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Deadwood Characteristics in Mature and Old-Growth Birch Stands and Their Implications for Carbon Storage

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Abstract: As one of the most abundant tree species in the hemiboreal zone, birch is important from both commercial and biodiversity perspectives. While old-growth deciduous stands are important for biodiversity conservation with an emphasis on deadwood availability, the role that deadwood in these stands plays in carbon sequestration remains unclear. We studied mature (71–110 years old) and old-growth (121–150 years old) birch stands on fertile mineral soils. The marginal mean deadwood volume was 43.5 ± 6.4 m^3 ha^{-1} in all mature stands, 51.3 ± 7.1 m^3 ha^{-1} in recently unmanaged mature stands, and 54.4 ± 4.4 m^3 ha^{-1} in old-growth stands; the marginal mean deadwood carbon pool for each stand type was 5.4 ± 0.8 t·ha^{-1}, 6.3 ± 0.9 t·ha^{-1}, and 7.9 ± 0.6 t·ha^{-1}, respectively. Deadwood volume was not related to stand productivity in terms of stand basal area, stand height, or stand age. The difference between mature and old-growth stands remained non-significant ($p < 0.05$). A high volume of deadwood was almost continuously present throughout the landscape in assessed unmanaged sites; moreover, 88% of sample plots in old-growth stands and 63% of sample plots in mature stands had a deadwood volume higher than 20 m^3·ha^{-1}. Old-growth stands had a slightly greater volume of large deadwood than unmanaged mature stands; in both, almost half of the deadwood was more than 30 cm in diameter and approximately one-fifth had a diameter greater than 40 cm. Both groups of stands had similar proportions of coniferous and deciduous deadwood and lying and standing deadwood. Old-growth stands had a higher volume of recently and weakly decayed wood, indicating increased dieback during recent years.

Keywords: birch senescence; decline; overmature; deadwood carbon pool

1. Introduction

Birch (*Betula pendula* Roth and *Betula pubescens* Ehrh.) is the most abundant deciduous tree species in Northern and Eastern Europe, as well as the most commercially important source of hardwood [1]. It is also the most abundant tree species in Latvia, where birch-dominated stands account for 24% of total standing volume and 27% of total forest area. Along with its commercial importance, birch is valuable from a biodiversity perspective. It is used to increase biodiversity in coniferous-dominated sites in boreal regions [2], reclaim land on poor sites [3], and reforest abandoned fields [4]. Birch is used by many species in various phases of succession: mycorrhiza-forming fungi [5], insect herbivores [6], wood-decaying fungi and bacteria [7], and saproxylic insects [8], including several red-listed species [9,10]. For the latter, large-diameter deadwood is particularly important.

Large debris persists longer and provides more stable microclimatic conditions due to its slower decay rate [11]. Its longevity facilitates coexistence of species with different ecological requirements; therefore, large-diameter deadwood hosts a higher number and greater diversity of deadwood-associated species than thin-diameter deadwood [12,13] and several studies have found that it is preferred by red-listed species [14,15].

The volume and characteristics of deadwood depend largely on disturbance and the management regime used [16], and to some extent on stand age [17]. Because it can be quite patchy in the landscape [18], relatively large data sets are required to assess these factors. Deadwood stock depends on the creation and decay of new deadwood, as well as the tree species and forest zone [19,20]. Therefore, we cannot rely on studies from other zones on other tree species to gain accurate estimates. Several studies have been conducted in the boreal forest, primarily with conifers (e.g., [16,18,21–23]), while no comprehensive study on hemiboreal forests and birch has been performed. Nevertheless, a comparison of mature and old-growth stands is needed to assess whether management practices should be modified to ensure the presence of certain deadwood characteristics. Furthermore, since deadwood characteristics are linked to stand characteristics [23], it is important to identify the stand variables that drive dynamics.

Deadwood is important as a carbon pool. Since the adoption of the Kyoto Protocol in the early 1990s, increased attention has been devoted to forest-based climate mitigation [24,25]. Forests are among the largest carbon pools, estimated to store approximately 45% of terrestrial carbon [26]. Nations that have signed the Kyoto Protocol are obligated to report carbon pools and fluxes in their forests. Forests absorb CO_2 from the atmosphere, store carbon in soil and biomass, and produce wood that replaces fossil fuels in some applications. Deadwood plays an important role as both a long-lived carbon pool and a carbon source through the release of CO_2 [27]. The dynamics of forest carbon are affected by various factors, such as forest zone, site type, and productivity, stand age and dominant species, the soil moisture regime, and disturbance dynamics [26]. As a result, accurate estimations of carbon balance for forest ecosystems are hampered by tremendous heterogeneity. Most research that assesses carbon balance has been performed in managed forests. There are contrasting theories on whether old-growth forests are a carbon sink or source [28–34], with recent studies agreeing that old-growth forests are carbon sinks (for an exception, see [35]). A few studies have recently addressed the carbon budget in hemiboreal birch stands [36–39] but have focused on stand age up to maturity. However, an assessment of carbon mass in old-growth forests is necessary to improve the accuracy of greenhouse gas emission and carbon sequestration models, which will provide better accuracy on how carbon balance changes with stand age. This study aims to quantify deadwood and its carbon pool in relation to stand characteristics in mature and old-growth birch stands in hemiboreal forests.

