patches of paludified *Myrtillus* spruce forest and *V. myrtillus* spruce mire (see Vanha-Majamaa and Jalonen, 2001 for details in biotope mapping on similar *Myrtillus* type sites, type definitions follow Laine and Vasander, 2005). The size of paludified patches varied up to one hectare (Lilja et al., 2005).

The treatments consisted of three levels of deadwood creation: 5, 30 and 60 m^3 ha^{-1}, cuttings with a volume of 50 m^3 ha^{-1} of standing evenly dispersed retention trees (on average 200 retained trees per ha), and burning treatments applied in half of the stands (Table 1). In addition, unburned stands without cutting treatments were used as references. Each treatment was replicated three times. The restorative cuttings carried out in spring 2002 were followed by burnings in summer 2002 (Lilja et al., 2005; Vanha-Majamaa et al., 2007). The 20 * 40 m sample plots were placed randomly inside each stand, in both the upland and paludified biotopes. The total number of sample plots in the experiment was 48 (Table 1).

The pre-treatment volume of living and standing dead trees did not differ between the upland and paludified biotopes (Lilja et al., 2005). The pre-treatment volume of downed deadwood was higher in the upland than in the paludified biotope owing to previous cuttings, which increased the volume of stumps and small-diameter fallen logs. The volume of downed deadwood before treatments consisted mainly of thinning residues and stumps.

In the Evo experiment, the immediate effects of restoration treatments on living tree volume and deadwood were examined in 2003 (Lilja et al., 2005). After one year, the variation in living tree volume between forest stands was generally high, especially after burning, and especially in the upland biotopes, with no significant differences between deadwood creation levels. Prescribed burning reduced the volume of living trees. The volumes of deadwood were highly variable as well. In the upland biotope, prescribed burning did not affect the total amount of deadwood across deadwood creation levels. However, the volume of standing dead trees was higher after burning. In the paludified biotopes, the highest amount of deadwood was formed after the highest level of deadwood creation and burning, whereas the lowest volume was found in the unburned reference stand. Retention without burning did not cause immediate tree mortality - the mean volume of snags and logs was less than 1 m^3 ha^{-1} across all deadwood creation levels in both biotopes (Lilja et al., 2005).

Table 1
Experimental design: number of replicates per treatment.

48 Norway spruce-dominated mature managed forest stands on mesic-site type								
	Standing retention 50 m^3/ha						No cuttings	
	Deadwood creation							
	5 m^3/ha		30 m^3/ha		60 m^3/ha			
	Burned	Unburned	Burned	Unburned	Burned	Unburned	Burned	Unburned
Biotope	Number of replicates							
Upland	3	3	3	3	3	3	3	3
Paludified	3	3	3	3	3	3	3	3

2.2. Field inventories

Inventories of living trees and deadwood by size, tree species, decay class and position were conducted before, one- and 16-years following restoration treatments. In 2001 and 2003 (pre-treatment and one year after treatment) the diameter and height of each tree of more than 2 m in height of more than 10 cm in diameter at the height of 1.3 m were measured within the sample plot and the 5 m buffer zone (Lilja et al., 2005). All visible pieces of FWD with diameter of 2–9 cm on the forest floor, and CWD with diameter of more than 10 cm were inventoried. The tree species, diameter, height or length, decay class, and type (snags, stumps, logs, and branches/fragments) were recorded. The decay class was assigned to each piece according to the following characteristics: 1) tree died recently, bark is present; 2) bark is mainly decomposed, knife blade penetrates a few millimetres into the wood; 3) knife blade penetrates 1–2 cm into the wood; 4) knife blade penetrates 2–5 cm into the wood; and 5) knife blade penetrates all the way into the wood (Karjalainen and Kuuluvainen, 2002, modified from Renvall, 1995). In 2018, all living trees and deadwood were measured analogously. The mortality mode was recorded for snags or logs as following: died naturally standing, dead naturally broken or uprooted, cut down.

2.3. Data analysis

The height or length of CWD pieces for the 2018 inventory were estimated using the tree species specific height-diameter relationships expressed as non-linear regression equations established separately for upland and paludified biotopes. The volume of each living tree or CWD item was calculated using the tree species specific equations (Laasasenaho, 1982).

We analyzed the relationships between deadwood and ecosystem characteristics before and 16 years after the treatments with linear

Table 2
Characteristics of deadwood before and after the restoration treatments. Means and (min-max) for each characteristic are presented. If the effects of biotope before treatments were significant (Supp. 1), the values are presented separately for upland and paludified biotopes. The significant effects of treatments on deadwood characteristics according to the generalized linear mixed models are marked with '+' or '-' (Suppl. 2).

