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Deadwood carbon stock in overmature coniferous forests on different soil types in the hemiboreal region

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Abstract

The amount of deadwood is a subject of heated debate regarding biodiversity conservation and carbon (C) storage as an instrument for climate change mitigation in north-eastern Europe. In the region, Scots pine (*Pinus sylvestris*) and Norway spruce (*Picea abies*) are among the principal forestry species providing a significant pool of stable deadwood, especially in overmature forests. Deadwood C stocks are highly variable, and regional deadwood estimates can be biased; thus, local data is vital, and accurately quantified deadwood C stocks, particularly in overmature stands on different soil types, are essential.

The study aims to characterise deadwood C stock, modes (standing or lying), and decay classes in hemiboreal overmature coniferous forest stands on dry mineral, drained, and wet organic soils. C stock in deadwood and forest inventory parameters were estimated in 95 overmature (aged 122 to 218 years) coniferous stands using the sample plot method, taking into account the form of deadwood standing, decomposition class and soil type.

Mean deadwood C stock (deadwood with a diameter ≥ 6.1 cm) in coniferous stands ranged from 4.59 C t ha^{-1} to 11.25 C t ha^{-1} in spruce stands on wet organic soil and pine stands on mineral soil, respectively. However, the amount of deadwood showed large spatial variability; at the same time, a statistically significant relationship between deadwood carbon stock and soil type, basal area, and the mean stand diameter at breast height, explaining a limited effect and maintaining high uncertainties. This suggests that the dynamics of deadwood were complex, driven by ageing, natural disturbances and any past management, perhaps carried out decades ago; for these reasons, the findings should be interpreted with caution due to the potential legacy effect of any disturbances in some stands. Nevertheless, the results highlight the crucial role of large-sized coniferous deadwood as a stable carbon store, contributing to both carbon storage and maintaining biodiversity, in the hemiboreal region.

Keywords: carbon stock; coarse woody debris; decay stage; organic soils; Norway spruce; Scots pine

Introduction

Forest ecosystems are some of the largest global biotic carbon (C) pools (Bonan 2008, Pan et al. 2011), playing an important role in the mitigation of climate change effects (Canadell and Raupach 2008). Estimates of C stock are essential for reporting the state of forest contribution to climate goals as defined by international legislation (Penman et al. 2003). The main C pools in forests are living tree biomass, soil, deadwood, and litter (Frouz et al. 2009, Ķēniņa et al. 2022). However, they show high regional and temporal variability; therefore, the uncertainty regarding individual components remains high (Müller and Bütler 2010), which needs clarification.

While C dynamics in young and middle-aged managed stands, as well as those for living trees, are relatively well understood (Uri et al. 2023, Kellomäki 2024), such dynamics in old, unmanaged stands are still poorly quantified due to scarcity and low economic interest. However, in the context of the European Union (EU) Nature Restoration Law, which aims at a significant increase in unmanaged forest areas, such areas will inevitably increase, leading to a greater extension of old-growth stands, associated natural mortality, and deadwood accumulation (EUR-Lex 2024). Although the primary ecological function of deadwood is to support biodiversity across spatial and temporal gradients (Felton et al. 2010), in doing so, deadwood serves as a temporary C stock, as it inevitably decomposes, releasing C back into the atmosphere (Humphrey et al. 2004, Mäkinen et al. 2006). Therefore, it is essential to estimate C stock in deadwood in overmature stands, which can already be done by a detailed survey of the existing forests falling under such a category.

The dynamics of deadwood C stock has regional and local characteristics, which are determined by natural

disturbance regime, forest management practices, stand age, successional stage, and climatic conditions, particularly soil microclimate and moisture conditions affecting decomposition rates (Köster et al. 2005, Garbarino et al. 2015, Jonsson et al. 2016, Vítková et al. 2018). Accordingly, regional extrapolations can be strongly biased, and local information is highly anticipated. In this regard, there is particular uncertainty regarding the impact of hydromelioration (drainage) of plantations on the dynamics of C stocks in deadwood, which is typical for the Eastern Baltic region (Ķēniņa et al. 2022).

The Eastern Baltic region, which is an important source of timber for the EU market (Jansson et al. 2017), is situated under a moist continental climate, where the excess of soil moisture is considered the main limiting factor for forest productivity (Zālītis 2012). Accordingly, since the 1960s, forest drainage, which has long-term effects on productivity, biodiversity, and C storage via altered growth, microclimate, and decomposition dynamics (Ranius and Fahrig 2006, Lõhmus et al. 2015, Tong et al. 2022), has been widely implemented (Zālītis 2012, Skaggs et al. 2016).

Due to their abundance, Scots pine (*Pinus sylvestris* L.) and Norway spruce (*Picea abies* L. Karst.) are main species for commercial forestry in north-eastern Europe, especially in the Eastern Baltic region (Caudullo et al. 2016, Durrant et al. 2016), where they also have high ecological value (Tērauds et al. 2011, Fahlvik et al. 2015). Thanks to well-developed forest-related sectors, the ecological and economic services, including C credits, are under special attention in Latvia, making the country a good model for assessing the potential impact of the Nature Restoration Law on C stocks and their dynamics. Currently, C stocks in old-growth birch (*Betula* spp.) and European aspen (*Populus tremula* L.) stands are assessed on mineral soils (Šēnhofa et al. 2020, 2021). However, the information on over-mature coniferous forest deadwood C stocks, which have different dynamics (Lassauce et al. 2011), is still awaited. In addition, Latvia is in the hemiboreal zone, where the climate-related changes and forests are expected to be pronounced (Buras and Menzel 2019).

The study aims to characterise deadwood C stock, modes (standing or lying), and decomposition classes in hemiboreal overmature coniferous stands on dry mineral, drained, and wet organic soils to illustrate the amount of deadwood in different stages of decay under natural conditions and to show the effect of drainage on deadwood C stock. We hypothesised that: 1) deadwood carbon stock is lower in stands on wet soils, compared to dry mineral and drained organic soils, *and* 2) stand characteristics are significant predictors of deadwood C stock.