2. Materials and Methods

This study was conducted in 25 unmanaged old-growth birch stands (*Betula pendula* Roth and *B. pubescens* Ehrh.) in hemiboreal forests (based on European forest types [40]). Throughout this paper, this group is referred to as ‘old-growth stands’ (121–150 years), with the degree of naturalness based on the Buchwald [41] classification ‘n6—Old-growth forest’. Stands were randomly pre-selected from protected forests (without documented management) across Latvia, based on the age limit (≥120 years), dominant species, and site type. Our study included birch stands on fertile mesic mineral soils (*Hylocomniosa* and *Oxalidosa* site types, according to the classification by Bušs [42]) and fertile wet mineral soils (*Myrtilloso-sphagnosa* and *Myrtilloso-polytrichosa* site types), because almost half (48%) of the birch-dominated stands in Latvia grow on these four site types. The selected stands were inspected—sites that did not meet the aforementioned requirements or which showed signs of former logging were excluded—and 6–8 sample plots per stand were established.

Overall, our study included 113 sample plots (mean 4.5 per stand; all plots with dominant species other than birch were excluded) in 122–148-year-old stands (Figure 1). In each sample plot (area 500 m^2), all living trees with a diameter at breast height (DBH) of ≥6.1 cm were measured and data on species and stand layer were noted. The heights of five overstorey trees of dominant species and three understorey trees were measured; stand height was estimated by corresponding height to the quadratic mean diameter of overstorey birch. The same overstorey trees were used to measure tree age by increment cores. For standing dead trees (stems and snags), we recorded DBH ≥6.1 cm, height, species (birch or another deciduous/coniferous species), and decay stage. Within each plot, we measured length (≥1.0 m) and the diameter at both ends of lying deadwood (diameter at thicker end ≥6.1 cm); we also noted species and decay stage at both ends. The decay stage was observed visually and using the 'knife method' and deadwood was divided into five groups: (1) recently dead, (2) weakly decayed, (3) moderately decayed, (4) very decayed, and (5) almost completely decomposed (applied from Mäkinen et al. [43]).