Characteristics	Pre-treatment		16 years after treatments						
	Biotope		Retention of live trees, deadwood creation (DWC), and burning					Burned only	No treatments
	Upland	Paludified	Post-treatment	Biotope	DWC	Burning	Biotope * DWR		
Volume of living trees, m^3 ha^{-1}	455 (296–666)	379 (230–600)	72 (0–375)	+	-	-	-	105 (18–210)	381 (220–530)
Volume of living trees, % from pre-treatment			17 (0–86)		+	+	+	27 (5–47)	77 (45–92)
Volume of deadwood, m^3 ha^{-1}	19 (0–64)	9 (0–33)	64 (9–107)		+	+	+	116 (23–214)	46 (9–149)
Dead / (dead + live), volume %	3 (0–18)		61 (2–100)		+	+	+	52 (13–92)	11 (3–34)
Volume of CWD, m^3 ha^{-1}	11 (0–56)	3 (0–11)	62 (6–106)	+	+	+	+	115 (19–214)	46 (8–149)
Volume of FWD, m^3 ha^{-1}	7 (0–33)		1 (0–5)		+		+	1 (0–4)	0 (0–1.5)
Volume of logs, m^3 ha^{-1}	4 (0–16)	1 (0–10)	55 (1–102)		+	+	+	103 (3–183)	28 (7–91)
Number of logs, # ha^{-1}	11 (0–60)		75 (7–200)		+	+	+	121 (14–226)	42 (20–87)
Volume of snags, m^3 ha^{-1}	2 (0–13)		9 (0–41)					12 (0–31)	18 (1–58)
Number of snags, # ha^{-1}	6 (0–33)		9 (0–27)					24 (0–60)	24 (7–53)
Share of fresh deadwood, %	1 (0–19)	0	3 (0–40)	+	+	+		15 (0–61)	28 (8–59)
Share of intermediately decomposed deadwood, %	64 (0–100)		39 (0–98)		+			68 (39–83)	48 (16–79)
Share of severely decomposed deadwood, %	22 (0–80)		58 (2–100)		+		+	17 (0–43)	25 (6–77)
Mean diameter of CWD, cm	20 (0–27)	15 (0–24)	22 (13–31)					22 (13–27)	18 (14–25)
Decay class diversity of CWD (Shannon index)	0.84 (0–4.60)	0.32 (0–1.35)	0.85 (0.47–1.93)					0.92 (0.59–1.68)	0.68 (0.61–0.75)
Volume of spruce CWD, m^3 ha^{-1}	10 (0–43)	2 (0–11)	52 (1–102)					110 (19–210)	44 (7–138)
Diversity (live trees)	43 (20–87)		34 (0–113)	-	+	-	+	33 (0–100)	71 (50–100)
Diversity (deadwood)	21 (0–75)		89 (25–163)		-	+		119 (50–200)	88 (50–188)

models (LM), generalised linear models (GLM), or generalized linear mixed models (GLMM) (Table 2; Supp. 1). The differences between characteristics of deadwood and live trees before and after treatments were examined using the Mann–Whitney U test. We used the rank-based Spearman's correlation to explore the pairwise correlations between deadwood volume and diversity. The characteristics of deadwood included total volume of deadwood, volume of CWD, volume of FWD on the forest surface, number of CWD pieces, volume of logs, number of logs, volume of snags, number of snags, the deadwood to living trees volume ratio, the share of fresh deadwood (decay class one), the share of intermediately decomposed wood (decay classes 2 and 3), the share of highly decomposed wood (decay classes 4 and 5), the decay class diversity of deadwood (Shannon index), and mean diameter of CWD. The diversity indices were calculated as suggested by Siitonen et al. (2000). The diversity of the living stand was estimated as the number of combinations formed by different tree species and 10 cm diameter classes. Diversity of CWD was calculated in a similar way as the number of combinations formed by tree species, quality (snags, logs), decay class and 10 cm diameter class. The cut stumps were ignored. The ecosystem characteristics (factors) were biotope (upland vs. paludified), burning (burned vs. non-burned), deadwood creation level (5, 30 and 60 m^3 ha^{-1}), as well the interrelation between them.

The 'community' of deadwood was analyzed using non-metric multidimensional scaling (NMDS, Vegan package, Oksanen et al., 2013). The characteristics included the total volume of deadwood, volume of CWD, volume of FWD on the forest surface, number of CWD pieces, volume of logs, number of logs, volume of snags, number of snags, the dead to live wood volume ratio, the share of deadwood of various decay classes, mean diameter of CWD, the decay class diversity (Shannon index), the tree species diversity (Shannon index) as well as the diversity of type (log, snag, stump, Shannon index) of CWD.

All analyses were performed in R (version 4.0.5 GUI 1.74 Catalina build (7950)).

3. Results

In the mature managed spruce forest, the pre-treatment volume of deadwood varied from 0 to 64 m^3 ha^{-1} with the mean of 14 m^3 ha^{-1}. However, the mean share of CWD was only 38%; deadwood consisted mainly of FWD. The volume of logs with diameter more than 10 cm averaged only three cubic meters per hectare, being slightly higher in upland biotopes, compared with paludified biotopes (Table 2, Supp. 1). The volume of snags was 2 m^3 ha^{-1}. The deadwood was mostly intermediately decomposed (Table 2).