Materials and methods

Study area

Latvia is located in north-eastern Europe between 58°05'N–55°40'N and 28°14'E–20°58'E (Figure 1), corresponding to the hemiboreal zone, an intermediate belt that incorporates elements of both the boreal and nemoral zones. Latvia has a cool, moist climate with strong maritime influences. The average temperature in January is –6°C and in July is +16°C. The average annual precipitation is 685 mm (LEGMC 2020).

Forests cover 53% of Latvia's terrestrial area. Scots pine and Norway spruce are among the most common tree species, together accounting for 45% of the forested area. Specifically, Scots pine-dominated stands comprise 25%, while Norway spruce-dominated stands comprise 20% of the total forest area (LSFRI 'Silava' 2023).

Selected forest stands correspond to *Oxalidosa* (fertile dry mineral soils), *Aegopodiosa* (fertile dry carbonate soils), *Caricoso-sphagnosa* (poor wet peat soils), and *Oxalidosa turf. mel.* (drained fertile peat soils) forest types according to the local classification in Latvia (Bušs 1997). Soil conditions and forest type were confirmed in the field by visual and physical inspections (including peat layer depth measurements), and further selected forest types used in this study are referred to as mineral, wet organic, and drained organic soils. All measured stands were un-

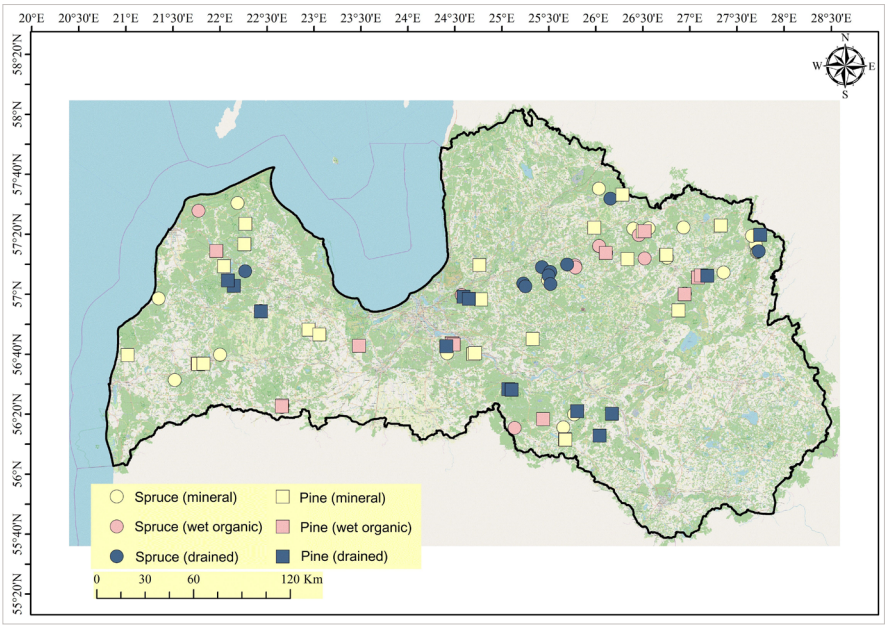

Figure 1. Locations of the study sites in Latvia

managed for at least 30 years (including no maintenance of forest drainage systems). Management history information and mean stand age were determined based on the State Forest Service database. The age of the study sites ranged from 122 to 218 years.

Data collection

In total, 600 sample plots were established and measured in 95 selected over-mature stands across Latvia, where old trees are the dominant forest elements. In each stand, six to eight 500-m^2 circular sample plots (radius = 12.62 m) were established randomly throughout the area of selected stands for measurements of main tree variables (tree species, DBH, tree height) to determine and calculate forest inventory parameters such as basal area, standing volume, and tree count per hectare (Table 1). For a more detailed sample description, see Ķēniņa et al. (2022).

Deadwood was characterised by using a concentric scheme with two distance steps: within a distance of 12.62 m, all deadwood with a diameter ≥ 14.1 cm, and within a distance of 5.64 m, deadwood with a diameter ≥ 6.1 cm was measured. The deadwood diameter threshold was based on the methodology of the National Forest Inventory (NFI). Modes of deadwood structures included lying deadwood and dead-standing trees. For lying deadwood, the diameter was measured at both ends of the log, and the length of the log was also measured. Standing deadwood was measured at breast height, and tree height was measured up to the top of the tree or the breakage point. The decay class of deadwood was observed visually and using the 'knife method', and decay was divided into five classes (Table 2; Stokland 2001, Köster et al. 2015).

Data analysis

Tree volume was calculated with locally developed equations (Liepa 1996). The volume of deadwood was calculated using Huber's formula (Eq. 1; for a more detailed methodology description, see Šēnhofa et al. 2021). Deadwood C stock was calculated by using the obtained deadwood volume and converting it to C stock by using decay class-specific wood density and C content for Norway spruce and Scots pine (Table 2; Köster et al. 2015).

Huber's formula takes the form as follows:

$$V = \frac{L \cdot \pi \cdot d_m^{\,2}}{4}, \qquad (1)$$

where

V – dead standing/lying dead tree volume,

L – length of the log or height of the snag/dead standing tree, *and*

d_m – mid-diameter of the log or the snag.