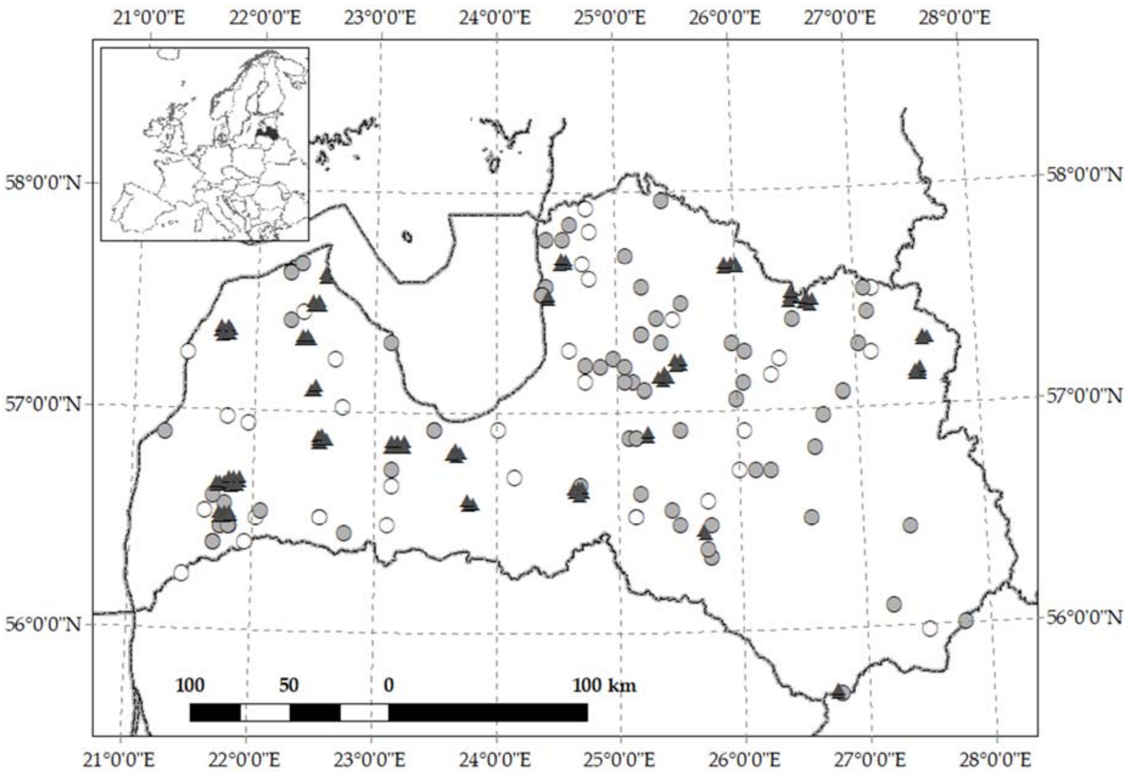

Figure 1. Distribution of sample plots in mature and old-growth stands. Triangles denote old-growth stands and circles denote mature stands, with dark-coloured circles indicating unmanaged mature stands.

National Forest Inventory (NFI, 2014–2018) data were used to select 102 sample plots (Figure 1) with (1) an overstorey dominated by birch; (2) overstorey tree age of 71–110 years; (3) *Hylocomniosa*, *Oxalidosa*, *Myrtilloso-sphagnosa*, and *Myrtilloso-polytrichosa* forest types. The selected NFI plots are referred to as 'mature stands' throughout this paper. NFI data were first used to characterise the average quantity of deadwood and deadwood carbon pool in mature stands across the country. For further assessment, we included only 'recently unmanaged mature' stands (referred to as 'unmanaged' stands; 70 sample plots). In these stands, no fresh stumps were found during the previous 15 years and no information on tree removal prior to that time was available. Measurements in these plots were performed as described by Jansons and Līcīte [44]. All measurements were conducted in circular sample plots with an area of 500 m^2. If the sample plot consisted of two distinctly different stands, it was divided into sectors; only plots with a sector area ≥400 m^2 were used. DBH was measured for all overstorey trees and stand basal area was calculated. Stand height was measured for 8–19 trees of each overstorey species, depending on the number of species in the overstorey. Stand age was measured using increment cores from three overstorey trees. Deadwood was measured in the same plot using a concentric design: within a 12.62 m radius, all deadwood with a diameter ≥14.1 cm was measured;

within a 5.64 m radius, all deadwood with a diameter ≥6.1 cm was measured. For lying deadwood, diameter at both ends (diameter at the thicker end ≥14.1 cm or ≥6.1 cm, according to the distance from centre of the sample plot) was measured. The height of all standing deadwood was measured, along with the length (≥1.0 m) of all lying deadwood; decay stage and species were noted. The decay stage was visually observed and deadwood was accordingly divided into three groups: (1) recently dead (wood hard, bark intact), (2) moderately decayed (all succeeding phases of decomposition starting from loose bark to the cover of epiphytic mosses on <10% of the visible stem surface), and (3) very decayed (cover of epiphytic mosses on ≥10% of the visible stem surface). Since NFI data had three decay stages while our measured data (old-growth stands) used a five-class division, we integrated decay stages for measured data according to their descriptions. To compare the volume of deadwood in various decay stages in mature and old-growth stands, we refer to adjusted decay stages as follows: (11) recently dead, (22) weakly decayed, and (33) moderately to almost completely decomposed.

For both data sets, the volume of whole (both living and dead) trees was calculated using equations developed by Liepa [45]. The volume of stumps and snags was calculated using Huber's formula (1); volume was then converted to mass using the decay stage-specific density. The values for deadwood density and carbon content for birch were obtained from a study by Köster et al. [46].

Huber's formula:

$$V = \frac{\mathrm{L}\,\pi\,\mathrm{d_m}^2}{4} \tag{1}$$

V = Stump/snag volume,
L = Length of the log or height of the stump, and
$\mathrm{d_m}$ = Mid-diameter of the log or the stump.

We hypothesised that (1) beyond stand maturity, deadwood increases with stand senescence; (2) sparse stands (lower basal area) consist of a higher proportion of deadwood; and (3) a larger quantity of deadwood is found in more fertile sites. Therefore, we tested the effects of stand age, basal area, and height on the quantity of deadwood and deadwood carbon pool using pooled data for unmanaged mature and old-growth stands. Data analysis was performed using SPSS 14.0 for Windows. Due to the nested design utilised in the old-growth stands (several plots were selected from the same stand), we used marginal means to assess how quantities of deadwood and deadwood carbon pool differed among site types according to stand age and adjusted decay stage. Mean values were used to characterise deadwood quantities among groups based on size and decay stage. We used generalised linear mixed models to assess the effect that stand age, basal area, and height had on the quantity of deadwood and the size of the deadwood carbon pool. All tests were performed at $\alpha = 0.05$.