At 16 years since the implementation of the treatments, the volume of living trees has decreased in all stands, in some cases by more than 80% i.e. tree mortality exceeded growth increment (Table 2). The amount and other characteristics of deadwood varied greatly (Table 2). The volume of deadwood varied from 9 to 107 m^3 ha^{-1}, with a mean of 65 m^3 ha^{-1} (Table 2, Fig. 1). The volume of logs with more than 10 cm in diameter varied from 1 to 102 m^3 ha^{-1}, with a mean of 55 m^3 ha^{-1} (Table 2, Fig. 2). Diverse deadwood profiles were formed (Table 2, Fig. 3). The amount of CWD increased, whereas the amount of FWD decreased over the 16-year period. Both the number and volume of logs and snags increased substantially. The share of both fresh and severely decomposed deadwood, as well as the share of spruce CWD increased, whereas the share of moderately decomposed deadwood decreased. Mean diameter of deadwood increased. The highest amounts of all deadwood, CWD and logs were recorded in the upland biotopes after prescribed burning without deadwood creation (Figs. 1,2,4). The index

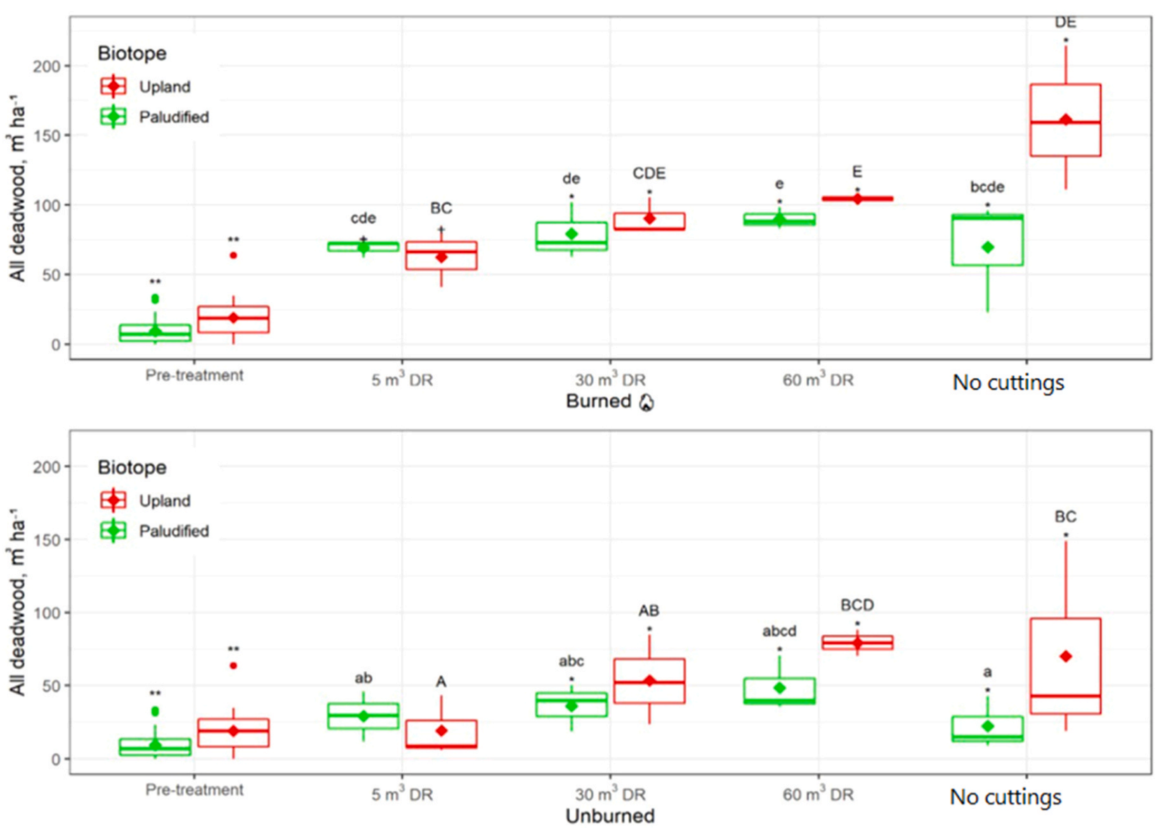

Fig. 1. Boxplots for the volume of all deadwood on the sample plots before restoration treatments and 16 years after prescribed burning (upper part) or without it (lower part) and 50 m^3 ha^{-1} of tree retention and 5, 30 and 60 m^3 ha^{-1} of downed deadwood creation. Median values, means, first and third quartiles, and maximum and minimum values are shown. Significant differences between the cases estimated based on generalized linear mixed models are indicated by letters (Piepho, 2018).