The Shapiro-Wilk test was used to check the normality of data distribution. Turkey's HSD was used for parametric variables to compare the means of different tree species in each soil type. The Mann-Whitney U test was used to observe significant differences in non-parametric variables. Linear mixed-effects models were developed to examine stand characteristics that influence deadwood C stocks. Initially, all available stand characteristic variables were included in the linear mixed-effects model. Subsequently, covarying variables were excluded. The dependent variable (deadwood C stock) was logarithmically transformed to meet normal distribution, and dominant tree species (2 levels: pine and spruce), soil type (3 levels: mineral, wet organic, drained organic), mean stand DBH (continuous variable), mean age (continuous variable), mean

Table 1. Main characteristics of studied forest stands and sample plots (mean values ± 95% confidence interval)

Tree species	Soil type	Number of study sites (n)	Number of sample plots (n)	Mean stand age, (years)	DBH (cm)	H (cm)	Total growing stock (m^3 ha^{-1})	Trees per ha (n)
Scots pine	Mineral	26	170	178 ± 15	47.1 ± 5.5	30.8 ± 2.3	568.3 ± 85.5	277 ± 69
Scots pine	Organic drained	13	78	150 ± 19	35.8 ± 2.0	27.9 ± 2.9	490.1 ± 133.5	370 ± 39
Scots pine	Organic wet	13	82	175 ± 15	27.6 ± 2.9	20.7 ± 2.4	293.2 ± 84.8	566 ± 172
Norway spruce	Mineral	17	114	177 ± 13	36.4 ± 6.2	28.5 ± 3.1	391.4 ± 100.0	239 ± 68
Norway spruce	Organic drained	13	78	151 ± 29	34.9 ± 3.9	29.4 ± 3.1	474.6 ± 126.8	349 ± 67
Norway spruce	Organic wet	13	78	159 ± 11	26.4 ± 2.6	24.3 ± 1.9	393.4 ± 96.6	554 ± 179

Table 2. Decay class description, dominant species carbon concentration and basic wood density (Köster et al. 2015)

Decay class	Decay class description	Scots pine		Norway spruce	
		basic density (kg m^{-3})	C concentration (%)	basic density (kg m^{-3})	C concentration (%)
1	The tree recently died, but the bark is intact and has retained colour	381.1	49.03	410.7	48.35
2	The bark has started to fall off, the stem is round, and the wood is still hard	337.2	49.26	354.2	48.31
3	Wood is becoming soft, bark covers < 50%, bark colour is intact	258.8	49.56	280.7	47.93
4	Wood is soft, no bark remains, and the wood structure has disintegrated	233.7	49.58	191.3	49.60
5	Parts of the stem are indistinguishable, wood is very soft and may be covered with plants or mosses	141.8	50.21	124.8	51.33

tree height (continuous variable), basal area (continuous variable), and trees per hectare (continuous variable) were used as fixed effects, but study site and sample plot as random effects. Significant variation ($p \leq 0.05$) in fixed effects was examined with the ANOVA type III Wald χ-square test. The pairwise comparison was used to compare the estimated marginal means of deadwood C stock. Data analysis was performed using the R statistical computing and graphics environment version 4.2.2 (R Core Team 2023), employing the packages "lme4" (Bates et al. 2015) and "emmeans" (Lenth 2025).

Results

Deadwood carbon stock, modes, and decay classes

Mean deadwood C stocks ranged from 4.59 C t ha^{-1} to 11.25 C t ha^{-1} and can be ranked in decreasing order based on soil type: mineral soil > drained organic soil > wet organic soil (Figure 2). Estimated ranges in C stocks exhibit relatively high variability, but, in general, in Scots pine stands, deadwood C stock tends to be higher compared to Norway spruce. The lowest deadwood C stock was observed in Norway spruce stands on wet organic soils (4.59 ± 1.10 t ha^{-1}), which was significantly ($p < 0.05$) lower compared to Scots pine-dominated stands (7.91 ± 2.87 t ha^{-1}). On mineral soils, the mean deadwood C stock for Scots pine was 11.25 ± 1.99 t ha^{-1} and larger by 19% compared to Norway spruce (9.47 ± 1.95 t ha^{-1}). Moreover, Scots pine deadwood C stock on drained organic soils was 9.74 ± 1.85 t ha^{-1} and larger by 9% compared to Norway spruce stands (8.96 ± 1.61 t ha^{-1}), yet, the differences between dominant tree species on mineral and drained organic soils were non-significant ($p > 0.05$).

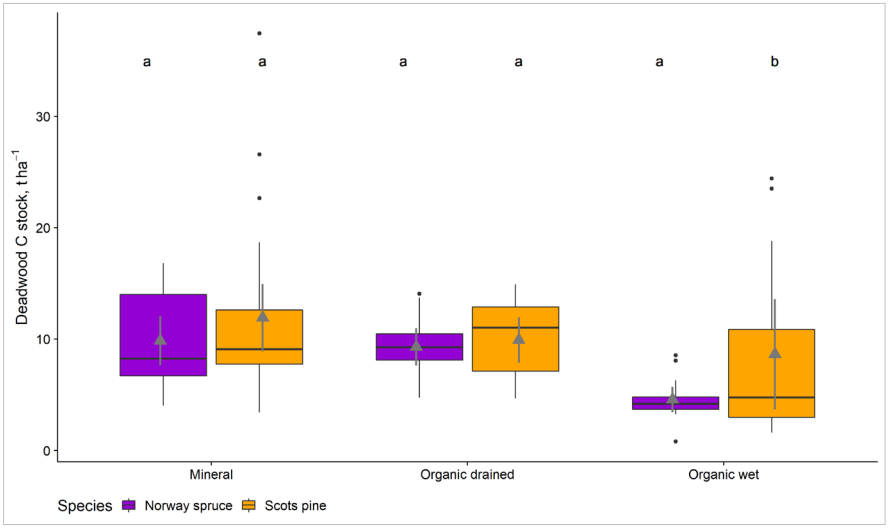

Figure 2. Mean deadwood C stock by soil type group for Scots pine and Norway spruce sample plots

Grey triangles indicate mean values ± 95% confidence intervals; the box plots represent median values and the 25% and 75% percentiles; the whiskers indicate the maximum and minimum values; different letters indicate significant differences.