3. Results

The marginal mean volume of deadwood was 49.1 ± 3.6 m^3 ha^{-1} (± standard error) in site types on mesic mineral soil and 45.8 ± 6.4 m^3 ha^{-1} in site types on wet mineral soil. The corresponding marginal mean deadwood carbon pools were found to be 6.4 ± 0.5 and 6.4 ± 0.9 t·ha^{-1}, respectively. Both the deadwood volume ($p > 0.05$) and the deadwood carbon pool were similar ($p > 0.05$) between site types on mesic and wet mineral soils; thus, we used pooled data from site type groups for subsequent analysis.

The marginal mean deadwood volume was 43.5 ± 6.4 m^3 ha^{-1} in all mature stands and 51.3 ± 7.1 m^3·ha^{-1} in unmanaged mature stands, which was similar to the 54.4 ± 4.4 m^3 ha^{-1} measured in the old-growth stands (all $p > 0.05$). Old-growth stands and unmanaged mature stands also had similar quantities of standing and lying deadwood (both $p > 0.05$) (Table 1). In all stand types, lying deadwood constituted the greater portion (68% overall) of total deadwood (Table 1). The deadwood carbon pool size was similar ($p > 0.05$) between all mature (5.4 ± 0.8 t·ha^{-1}) and recently unmanaged mature stands (6.3 ± 0.9 t·ha^{-1}), and they both differed significantly from that in old-growth stands (7.9 ± 0.6 t·ha^{-1}).

Table 1. Deadwood volume and deadwood carbon pool size in all mature (71–110), recently unmanaged mature (71–110), and old-growth (121–150) birch stands by deadwood position.

Deadwood Characteristics	Deadwood Position	Stand Type	Marginal Mean	Standard Error	95% Confidence Interval	
					Min	Max
Deadwood volume, m^3·ha^{-1}	Standing	all mature	13.8	2.4	9.2	18.5
		unmanaged mature	16.3	2.7	11.1	21.6
		old-growth	17.2	1.7	13.8	20.6
	Lying	all mature	29.7	5.5	18.8	40.5
		unmanaged mature	34.9	6.2	22.6	47.2
		old-growth	37.2	4.1	29.2	45.2
	Total	all mature	43.5	6.4	31.0	56.0
		unmanaged mature	51.3	7.1	37.3	65.3
		old-growth	54.4	4.6	45.3	63.5
Deadwood carbon pool, t·ha^{-1}	Standing	all mature	1.9	0.3	1.2	3.0
		unmanaged mature	2.2	0.4	1.4	2.9
		old-growth	2.6	0.3	2.1	3.0
	Lying	all mature	3.5	0.6	2.1	4.8
		unmanaged mature	4.1	0.8	2.6	5.6
		old-growth	5.3	0.5	4.3	6.3
	Total	all mature	5.4	0.8	3.8	7.0
		unmanaged mature	6.3	0.9	4.5	8.1
		old-growth	7.9	0.6	6.7	9.0

Within unmanaged stands, none of the tested stand parameters had an effect (all $p > 0.05$) on deadwood volume; significant variability occurred (Figure 2). A weak positive correlation was found between deadwood carbon pool size and stand age ($p < 0.01$, $r = 0.2$).