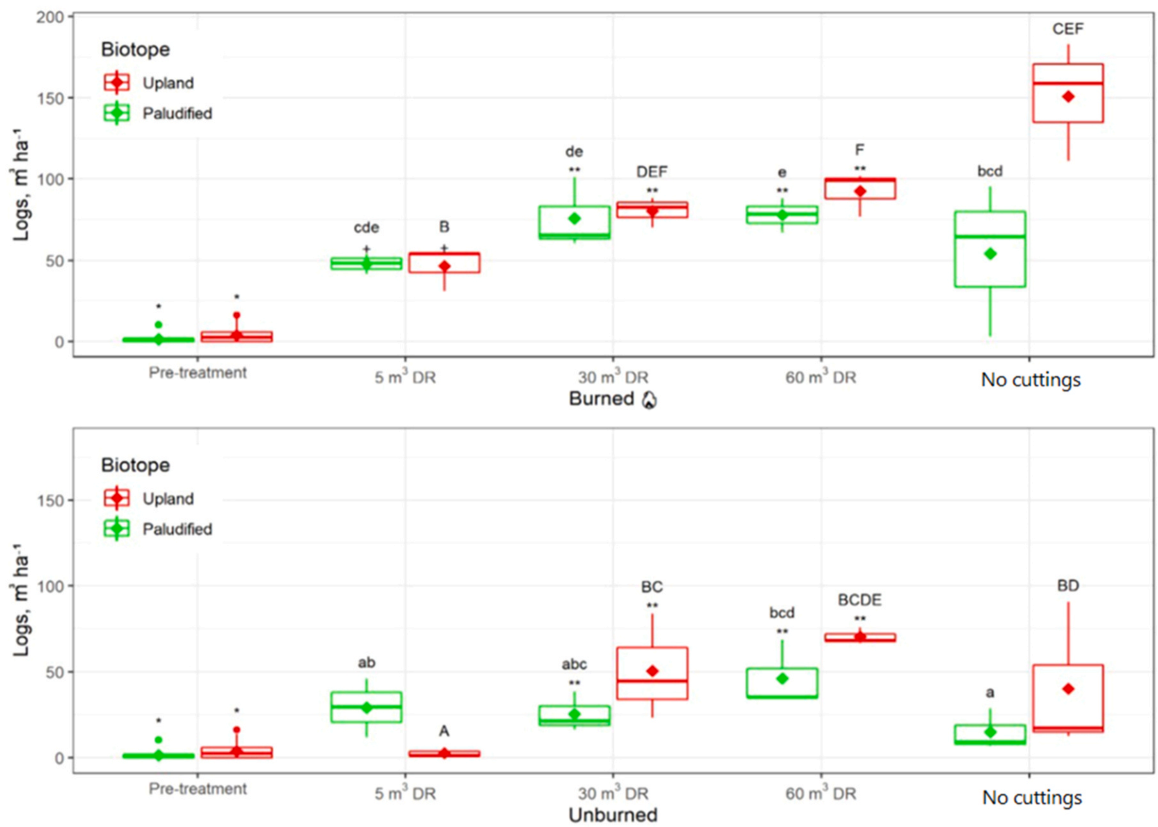

Fig. 2. Boxplots for the volume of logs with diameter more than 10 cm on the sample plots before restoration treatments and 16 years after prescribed burning (upper part) or without it (lower part) and 50 m^3 ha^{-1} of tree retention and 5, 30 and 60 m^3 ha^{-1} of downed deadwood creation. Median values, means, first and third quartiles, and maximum and minimum values are shown. Significant differences between the cases estimated based on generalized linear mixed models are indicated by letters (Piepho, 2018).