Estimated deadwood C stock are higher compared to that, observed in mature, managed spruce forests (2.6 t ha^{-1}) in Switzerland (Weggler et al. 2012), Sweden (ca 6.4 t ha^{-1}; Fridman and Walheim 2000), and old-growth birch forests (6.3–7.9 t ha^{-1}) on mineral soils in Latvia (Šēnhofa et al. 2020), but similar to old-growth, unmanaged aspen forests (8.2–12.5 t ha^{-1}) on mineral soils and coniferous forests (10–11 t ha^{-1}) on organic soils in Latvia (Šēnhofa et al. 2021, Ķēniņa et al. 2022), and overmature coniferous dominated forests in Scandinavia (ca. 7–11.2 t ha^{-1}; Jonsson et al. 2016).

However, estimated deadwood C stock in this study is lower than that observed in old-growth spruce forests (13 t ha^{-1} of which 7 t ha^{-1} for snags, and 6 t ha^{-1} for lying deadwood) in the Czech Republic (Seedre et al. 2015) and in Estonian mature spruce forests, where deadwood C ranges from 14.5 to 20.6 t ha^{-1} (Rosenvald et al. 2025) but in old-growth coniferous forests from ca. 8–53.5 t ha^{-1} for snags and 3.7–71.6 t ha^{-1} for logs (Lõhmus and Kraut 2010). In addition, the deadwood C observed in virgin forests dominated by European beech (*Fagus sylvatica* L.) and Silver fir (*Abies alba* Mill.) in Romania ranges from 0.4 to 41.2 t ha^{-1} (Petritan et al. 2023). In general, the estimated and compared deadwood C stocks are highly variable. Lower deadwood C stocks in Norway spruce stands on wet organic soils could be explained by lower standing volume and tree dimensions due to harsher growing conditions (due to high soil moisture), where larger tree dimensions, biomass, and C stock can be reached more slowly compared to drained organic or dry mineral soils (Ranius and Fahrig 2006). This partly confirms our first hypothesis that deadwood C stocks are lower in forest stands on wet organic soils; however, this trend did not hold for Scots pine on wet organic soils, where the deadwood C stock was nearly identical to that found in drained organic soils. The highest deadwood values were observed for Scots pine-dominated stands on mineral and drained organic soils, as more productive forests tend to have higher amounts of deadwood due to higher biomass growth rates (Framstad et al. 2013). Estimated higher deadwood C stock in overmature coniferous forests than in old-growth deciduous forests, particularly in birch dominated stands, indicate that coniferous deadwood is more persistent and deciduous trees decompose more rapidly, due to differences in wood density and chemistry, leading to more rapid C loss (Mäkinen et al. 2006, Menichetti et al. 2021), thus coniferous deadwood provides more stable C stocks in the long term.

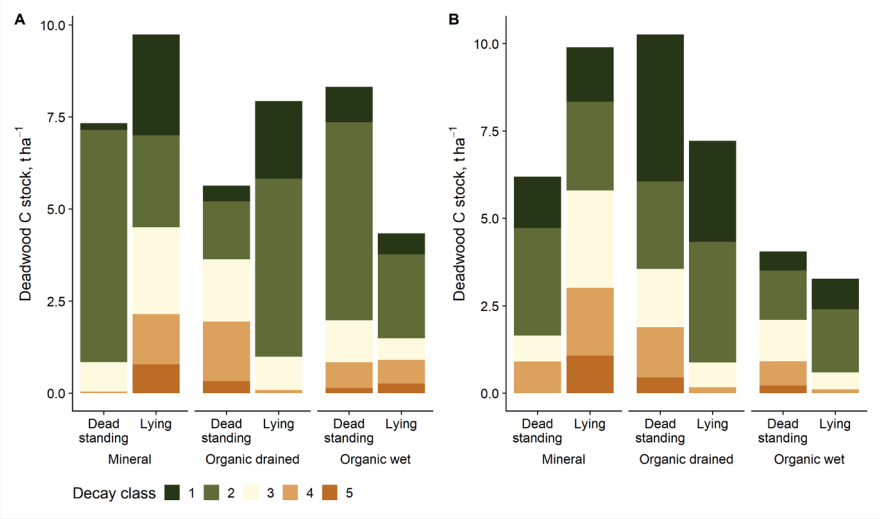

Figure 3. Distribution of deadwood modes (lying deadwood or dead standing tree) and decay classes (1–5) by deadwood C stock in Scots pine (A) and Norway spruce (B) stands on mineral, drained organic, and wet organic soils

The study results indicated variability in C stock across different deadwood modes (Figure 3). In Scots pine stands on mineral soils, dead standing trees and lying deadwood had similar mean C stocks (5.81 ± 0.88 t ha^{-1} and 5.44 ± 1.33 t ha^{-1}, respectively), indicating a relatively balanced distribution between deadwood modes (Figure 3A). On drained organic soils, lying deadwood held more C (5.88 ± 1.02 t ha^{-1}) than dead standing trees (3.86 ± 0.65 t ha^{-1}). In contrast, wet organic soils showed the opposite trend: dead standing trees deadwood C stock was more prominent (5.03 ± 2.04 t ha^{-1}) than lying deadwood (2.89 ± 0.53 t ha^{-1}). In Norway spruce stands on mineral soils, lying deadwood had the highest C stock (6.44 ± 1.34 t ha^{-1}), more than double that of dead standing trees (3.03 ± 1.0 t ha^{-1}). On drained organic soils, C stocks were more evenly distributed, with 4.65 ± 0.73 t ha^{-1} in standing trees and 4.31 ± 0.98 t ha^{-1} in lying deadwood (Figure 3B).

Wet organic soils exhibited low C stocks in both modes: 2.41 ± 0.43 t ha^{-1} in lying deadwood and 2.18 ± 0.49 t ha^{-1} in standing trees. Variability in deadwood C stocks between different soil types and dominant tree species suggests different causes of tree die-off: the natural disturbance, such as bark beetle (*Ips typographus*) infestation, leaves much of the deadwood standing, while windblow uproots dead trees. Moreover, after tree dieback, dead standing trees can remain standing for up to 40 years (Mäkinen et al. 2006) and decompose more slowly due to different microclimate conditions than lying dead wood (Peltola et al. 2000, Šēnhofa et al. 2020).