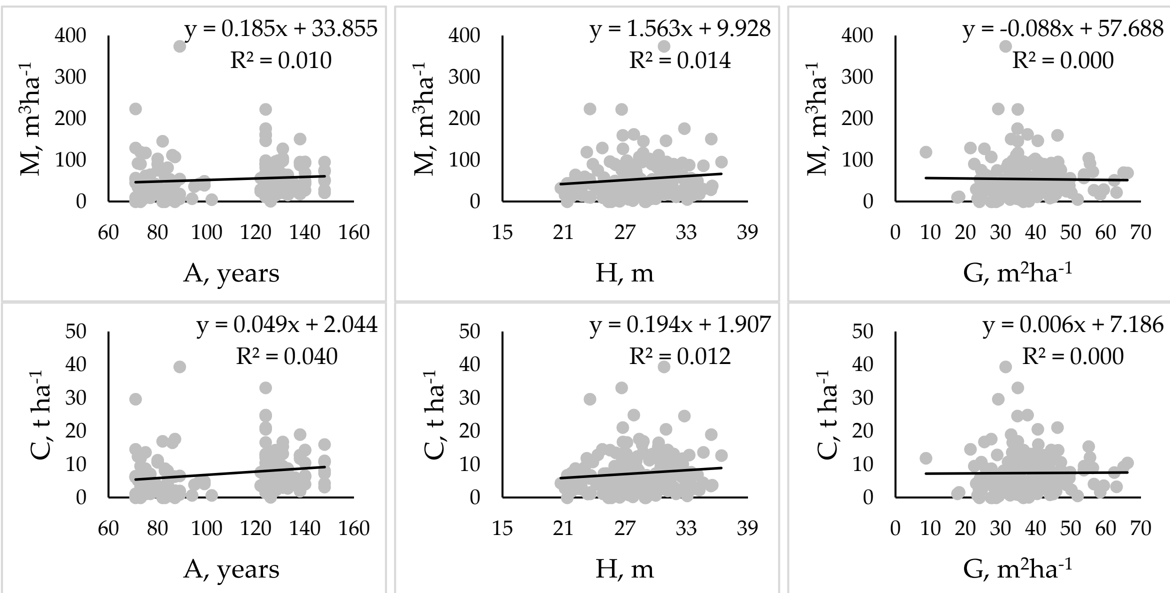

Figure 2. Volume of deadwood (M) and deadwood carbon pool size (C) in relation to stand age (A), stand height (H), and stand basal area (G) in unmanaged stands.

A large amount of deadwood was almost continuously present in assessed unmanaged stands: 88% of sample plots in old-growth stands and 63% of sample plots in unmanaged mature stands had a deadwood volume greater than 20 m^3·ha^{-1}. Moreover, a deadwood volume greater than 30 m^3·ha^{-1} was present in 74% of sample plots in old-growth stands and in 54% of plots in unmanaged mature stands. Deadwood volumes of at least 40 $m^3 \cdot ha^{-1}$ were found in 64% of sample plots in old-growth stands and 41% of plots in unmanaged mature stands.

Most of the deadwood consisted of coniferous species and birch, with these groups constituting similar proportions in both old-growth and unmanaged mature stands (both $p > 0.05$) (Table 2). However, the proportion of deadwood formed from other deciduous species (mostly *Populus tremula* L., *Alnus glutinosa* (L.) Gaertn., *Alnus incana* (L.) Moench, and *Salix caprea* L.) differed significantly; old-growth stands had a substantially lower proportion than mature stands (9% and 25%, respectively).

Table 2. Proportion of deadwood in recently unmanaged mature (71–110) and old-growth (121–150) stands by groups of species.

Stand Age, Years	Species	Proportion of Deadwood, %	Standard Error	95% Confidence Interval	
				Min	Max
71–110	Birch	35.8	4.0	28.8	44.6
	Other deciduous	25.4	3.1	19.9	32.3
	Coniferous	38.8	4.2	31.5	48.1
121–150	Birch	37.9	3.0	31.9	43.9
	Other deciduous	9.1	2.4	4.4	13.8
	Coniferous	53.0	3.2	46.7	59.2

Old-growth stands had a slightly but not significantly ($p > 0.05$) higher volume of large deadwood (pooled standing and lying) compared to unmanaged mature stands (Figure 3). Approximately half of the deadwood volume consisted of logs larger than 30 cm in diameter: 47% (22.8 ± 4.6 $m^3 \cdot ha^{-1}$) in unmanaged mature stands and 53% (30.9 ± 3.6 m^3 ha^{-1}) in old-growth stands. Moreover, 23% (11.1 ± 3.5 $m^3 \cdot ha^{-1}$) of the deadwood volume in unmanaged mature stands and 22% (13.1 ± 2.7 m^3 ha^{-1}) in old-growth stands was formed by debris with a diameter greater than 40 cm.

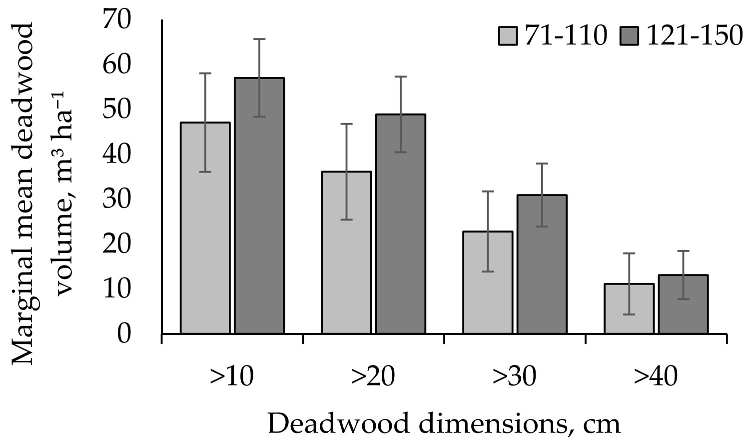

Figure 3. Volume of deadwood (± confidence interval) in recently unmanaged mature (71–110) and old-growth (121–150) stands by groups of deadwood dimensions.

Adjusted decay stages were used to assess differences in deadwood volume between unmanaged mature and old-growth stands (Figure 4). Both stand types had similar ($p < 0.05$) volumes of weakly decayed deadwood (19.2 ± 2.9 and 22.7 ± 2.3 $m^3 \cdot ha^{-1}$, respectively) and moderately to almost completely decomposed deadwood (28.0 ± 3.8 and 22.4 ± 3.0 $m^3 \cdot ha^{-1}$, respectively). However, the volume of recently dead trees differed significantly.