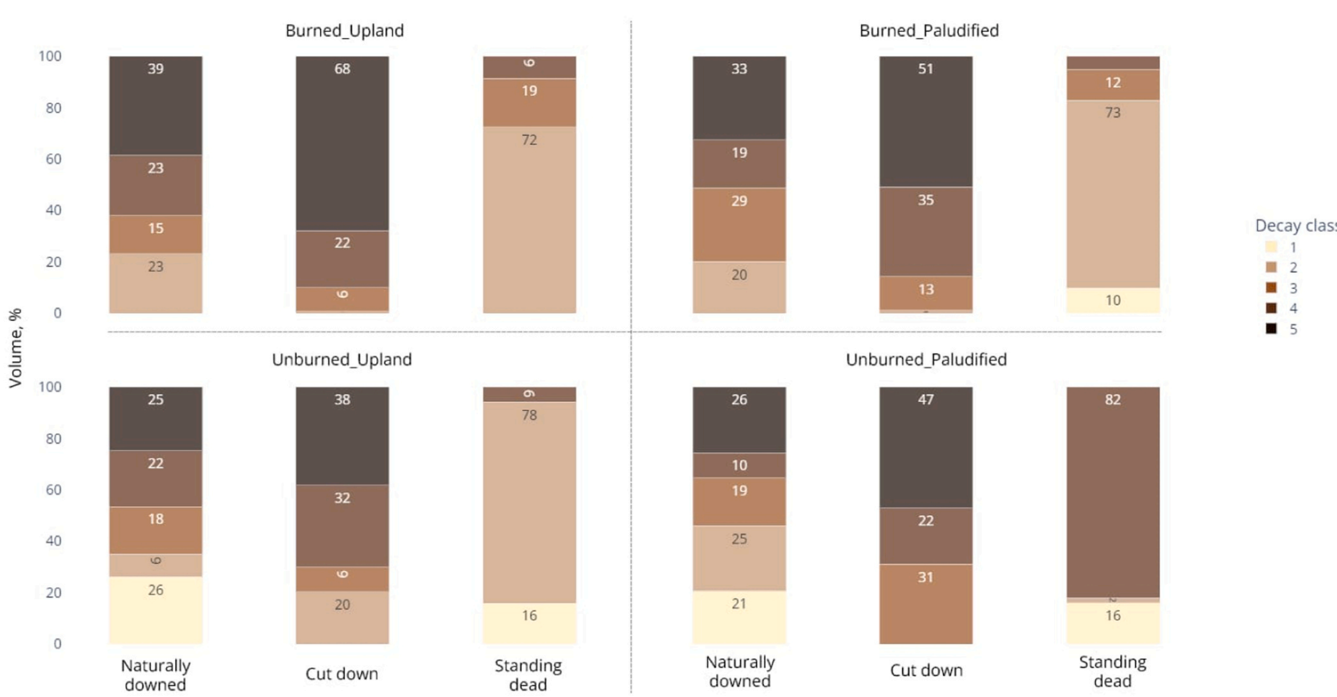

Fig. 3. Distribution of coarse woody debris volume by decay class and tree mortality mode 16 years after tree retention and deadwood creation with or without prescribed burning in the upland and paludified biotopes.

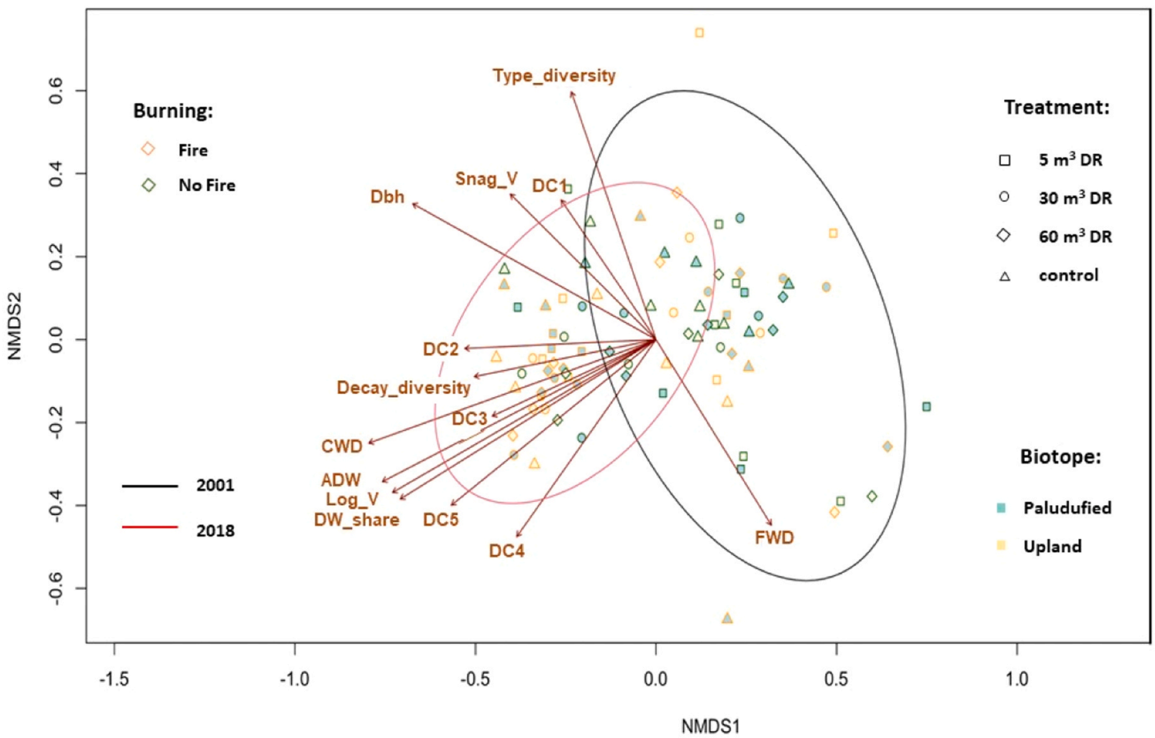

Fig. 4. NMDS ordination of the study plots before and 16 years after treatments. Ordination scores along the two dimensions were averaged for 'before vs after treatments' (Supp. 3). Ellipses are the SDs of the means. The vectors fitted to the ordination are ranked by decreasing r^2 value: Decay class (DC) 2, Decay diversity (Shannon index), Volume of CWD (coarse woody debris), DC3, Volume of all deadwood (ADV), Log diameter at the height of 1.3 m, Volume (V) of logs, Deadwood share, Volume of living trees, DC 5, Volume of snags, DC 4, DC 1, Volume of FWD (fine woody debris), Diversity of deadwood types, Shannon index (Supp. 3).

of deadwood diversity increased substantially over the 16 years (Table 2; Supp. 2). All characteristics listed in the Table 2, except the diversity of live trees, were significantly different before than after the treatments. The correlation coefficient between deadwood volume and diversity was 0.81 ($p<0.001$) and 0.63 ($p<0.001$) before the treatments and 16 years following the treatments, respectively. The 'deadwood community' was different before and after the treatments (Fig. 4, Supp. 3).