The degree of deadwood decomposition was classified into decomposition classes (Köster et al. 2015): deadwood with decomposition classes 1–3, due to its prevalence in most sample plots, accounted for the largest proportion of deadwood C stock among the analysed tree species, deadwood decomposition forms and soil type groups. Furthermore, the proportion of deadwood C stock in decay classes 1 to 3 varied by soil type and ranged from 64% to 100% of total deadwood C, while decay class 2 formed the largest proportion in most cases, and decay class 5 was not observed in all soil types and deadwood structures. However, in old-growth forests in Estonia, deadwood in decay class 5 has been observed in relatively higher proportion (Lõhmus and Kraut 2010), thus indicating possible past-management impact in our study sites even more than 30 years ago.

A relatively high proportion of decomposition class 2 indicates slow decomposition at the beginning of tree dieback, as this class represents deadwood, which is still hard. Moreover, the decomposition rates of coniferous trees are not constant, but highly variable and non-linear, with an initial slow decomposition phase after tree mortality, followed by a rapid decay period and a more moderate decomposition phase (Mäkinen et al. 2006). In addition, decomposition rates may vary depending on the mode of deadwood and site conditions (wet or dry), as dead standing trees and branches tend to decompose more slowly than lying deadwood, and C release occurs faster in moist soil (Mäkinen et al. 2006).

Factors affecting deadwood carbon stock in coniferous forests

Deadwood C stock was significantly influenced by soil type (p = 0.03), mean stand DBH (p = 0.03), and stand basal area (p = 0.004), while all other tested parameters were insignificant (Table 3). The model's conditional R^2 was high (0.88), while the marginal R^2 was low (0.11). Stand age and DBH are commonly used as predictors for coarse deadwood volumes (Pregitzer and Euskirchen 2004, Siipilehto et al. 2021). Forest C stocks are generally linked to stand age because higher stand age increases tree mortality caused by competition, self-thinning, senescence, and disturbances (Karjalainen and Kuuluvainen 2002, Kapusta et al. 2020), but our results indicate that stand age in overmature forests is a weak predictor of deadwood C stock.

Table 3. Stand characteristic variables affecting deadwood C stock

Variables	χ^2	*p*-value
(Intercept)	0.39	0.53
Species	2.48	0.12
Soil type	7.16	0.028 **
Stand age	0.01	0.92
Mean stand DBH	4.90	0.027 **
Mean tree height	0.66	0.42
Basal area	8.26	0.004 **
Trees per ha	0.82	0.36

Note: Significant variables ($p < 0.05$) marked with **.

An insignificant relationship between C stock and stand age in most cases may be attributed to the analysis being restricted to overmature stands. The assessed study stands had not been managed for at least the last 30 years; however, a full management history, allowing for the effects of neglecting past management practices and natural disturbances on deadwood abundance to be taken into account, was not available. Past management and natural disturbances can significantly alter stand age and DBH distribution; thus, the insignificance of stand age and deadwood C stock relationship in most cases is not surprising. Similar findings have been reported in local studies in the hemiboreal region (Ķēniņa et al. 2018, Ķēniņa et al. 2022). The results indicate significantly lower deadwood C stock in stands on wet organic soils, emphasising the differences in the tree dimensions and consequently deadwood dimensions in wet soils compared to mineral or drained soils. Overall, our second hypothesis was thus not confirmed, since the significant factors affecting deadwood C stock were soil types, mean stand DBH, and basal area; high uncertainty between study sites and sample plots was also observed, indicating strong other factors (e.g. past disturbances or past management) influence on deadwood C stock.

Past management, even that conducted decades ago, can have a lasting impact on deadwood C stock, as it can shift stand dynamics by promoting homogenization of forest structures and reducing natural mortality rates (Schulte et al. 2007). Moreover, historic thinnings or sanitary cuttings directly reduce the potential of deadwood accumulation and presence in the stand (Rosenvald et al. 2025). Consequently, even forests that appear unmanaged today may retain legacy effects of past management, and any assessment of their deadwood C stock must consider possible historical disturbances.

Tree senescence is also associated with declining growth rates and increased vulnerability of overmature stands (Siipilehto et al. 2021). In combination with senescence, exogenous and endogenous disturbances regulate the influx into the deadwood C pool in unmanaged forests. Natural disturbance sensitivity is often related to the presence of numerous trees nearing their maximum age, either in sparse stands with a few large-diameter trees or in denser stands with a high average diameter. High variability in small- and large-scale die-off and regeneration dynamics in overmature forests results in transitional states both in the C stock of deadwood and in the wider forest ecosystem (Frelich et al. 2020, Palm-Hellenurm et al. 2024).

Natural disturbances play a crucial role in deadwood dynamics (Krankina and Harmon 1995), and the disturbance cycle exhibits considerable variation, as indicated by maximum and minimum deadwood C stocks in sample plots. Tree mortality in forests is a complex process, and rare events, such as wind-throws and bark beetle infestation, are difficult to predict but can significantly impact the presence and size of the deadwood stock. Due to the lack of consistent data on natural disturbance types, gap dynamics were assumed to be the dominant disturbance process in hemiboreal coniferous stands (Angelstam and Kuuluvainen 2004). Surprisingly, the gap dynamics that could lead to a demographic transition appear to be delayed. This delayed transition, combined with the high mortality of large trees, can result in a sudden increase in deadwood C stock. Nevertheless, the deadwood C stock of conifers can have long-lasting storage, which contributes to both biodiversity and C storage goals (Menichetti et al. 2021). This is a very valuable aspect of the changing climate and expected shift in living forest composition (D'Amato et al. 2017).

Conclusions

The estimated moderate C stocks in deadwood showed explicit spatial variability, whilst stand characteristics exhibited limited effects, thus maintaining high uncertainties regarding underlying causes. The estimates were higher than those in conventionally managed commercial stands; however, reported deadwood C stocks in over-mature and old-growth forests in boreal and hemiboreal regions, implying that overmature stands were still in low senescence and deadwood C stocks can increase significantly in the future; however, much is dependent on any disturbances in the forest ecosystems. The high variability of deadwood mode C stocks and decomposition classes indicated inconsistent changes in deadwood C stocks and C release rates, highlighting that deadwood is a dynamic yet depleting C store; however, given the values of carbon storage and biodiversity, larger deadwood sizes are of particular importance, as hinted by relationships with mean diameter.