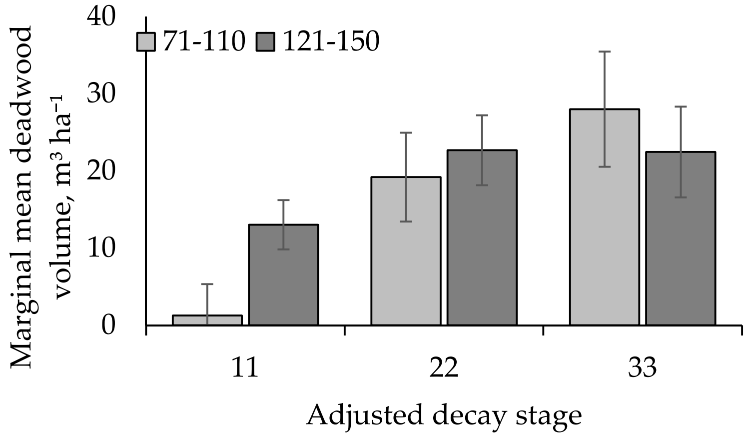

Figure 4. Volume of deadwood (± confidence interval) in recently unmanaged mature (71–110) and old-growth (121–150) stands by adjusted decay stages: (11) recently dead, (22) weakly decayed, and (33) moderately to almost completely decomposed.

In old-growth stands, deadwood distribution was categorised into five decay stages. Most of the deadwood was in decay stages 1–3 (Figure 5), comprising 83% of total deadwood volume. Weakly decayed wood formed 39%, while very decayed and almost completely decomposed wood accounted for 13% and 5% of total deadwood, respectively.

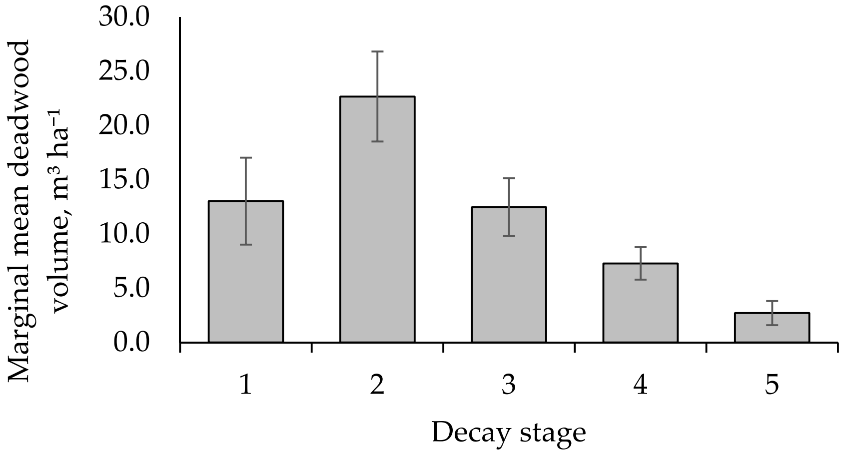

Figure 5. Volume of deadwood (± confidence interval) in old-growth stands by decay stage (applied by Mäkinen et al. [43]): (1) recently dead, (2) weakly decayed, (3) moderately decayed, (4) very decayed, and (5) almost completely decomposed.

4. Discussion

Deadwood volume in forests depends on accretion factors (disturbance, self-thinning, and senescence) and depletion factors (harvesting and decay) [47]. The great variability in deadwood volume revealed in our results is consistent with other studies. This variability results from many factors, including site productivity [48], stand age [22], tree species composition [21], deadwood turnover rate [45], forest management [34], and history of natural disturbance [49]. Our estimated marginal mean deadwood volume was 43.5 $m^3 \cdot ha^{-1}$ in all mature stands and 54.4 m^3 ha^{-1} in old-growth birch stands. This exceeds the most frequently reported threshold values for deadwood volume (from any species) in both boreal (20–30 $m^3 \cdot ha^{-1}$) and temperate lowland (30–50 $m^3 \cdot ha^{-1}$) forests [50]. Unmanaged forests at some successional stages—especially after disturbances—are often found to store more deadwood than conventionally managed forests [22,51–53], due to continuous removal of large timber from the latter. In managed boreal and temperate forests, deadwood volume is often found to be as low as 2%–30% of the volume found in unmanaged forests [16,21].