3.1. Biotope-related variation

Before the treatments, forest stands in the upland biotopes had higher volumes of living trees as well as higher amounts of more diverse and larger deadwood and CWD as compared to forests in the paludified biotopes (Table 2, Fig. 4). The volume of FWD, number of logs, dead to live wood volume ratio, share of fresh deadwood did not depend on biotope characteristics.

After 16 years, the patterns of higher CWD volumes and higher shares of fresh deadwood in the upland than in the paludified biotopes persisted. The mean volumes of CWD were 67 (range 6–105) and 57 (range 12–101) m^3 ha^{-1} in the upland and paludified biotopes, respectively. The positive effect of wood retention on the total deadwood volume was higher in the upland biotopes (Table 2). For other deadwood characteristics, the effect of biotope was not significant. The 'deadwood community' was independent of biotope type (Fig. 4, Supp. 3).

3.2. Effects of burning

Prescribed burning increased volumes of all deadwood, CWD, logs, fresh (decay class one) and highly decomposed (decay classes 4 and 5) wood, deadwood: live trees ratio, as well as the numbers of CWD pieces and logs (Table 2, Supp. 2). The volumes of all deadwood, CWD, logs and snags, the numbers of logs and snags, as well as the share of fresh deadwood were higher after burning only as compared to burning with deadwood creation or deadwood creation only (Table 2, Supp. 2, Figs. 1, 2). Burning had a negative effect on the diversity of living trees and a positive effect on the diversity of CWD (Table 2). The 'deadwood community' was slightly different with vs. without burning (Supp. 3).

3.3. Retention of live trees and creation of deadwood

The volume of all deadwood and CWD, volume and number of logs, as well as dead to live volume ratio increased with the increasing level of deadwood creation, especially in the upland biotopes (Table 2, Supp. 2). Mean diameter of CWD, volume of snags, number of snags, decay class diversity, and species composition of CWD did not depend on the level of deadwood creation. After 16 years since live tree retention and deadwood creation, the diversity of deadwood decreased, whereas the diversity of live trees increased (Table 2). All characteristics of deadwood, when considered together, were highly variable independent of the original treatment level of deadwood creation (Fig. 4).

4. Discussion

4.1. Deadwood amounts and diversity

In 89% of studied forest stands, applied restoration treatments resulted in the volume of deadwood of more than 20 m^3 ha^{-1} - the threshold volume suggested for the majority of saproxylic species and communities to be present in boreal forests (Müller and Bütler, 2010; Hekkala et al., 2023). For comparison, the deadwood volume in commercial forests in Southern Finland averages 4.4 m^3 ha^{-1} (Korhonen et al., 2021). Before treatments, the deadwood composed mainly of thinning residues: small-diameter fallen logs, branches and stumps consisting of mostly intermediately decayed wood. In the short-term, restoration based on deadwood creation and burning, increased both the volume and diversity of deadwood, whereas deadwood creation only increased merely the volume of deadwood (Lilja et al., 2005). Similar results were reported by Hekkala et al. (2016). After 16 years since prescribed burning with or without deadwood creation, the cut down and naturally downed logs were relatively evenly distributed by decay classes; standing deadwood in various decay classes were also presented (Fig. 3 and Fig. 5). Thus, the applied restoration treatments not only increased the deadwood amounts, but also diversified the deadwood patterns for decades. The volume and diversity of deadwood correlated. The increased deadwood diversity two decades after restoration burning coupled with retention of living trees has been reported also by Nirhamo et al. (2023).

The observed high variation in all deadwood characteristics between forests stands is due to both initial differences and variability in subsequent mortality of legacy trees, as well as varying decomposition rates of deadwood. Tree mortality in mature boreal forests in the absence of severe disturbances is mainly competition-induced, and possibly increased by droughts (Kulha et al., 2023). The interrelated effects of burning, live tree retention and downed deadwood creation influenced the background tree mortality. The tree mortality one year after prescribed burning was the highest when coupled with the highest level of deadwood creation (60 m^3 ha^{-1}), and where the trees were scorched, using downed wood and slash as a ladder. This happened even in the paludified biotopes. Varying patterns of tree mortality led to varying inputs of deadwood and consequently diverse deadwood profiles.

Burning with dispersed living tree retention and low and intermediate treatment levels of downed deadwood creation (5 and 30 m^3 ha^{-1}) did not cause immediate tree mortality (Lilja et al., 2005). Burning effects on tree mortality may depend on spatial distribution of retained trees. Nirhamo et al. (2023) recorded high immediate tree mortality in retention tree groups facilitated by burning in stands dominated by fire-resistant *P. sylvestris*. The lowest immediate tree mortality was recorded in burned stands without cutting treatments. There fuel load was much lower due to absence of logging slash, leading to less intensive surface fire with patchy burn severity, especially in the paludified biotopes. The amount and size of created deadwood in the Evo experiment affected the populations of bark beetles (Eriksson et al., 2006), which in turn possibly affect subsequent tree mortality of retained trees and future deadwood decomposition patterns. An increase in the total number of downed spruce trees decreased the proportion of logs colonized by *Ips typographus* (L.), but increased the total number of colonized logs. *Pityogenes chalcographus* (L.) colonized almost 100% of felled spruces. The number of *I. typographus* egg galleries increased with the number of large spruce logs. Burning treatment diminished the breeding success of *I. typographus,* especially at the highest level of downed deadwood creation, where the intensity of fire was also the highest (Eriksson et al., 2006). Over the 16-year period, the volume of living trees decreased substantially, especially in the upland biotopes.