On the other hand, ageing and larger dimensions of trees increase the vulnerability of the overmature stands to natural disturbances, which would inevitably boost the transition of deadwood C stock as observed in some old-growth and virgin forests.

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References

Angelstam, P. and Kuuluvainen, T. 2004. Boreal forest disturbance regimes, successional dynamics, and landscape structures: A European perspective. *Ecological Bulletins* 51: 117–136.

Bates, D., Mächler, M., Bolker, B. and Walker, S. 2015. Fitting linear mixed-effects models using lme4. *Journal of Statistical Software* 67(1): 1–48; https://doi.org/10.18637/jss.v067.i01.

Bonan, G.B. 2008. Forests and climate change: Forcings, feedbacks, and the climate benefits of forests. *Science* 320: 1444–1449; https://doi.org/10.1126/science.1155121.

Buras, A. and Menzel, A. 2019. Projecting tree species composition changes of European forests for 2061–2090 under RCP 4.5 and RCP 8.5 scenarios. *Frontiers in Plant Science* 9: 1986; https://doi.org/10.3389/fpls.2018.01986.

Bušs, K. 1997. Forest ecosystem classification in Latvia. *Proceedings of the Latvian Academy of Sciences. Section B* 51(5/6): 204–218.

Canadell, J.G. and Raupach, M.R. 2008. Managing forests for climate change mitigation. *Science* 320(5882): 1456–1457; https://doi.org/10.1126/science.1155458.

Caudullo, G., Tinner, W. and de Rigo, D. 2016. *Picea abies* in Europe: distribution, habitat, usage and threats. *European Atlas of Forest Tree Species* 14: 114–116.

D'Amato, A.W., Orwig, D.A., Foster, D.R., Barker Plotkin, A., Schoonmaker, P.K. and Wagner, M.R. 2017. Long-term structural and biomass dynamics of virgin Tsuga canadensis – *Pinus strobus* forests after hurricane disturbance. *Ecology* 98: 721–733; https://doi.org/10.1002/ecy.1684.

Durrant, T.H., de Rigo, D. and Caudullo, G. 2016. *Pinus sylvestris* in Europe: Distribution, Habitat, Usage and Threats. *European Atlas of Forest Tree Species* 14: 845–846.

EUR-Lex. 2024. Regulation (EU) 2024/1991 of the European Parliament and of the Council of 24 June 2024 on nature restoration and amending Regulation (EU) 2022/869 (Text with EEA relevance). PE/74/2023/REV/1. Available online at: http://data.europa.eu/eli/reg/2024/1991/oj (accessed: 18 June 2025).

Fahlvik, N., Ekö, P.M. and Petersson, N. 2015. Effects of precommercial thinning strategies on stand structure and growth in a mixed even-aged stand of Scots pine, Norway spruce and birch in southern Sweden. *Silva Fennica* 49(3): 1302; https://doi.org/10.14214/sf.1302.

Felton, A., Lindbladh, M., Brunet, J. and Fritz, Ö. 2010. Replacing coniferous monocultures with mixed-species production stands: an assessment of the potential benefits for forest biodiversity in northern Europe. *Forest Ecology and Management* 260(6): 939–947; https://doi.org/10.1016/j.foreco.2010.06.011.

Framstad, E., de Wit, H., Mäkipää, R., Larjavaar, M., Vesterdal, L. and Karltun, E. 2013. Biodiversity, Carbon Storage and Dynamics of Old Northern Forests. Copenhagen (Denmark): Nordic Council of Ministers, 507 pp.

Frelich, L.E., Jõgiste, K., Stanturf, J., Jansons, A. and Vodde, F. 2020. Are secondary forests ready for climate change? It depends on magnitude of climate change, landscape diversity and ecosystem legacies. *Forests* 11: 965; https://doi.org/10.3390/f11090965.

Fridman, J. and Walheim, M. 2000. Amount, structure, and dynamics of dead wood on managed forestland in Sweden. *Forest Ecology and Management* 131(1-3): 23–36; https://doi.org/10.1016/S0378-1127(99)00208-X.

Frouz, J., Pižl, V., Cienciala, E. and Kalčík, J. 2009. Carbon storage in post-mining forest soil, the role of tree biomass and soil bioturbation. *Biogeochemistry* 94: 111–121; https://doi.org/10.1007/s10533-009-9313-0.

Garbarino, M., Marzano, R., Shaw, J.D. and Long, J.N. 2015. Environmental drivers of deadwood dynamics in woodlands and forests. *Ecosphere* 6: 30; https://doi.org/10.1890/ES14-00342.1.

Humphrey, J.W., Sippola, A.L., Lempérière, G., Dodelin, B., Alexander, K.N.A. and Butler, J.E. 2004. Deadwood as an indicator of biodiversity in European forests: from theory to operational guidance. In: Marchetti, M. (Ed.) Monitoring and indicators of forest biodiversity in Europe – from ideas to operationality. Joensuu (Finland): European Forest Institute (EFI), EFI Proceedings No. 51, p. 193–206.

Jansson, G., Hansen, J.K., Haapanen, M., Kvaalen, H. and Steffenrem, A. 2017. The genetic and economic gains from forest tree breeding programmes in Scandinavia and Finland. *Scandinavian Journal of Forest Research* 32(4): 273–286.

Jonsson, B.G., Ekström, M., Esseen, P.A., Grafström, A., Ståhl, G. and Westerlund, B. 2016. Dead wood availability in managed Swedish forests – Policy outcomes and implications for biodiversity. *Forest Ecology and Management* 376: 174–182; https://doi.org/10.1016/j.foreco.2016.06.017.