Our estimated values for managed stands are rather high compared to other countries in the hemiboreal zone. Reported national deadwood volume averages are 5.9 and 7.6 $m^3 \cdot ha^{-1}$ for managed stands in Finland and Sweden, respectively, and 13.7 $m^3 \cdot ha^{-1}$ across forests in Estonia [16,54,55]. Our results also exceed the mean deadwood volume across forests in Latvia—according to NFI, 19.8 m^3 ha^{-1}—though this figure refers to managed and unmanaged stands together. Much higher deadwood volumes, although with large variation, have been reported in old-growth unmanaged boreal and hemiboreal forests. For example, deadwood volume in pine-dominated (*Pinus sylvestris* L.) managed and semi-natural stands in eastern Finland was similar to our results, with 8.7 and 22.1 m^3 ha^{-1} at age 70 years, 42.4 and 73.1 $m^3 \cdot ha^{-1}$ at age 110 years, and 46.9 and 54.4 $m^3 \cdot ha^{-1}$ at age 150 years and above, respectively [56]. However, leaving forests unmanaged does not spontaneously lead to high volumes of deadwood. Notable differences in deadwood volume were found in a study conducted in two national parks in Estonia, where the mean deadwood volumes were 48.5 $m^3 \cdot ha^{-1}$ (0.6–148.6 $m^3 \cdot ha^{-1}$) and 27.6 $m^3 \cdot ha^{-1}$ (0.2–193.7 $m^3 \cdot ha^{-1}$). In these two sites, the mean deadwood volumes in mature (age ≥75 years) birch-dominated stands were 52.9 and 9.6 $m^3 \cdot ha^{-1}$ [57]. A much higher volume has been found in old-growth hemiboreal forests—a mean deadwood volume of 129 $m^3 \cdot ha^{-1}$ with a range from 36 to 198 $m^3 \cdot ha^{-1}$ across site types [58]. However, the high deadwood volume is also present in relatively small patches in production forest landscapes—the mean deadwood volume in woodland key habitats in Latvia was found to be 38.2–149.5 $m^3 \cdot ha^{-1}$, with the highest volumes found in deciduous stands affected by ash dieback [53].

Contrary to our hypothesis, stand age showed no relation to deadwood volume (Figure 2). Higher stand age increases mortality, which is caused initially by competition, self-thinning, and senescence and later by exogenous disturbances [22]. Other studies have found that deadwood volume increases with stand age beyond the stand maturity [16,17,59]. For instance, in boreal mesic spruce (*Picea abies* (L.) Karst.) forests in southern Finland, deadwood volume was found to be 14 $m^3 \cdot ha^{-1}$ (range 2–28 $m^3 \cdot ha^{-1}$) in managed mature stands, 22 $m^3 \cdot ha^{-1}$ (7–38 $m^3 \cdot ha^{-1}$) in managed overmature stands, and 111 $m^3 \cdot ha^{-1}$ (70–184 $m^3 \cdot ha^{-1}$) in old-growth stands [22]. Furthermore, we found no relation between deadwood volume and stand productivity (as measured by stand basal area and stand height). Generally, more productive forests tend to have more deadwood [60], but studies have reported disparate results. For example, one study found a constant proportion of standing dead trees regardless of stand basal area, suggesting that the volume of deadwood in old-growth forests is directly proportional to productivity [19]. In another study, deadwood volume in two old-growth coniferous-dominated hemiboreal forests depended on site index class [57]. It varied from 6% of the total timber volume in the lowest site index class (least productive) to 24% in the highest site index classes in one nature park and from 15% to 19% in another. Similarly, more deadwood has been found in European beech (*Fagus sylvatica* L.) forest reserves with higher volumes of living wood [48]. Conversely, in old-growth stands, this relationship is reversed due to tree death from senescence and natural disturbance. For example, in 129–198-year-old spruce forests, the basal area of the living stand correlated negatively ($r^2 = -0.77$) with deadwood volume and was positively related with the degree of disturbance—a smaller stand basal area was correlated with a larger proportion of windfall gaps and a higher deadwood volume [22]. The absence of this pattern in our study might result from multiple factors. We selected stands where old birch still formed the dominant cohort. Therefore, stands where the transition to climax species had already occurred (i.e., most of the old birch trees had died and formed deadwood) were not included. Furthermore, the basal area of old-growth stands was similar to that in the mature stands (data not shown). In conjunction with the high deadwood volume found in these sites, this suggests that the basal area of old-growth stands at the time of their maturity was very high. Therefore, the chronosequence approach [61] taken in our study may not account for the diversity of potential successional development pathways in a birch stand as it ages.