The highest values of all deadwood, CWD, logs, and snags observed in reference stands in our study reflect natural successional processes in mature forests. Prescribed burning facilitated tree mortality, especially for poorly fire-adapted spruce (Engelmark et al., 1994). The variability in CWD parameters in reference stands and after the treatments exceed those in the spruce dominated old-growth forests in the Evo-Vesijako region (Anon, 1995, 2011), measured by Penttilä et al. (2006) (Häme plots, Appendix 1 in Penttilä et al., 2006) (Fig. 5).

In our study, both before and after the restoration treatments, mean amounts of deadwood and their variation were higher in the upland than in the paludified biotopes. Apparently, deadwood patterns related to biotope variation depend on the size of the site, productivity, dominant tree species, forest management history and landscape context. Low-productivity forests and forested mires have been reported to support lower amount and diversity of CWD (Hämäläinen et al., 2018, Jönsson and Snäll, 2020, Kyaschenko et al., 2022; Jönsson et al., 2023). In the Evo region, natural spruce mires exhibit high variability in deadwood amount, with values not less than 20 m^3 ha^{-1} (Nupponen, 2011). Jalonen and Vanha-Majamaa (2001) found higher volumes of deadwood in paludified biotopes in similar mesic Norway spruce stands, but in Eastern Finland. In our forest stands, the recent thinnings had led to increased volume of dead wood in the upland biotopes before the restoration treatments (Lilja et al., 2005). In cases when prescribed burning was applied, higher burning severity in the upland biotopes had probably led to higher deadwood amounts as compared to paludified biotopes.

The restoration treatments created forest stands with abundant and diverse deadwood, to some extent resembling early post-disturbance successional stages in natural forests with distinctive characteristics,

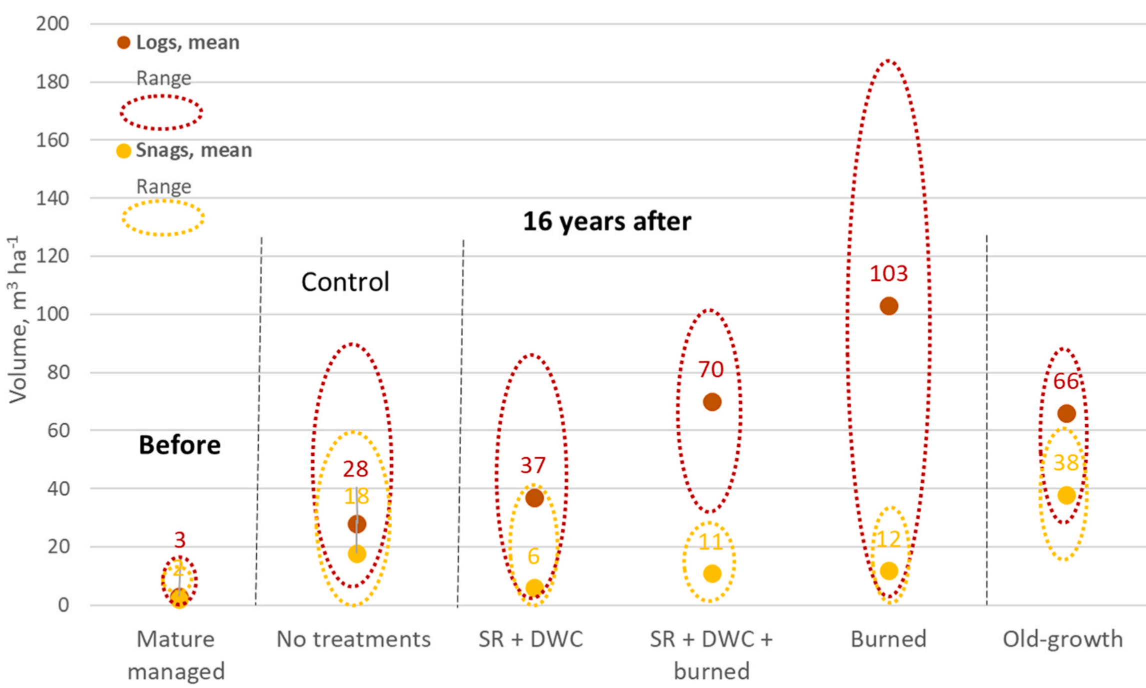

Fig. 5. Volume of logs with diameter more than 10 cm and snags before and 16 years after restoration treatments, compared to old-growth forests (Penttilä et al., 2006). SR – standing wood retention, DWC – deadwood creation.

including high species diversity, as well as complex food webs and ecosystem processes (Kuuluvainen and Gauthier, 2018; Martin et al., 2022, 2023), which are mainly absent in managed forest landscapes (Uotila et al., 2001). The patterns of downed deadwood created in the experiment and later formed deadwood owing to natural tree mortality deviate from those of traditional clear-cuts, represented mainly by fresh fine woody debris, stumps and log fragments (Eräjää et al., 2010). Relatively even distribution of deadwood by position and decay class refers to diverse ecological niches for wood-inhabiting species and variable wood decomposition and nutrient turnover rates. Consequently, high biodiversity can be expected in the forest stands for few decades. In managed forest landscapes, such restored patches can be potential biodiversity hotspots.