Kapusta, P., Kurek, P., Piechnik, Ł., Szarek-Łukaszewska, G., Zielonka, T., Żywiec, M. and Holeksa, J. 2020. Natural and human-related determinants of dead wood quantity and quality in a managed European lowland temperate forest. *Forest Ecology and Management* 459: 117845; https://doi.org/10.1016/j.foreco.2019.117845.

Karjalainen, L. and Kuuluvainen, T. 2002. Amount and diversity of coarse woody debris within a boreal forest landscape dominated by *Pinus sylvestris* in Vienansalo wilderness, eastern Fennoscandia. *Silva Fennica* 36(1): 147–167.

Kellomäki, S. 2024. Dynamics of Carbon in Boreal Forest Ecosystems. In: Forest Management for Timber Production and Climate Change Mitigation. Linking Dynamics of Carbon Cycle in Ecosystem Management. Cham: Springer, Managing Forest Ecosystems, Vol. 44, p. 31–48; https://doi.org/10.1007/978-3-031-71575-4_3.

Ķēniņa, L., Elferts, D., Bāders, E. and Jansons, Ā. 2018. Carbon pools in a hemiboreal over-mature Norway spruce stands. *Forests* 9(7): 435; https://doi.org/10.3390/f9070435.

Ķēniņa, L., Zute, D., Jaunslaviete, I., Samariks, V. and Jansons, Ā. 2022. Old-Growth Coniferous Stands on Fertile Drained Organic Soil: First Results of Tree Biomass and Deadwood Carbon Stocks in Hemiboreal Latvia. *Forests* 13(2): 279; https://doi.org/10.3390/f13020279.

Köster, K., Jõgiste, K., Tukia, H., Niklasson, M. and Möls, T. 2005. Variation and ecological characteristics of coarse

woody debris in Lahemaa and Karula National Parks, Estonia. *Scandinavian Journal of Forest Research* 20: 102–111; https://doi.org/10.1080/14004080510042137.

Köster, K., Metslaid, M., Engelhart, J. and Köster, E. 2015. Dead wood basic density, and the concentration of carbon and nitrogen for main tree species in managed hemiboreal forests. *Forest Ecology and Management* 354: 35–42; https://doi.org/10.1016/j.foreco.2015.06.039.

Krankina, O.N. and Harmon, M.E. 1995. Dynamics of the dead wood carbon pool in northwestern Russian boreal forests. *Water Air Soil Pollution* 82: 227–238; https://doi.org/10.1007/BF01182836.

Lassauce, A., Paillet, Y., Jactel, H. and Bouget, C. 2011. Deadwood as a surrogate for forest biodiversity: meta-analysis of correlations between deadwood volume and species richness of saproxylic organisms. *Ecological Indicators* 11(5): 1027–1039; https://doi.org/10.1016/j.ecolind.2011.02.004.

LEGMC. 2020. The Climate of Latvia. Latvian Environment, Geology and Meteorology Centre. Available online at: https://videscentrs.lvgmc.lv/lapas/latvijas-klimats (in Latvian; accessed on 30 November 2024).

Lenth, R. 2025. emmeans: Estimated Marginal Means, aka Least-Squares Means. R package, version 1.11. R-universe, 106 pp.

Liepa, I. 1996. Pieauguma mācība [Timber increment]. Jelgava (Latvia): LUA, 121 pp. (in Latvian).

Lõhmus, A. and Kraut, A. 2010. Stand structure of hemiboreal old-growth forests: characteristic features, variation among site types, and a comparison with FSC-certified mature stands in Estonia. *Forest Ecology and Management* 260(1): 155–165.

Lõhmus, A., Remm, L. and Rannap, R. 2015. Just a ditch in forest? Reconsidering draining in the context of sustainable forest management. *Bioscience* 65(11): 1066–1076; https://doi.org/10.1093/biosci/biv136.

LSFRI 'Silava'. 2023. National Forest Inventory (NFI). Latvian State Forest Research Institute 'Silava'. Available online at: https://silava.lv/en/research/projects/national-forest-inventory (accessed: 3 November 2024).

Mäkinen, H., Hynynen, J., Siitonen, J. and Sievänen, R. 2006. Predicting the decomposition of Scots pine, Norway spruce, and birch stems in Finland. *Ecological Applications* 16(5): 1865–1879; https://doi.org/10.1890/1051-0761(2006)016[1865:PTDOSP]2.0.CO;2.

Menichetti, L., Mäkinen, H., Stendahl, J., Ågren, G.I. and Hyvönen, R. 2021. Modeling persistence of coarse woody debris residuals in boreal forests as an ecological property. *Ecosphere* 12(11): 03792; https://doi.org/10.1002/ecs2.3792.

Müller, J. and Bütler, R. 2010. A review of habitat thresholds for dead wood: a baseline for management recommendations in European forests. *European Journal of Forest Research* 129(6): 981–992; https://doi.org/10.1007/s10342-010-0400-5.

Palm-Hellenurm, K., Bāders, E., Frelich, L.E., Köster, K., Metslaid, M., Polyachenko, O., Seedre, M., Shorohova, E., Stanturf, J.A., Vodde, F. and Jõgiste, K. 2024. The fate of remnant trees after wind disturbances in boreal and temperate forests. *Frontiers in Forests and Global Change* 7: 1405430; https://doi.org/10.3389/ffgc.2024.1405430.

Pan, Y., Birdsey, R.A., Fang, J., Houghton, R., Kauppi, P.E., Kurz, W.A., Phillips, O.L., Shvidenko, A., Lewis, S.L., Canadell, J.G. and Ciais, P. 2011. A large and persistent carbon sink in the world's forests. *Science* 333(6045): 988–993; https://doi.org/10.1126/science.12016.