For both carbon balance calculations and wildlife habitat availability assessments, deadwood structure and decay stages are important factors. In our study sites, deadwood was rather diverse in species composition, debris position, and the distribution of dimensions and decay stages. We found an almost equal proportion of deciduous (birch and other species) and coniferous tree species in deadwood in both stand groups. From a biodiversity perspective, wildlife habitat occurrence depends heavily on deadwood species richness, especially regarding temperate deciduous species [16]. The tree species composition of a stand affects the proportion of lying and standing deadwood; because spruce tends to uproot, pine trees remain as standing snags while birch and aspen often form broken snags and crumble into small pieces. The wood properties of a species and the position of deadwood (contact with the ground) determine the decomposition rate of the debris, thus affecting deadwood's life span. We found an equal proportion of lying deadwood in mature and old-growth stands (68% of total deadwood volume in both stand types). Several studies have found similar results, reporting 2–3 times more lying (approximately 60%–70%) than standing deadwood regardless of the dominant species [18,19,22,59], while proportions as low as 11% have been reported in mature unmanaged birch stands [57].

The abundance of large-diameter deadwood is particularly important for red-listed species [62,63]. We found high proportions of large-dimension deadwood—in both mature and old-growth stands, approximately half of the deadwood volume consisted of debris with diameters larger than 30 cm and approximately one-fifth of debris had diameters larger than 40 cm. In absolute numbers, deadwood larger than 30 cm in diameter comprised 22.8 and 30.9 $m^3 \cdot ha^{-1}$ (in unmanaged mature and old-growth stands, respectively). To some extent, our results align with other studies that have found increased large deadwood volume with stand age [17,22]; this is also affected by management regime, e.g., the frequency and intensity of wood removal during commercial thinning. Regardless of stand age, similar deadwood volumes were found for weakly decayed and moderately to almost completely decomposed debris. However, the volume of recently dead trees was more than tenfold higher in the old-growth stands. In addition, almost 40% of the deadwood in old-growth stands was weakly decayed and approximately 20% was fresh, indicating increased dieback over recent years. Birch is susceptible to brown heart rot—the incidence of which rapidly increases after age 50–60 [64]—rendering trees more prone to uprooting. The overall vitality of birch trees decreases before the age of 100 years [1], with the natural lifespan being approximately 150 years [65]. This is also supported by our observations during the stand selection process. Numerous old-growth birch stands in unmanaged territories were 130–140 years old, based on forest inventory data; however, field inspection revealed that old birch was no longer the dominant cohort, as they had declined.

In our study, deadwood was assessed as both a carbon pool and a biodiversity indicator. Overall, it appears that forest maintenance for biodiversity aligns well with a carbon sequestration objective. With carefully practised management, both can be achieved for a certain period of time [66], although the direct causative relationship between these two ecosystem services is questionable [67]. Moreover, this relationship depends on tree species and vegetative zone and persists only to the point that dieback rates of old trees become significant—that is, when the negative correlation between stand basal area of living trees and the volume of deadwood becomes strong. Changes in stand structure, caused by disturbances or senescence among dominant trees, impact stand carbon balance by reducing photosynthesis and increasing heterotrophic respiration. This has been demonstrated in primary boreal forest, where relatively small patches of disturbance yielded increased proportions of deadwood [35]. As a consequence, net emissions from deadwood increased, altering overall ecosystem respiration and turning the forest from a carbon sink to a source of CO_2 to the atmosphere [35]. However, small-scale disturbances do not necessarily lead to a forest becoming a carbon source. Depending on tree species and vegetation zone, deadwood decomposition may last for decades, whereas rapid natural regeneration or abundant understorey trees could compensate for the loss of dominant trees and mitigate increased respiration [31]. Likewise, a study on an overmature forest shifting from early successional species to later successional species showed stable ecosystem production during the first few years after moderate forest disturbance, although the enlarged deadwood volume substantially increased heterotrophic respiration [68]. Although a long-term increase in old-growth forest carbon pools may be possible in some conditions [69], it is still not the general rule. The decline in net primary productivity with stand age reduces the carbon pool [70]. A smaller increase in carbon pool per year has been observed in relatively long-lived species like spruce [71] and these processes are even faster for species with shorter life spans, including birch [39]. Moreover, the impact of natural disturbances increases [72] as older forests become more susceptible [73]; and in cases of severe stand-replacing disturbances, large amounts of carbon are released into the atmosphere [74].

5. Conclusions

We aimed to quantify deadwood and evaluate its implications for carbon storage in relation to stand characteristics in mature and old-growth birch stands in hemiboreal forests. High volumes of deadwood were present in both mature and old-growth birch-dominated stands and were found almost continuously across the studied stands. Deadwood volume was not related to stand productivity in terms of stand basal area and stand height, nor was it related to stand age; the difference between recently unmanaged mature stands and old-growth stands remained non-significant. We found that deadwood was diverse in species composition and decay stages and composed substantially of large-dimension debris. The high proportion of recently and weakly decayed deadwood indicates increased dieback in old-growth stands during recent years. Further monitoring studies of old-growth stands would provide additional insights into how long-term stand development progresses through successional transition and further elucidate ongoing deadwood dynamics for this widespread but, in this respect, poorly studied tree species.

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