The results from a multidisciplinary experimental study in Evo show that focusing only on a few species groups can give a biased picture of the overall effects of restoration treatments on the diversity of wood-inhabiting communities (Vanha-Majamaa et al., 2007). In the burned stands, sun-exposed deadwood increased the diversity of pioneer wood-inhabiting fungi (Penttilä and Kotiranta, 1996; Berglund et al., 2011), and later especially threatened polypore species (Ramberg et al., 2023). The beetle diversity and abundance of rare and red-listed beetle species showed a substantial increase after burning as compared to the unburned sites (Toivanen and Kotiaho, 2007). At the same time, the benefit of burning for epixylic bryophytes is questionable. There is a clear lack of knowledge in relation to colonization of bryophytes on burned wood (Ryömä and Laaka-Lindberg, 2005). Most often fire destroys the epixylic vegetation cover almost completely (Vanha-Majamaa et al., 2007), and the surviving bryophyte shoots seem to die owing to desiccation within one-two years after the fire. Further the dispersal ability becomes a major limiting factor, especially for the distribution of bryophyte species occupying temporal, patchy habitats such as logs (Ryömä and Laaka-Lindberg, 2005). Over 16 years, few living trees were left from the initial forest stands with dispersed retention, when high downed deadwood creation levels were applied. Leaving retention tree groups instead of creating too much downed wood at one time might ensure the stand scale deadwood continuum, including better snag survival (Halpern et al. 2022) in the long term and possibly favorable microclimate for some species groups, e.g. for bryophytes (Táborská et al., 2020). Combinations of forest stands with different degrees of structural diversity most likely optimize taxonomic diversity at the landscape level (Storch et al., 2023).

4.2. Implications for deadwood management

Increasing the amount and diversity of deadwood is pivotal to maintain key forest ecosystem processes and biodiversity (Jonsson et al., 2016; Vítková et al., 2018). The current scarcity and slow increase of deadwood in European forests (Mansuy et al., 2023) requires more effective closer-to-nature forest management and restoration actions in reaching EU climate mitigation and biodiversity targets and keeping European forests healthy (Halme et al., 2013; Similä and Junninen, 2012; Bernes et al., 2015; Jonsson et al., 2016; Anon, 2022).

Avoiding damage to already existing deadwood and leaving habitat trees (Kraus et al., 2016) do not increase harvesting costs considerably (Koivula and Vanha-Majamaa, 2020). For the short-term effects, downed wood retention is beneficial. Even though in our experimental stands the restoration treatments did not cause insect outbreaks in neighbouring areas (Eriksson et al., 2006), the potential risk should be taken into account in planning restoration actions.

From the ecosystem management and ecological restoration point of view, prescribed burning has a positive effect on almost all characteristics of deadwood. Prescribed burning alone can be an effective measure to restore natural deadwood patterns and related biodiversity (this study, Sandström et al., 2019, Ramberg et al., 2023). Tree retention with prescribed burning can produce significant amounts of various types of CWD over long time scales, thus ensuring CWD continuum. Therefore, it can be an effective tool to restore ecosystem structures and processes in commercial forests, set-asides, and conservation areas in Fennoscandia.

To achieve multiple objectives of European Green Deal, it is essential to define consistent and cost-efficient thresholds for tree retention and deadwood creation, tailored to local or regional forest conditions (Vítková et al., 2018; Mansuy et al., 2023). This is a challenge for future research. Both stand- and landscape-scale deadwood enrichment strategies in protected and commercial forests should be developed. Applying high levels of deadwood creation can mimic disturbance dynamics and restore early successional post-disturbance habitats. Prescribed burning, with higher share of aggregated or dispersed live tree retention, instead of high level deadwood creation at one time could result in slower but longer supply of deadwood, and thereby ensure the desired CWD continuum.

5. Conclusion

Our results highlight the long-term potential of prescribed burning, dispersed tree retention and downed deadwood creation in restoration, or closer-to-nature forest management, for maintaining deadwood diversity and ecosystem functioning in North European forests.

CRediT authorship contribution statement

Ekaterina Shorohova: Writing – original draft, Visualization, Conceptualization. **Ilkka Vanha-Majamaa:** Writing – review & editing. **Timo Kuuluvainen:** Writing – review & editing, Methodology, Conceptualization. **Henrik Lindberg:** Writing – review & editing, Methodology, 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.

Data Availability

Data will be made available on request.

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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.2024.122013.

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