Penman, J., Gytarsky, M., Hiraishi, T., Krug, T., Kruger, D., Pipatti, R., Buendia, L., Miwa, K., Ngara, T., Tanabe, K. and Wagner, F. 2003. Good practice guidance for land use, land-use change and forestry. Good practice guidance for land use, land-use change and forestry. IPCC National Greenhouse Gas Inventories Programme. Technical Support Unit. Kanagawa (Japan): Institute for Global Environmental Strategies (IGES) for the IPCC, 590 pp. Available online at: https://www.ipcc.ch/site/assets/uploads/2018/03/GPG_LULUCF_FULLEN.pdf.

Peltola, H., Kellomäki, S., Hassinen, A. and Granander, M. 2000. Mechanical stability of Scots pine, Norway spruce and birch: an analysis of tree-pulling experiments in Finland. *Forest Ecology and Management* 135(1-3): 143–153; https://doi.org/10.1016/S0378-1127(00)00306-6.

Petritan, I.C., Mihăilă, V.V., Yuste, J.C., Bouriaud, O. and Petritan, A.M. 2023. Deadwood density, C stocks and their controlling factors in a beech-silver fir mixed virgin European forest. *Forest Ecology and Management* 539: 121007; https://doi.org/10.1016/j.foreco.2023.121007.

Pregitzer, K.S. and Euskirchen, E.S. 2004. Carbon cycling and storage in world forests: biome patterns related to forest age. *Global Change Biology* 10(12): 2052–2077; https://doi.org/10.1111/j.1365-2486.2004.00866.x.

R Core Team. 2023. R: A Language and Environment for Statistical Computing, version 4.2.2. Vienna (Austria): R Foundation for Statistical Computing. *URL*: https://www.R-project.org (accessed on 18 March 2023).

Ranius, T. and Fahrig, L. 2006. Targets for maintenance of dead wood for biodiversity conservation based on extinction thresholds. *Scandinavian Journal of Forest Research* 21(3): 201–208; https://doi.org/10.1080/02827580600688269.

Rosenvald, R., Rosenvald, K., Drenkhan, R., Drenkhan-Maaten, T., Hobolainen, M., Lõhmus, P., Štšjogolev, S., Tedersoo, L. and Runnel, K. 2025. Balancing biodiversity, carbon, and profit with pathogen risk: Effects of felling age and thinning in spruce forests. *Journal of Environmental Management* 389: 126066.

Schulte, L.A., Mladenoff, D.J., Crow, T.R., Merrick, L.C., Cleland, D.T. 2007. Homogenization of northern US Great Lakes forests due to land use. *Landscape Ecology* 22, 1089– 1103; https://doi.org/10.1007/s10980-007-9095-5.

Seedre, M., Kopáček, J., Janda, P., Bače, R. and Svoboda, M. 2015. Carbon pools in a montane old-growth Norway spruce ecosystem in Bohemian Forest: Effects of stand age and elevation. *Forest Ecology and Management* 346: 106–113; https://doi.org/10.1016/j.foreco.2015.02.034.

Siipilehto, J., Mäkinen, H., Andreassen, K. and Peltoniemi, M. 2021. Models for integrating and identifying the effect of senescence on individual tree survival probability for Norway spruce. *Silva Fennica* 55(2): 10496; https://doi.org/10.14214/sf.10496.

Skaggs, R.W., Tian, S., Chescheir, G.M., Amatya, D.M., and Youssef, M.A. 2016. Forest drainage. In: Amatya, D.M., Williams, T.M., Bren, L. and de Jong, C. (Eds.) Forest hydrology: processes, management and assessment. Wallingford, OX (UK): CABI, p. 124–140.

Stokland, J.N. 2001. The coarse woody debris profile: an archive of recent forest history and an important biodiversity indicator. *Ecological Bulletins* 49: 71–83.

Šēnhofa, S., Jaunslaviete, I., Šņepsts, G., Jansons, J., Liepa, L. and Jansons, Ā. 2020. Deadwood characteristics in mature and old-growth birch stands and their implications for carbon storage. *Forests* 11(5): 536; https://doi.org/10.3390/f11050536.

Šēnhofa, S., Šņepsts, G., Bičkovskis, K., Jaunslaviete, I., Liepa, L., Straupe, I. and Jansons, Ā. 2021. Availability

and structure of coarse woody debris in hemiboreal mature to old-growth aspen stands and its implications for forest carbon pool. *Forests* 12(7): 901; https://doi.org/10.3390/f12070901.

Tērauds, A., Brūmelis, G. and Nikodemus, O. 2011. Seventy-year changes in tree species composition and tree ages in state-owned forests in Latvia. *Scandinavian Journal of Forest Research* 26(5): 446–456; https://doi.org/10.1080/02827581.2011.586647.

Tong, C.H.M., Nilsson, M.B., Drott, A. and Peichl, M. 2022. Drainage ditch cleaning has no impact on the carbon and greenhouse gas balances in a recent forest clear-cut in boreal Sweden. *Forests* 13(6): 842; https://doi.org/10.3390/f13060842.

Uri, V., Kukumägi, M., Aosaar, J., Varik, M., Becker, H., Aun, K., Lõhmus, K., Soosaar, K., Astover, A., Uri, M., Buht, M., Sepaste, A. and Padari, A. 2022. The dynamics of the carbon storage and fluxes in Scots pine (*Pinus sylvestris*) chronosequence. *Science of the Total Environment* 817: 152973; https://doi.org/10.1016/j.scitotenv.2022.152973.

Vítková, L., Bače, R., Kjučukov, P. and Svoboda, M. 2018. Deadwood management in Central European forests: Key considerations for practical implementation. *Forest Ecology and Management* 429: 394–405; https://doi.org/10.1016/j.foreco.2018.07.034.

Weggler, K., Dobbertin, M., Jüngling, E., Kaufmann, E. and Thürig, E. 2012. Dead wood volume to dead wood carbon: the issue of conversion factors. *European Journal of Forest Research* 131: 1423–1438; https://doi.org/10.1007/s10342-012-0610-0.

Zālītis, P. 2012. Mežs un ūdens [Forest and Water]. Salaspils (Latvia): LSFRI 'Silava', 356 pp. (in Latvian).