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Deadwood Diversity of Boreal and Sub-boreal Old-growth Forests in Southern Finland

Isabella De Meo[1,*], Roberta Pastorelli[1], Francesco Vitali[1], Alessandro Paletto[2]

(1) Consiglio per la ricerca in agricoltura e l'analisi dell'economia agraria (CREA), Research Centre for Agriculture and Environment, Via di Lanciola 12/A, I-50125 Firenze, Italy; **(2)** Consiglio per la ricerca in agricoltura e l'analisi dell'economia agraria (CREA), Research Centre for Forestry and Wood, p.za Nicolini 6, I-38123 Trento, Italy

***Correspondence:** e-mail: isabella.deme@crea.gov.it

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ABSTRACT

In the last century, old-growth forests in boreal and sub-boreal zone have decreased, along with their contribution to biological diversity. In order to carry on management strategies aimed at maintaining deadwood diversity in old-growth forests, it is fundamental to identify simply and readily measurable indicators. This study investigated the deadwood diversity in four old-growth forests in southern Finland. Five indicators of deadwood diversity (deadwood amount and diversity by species, component, decay class, water reservoir in logs) were estimated and analysed. The results showed an average deadwood volume of approximately 85±28 $m^3 \cdot ha^{-1}$ diversified by decay class and component. Besides, the results showed average Shannon index values four the four old-growth forests equal to 0.488 for deadwood species diversity, 0.932 for component diversity, and 1.286 for decay class diversity. The set of deadwood diversity indicators used in this study successfully supported the analysis of deadwood diversity in boreal and sub-boreal old-growth forests.

Keywords: biodiversity conservation; logs; snags; stumps; decay class; indicators

INTRODUCTION

In the last decades, the number of old-growth forests has been rapidly decreasing throughout the boreal and sub-boreal zone as highlighted by many authors (Axelsson et al. 2002, Shorohova et al. 2011, Martin et al. 2021a). This has led to a significant loss of biodiversity and other ecosystem services provided by boreal and sub-boreal forests (Thingstad et al. 2003, Betts et al. 2017). As emphasized by the new EU Forest Strategy for 2030, the old-growth forests "are not only among the richest EU forest ecosystems, but they store significant carbon stocks and also remove carbon from the atmosphere, while being of paramount importance for biodiversity and the provision of critical ecosystem services". Currently, the old-growth forests cover only 3% of EU forested land and their patches are generally small and fragmented (EC 2021), but despite this they play a key role as hot spots of biodiversity.

In literature, there are several definitions of old-growth forests, but explanations of the elements that constitute an old-growth forest are often ambiguous (Wirth et al. 2009). Since old-growth forests are complex dynamic systems, most definitions use multiple criteria that can be categorized into three groups: structural, successional, and biogeochemical (Wirth et al. 2009, Cristea et al. 2019). According to Frelich and Reich (2003), old-growth forests are forests that have reached some context-specific thresholds (e.g. a minimum stand age, a minimum age or size of trees, a stage of development and succession, a degree of naturalness) that has been determined by a scientific or political process. Other authors emphasize that old-growth is the final stage of stand development (Oliver and Larson 1990) or that old-growth forests are those characterized by high complexity and largest and oldest trees (Spies 2004). Regardless of the definition adopted, old-growth forests are complex ecosystems that can be distinguished from the earlier stand development stages by the following attributes (Kneeshaw and Gauthier 2003, Larson et al. 2015): tree size and age, tree mortality regime, tree species composition, number of canopy layers, complex ecological relationships, high spatial heterogeneity, and accumulations of large deadwood material. The last can be found either as standing dead trees or as fallen logs and stumps, in various decay stages (Paillet et al. 2015, Martin et al. 2021a).

Deadwood in forests contributes to ecosystem functioning, productivity and fluxes, facilitates natural tree regeneration, and contributes to nutrient cycling and soil formation (Harmon et al. 1986, Siitonen et al. 2000, Humphrey et al. 2004, Franklin et al. 2006, Hekkala et al. 2016). In addition, the volume and diversity of deadwood in terms of tree species, size, and the degree of decay determine the richness of many deadwood-dependent species (Martikainen et al. 2000, Lassauce et al. 2011). Standing dead trees, logs, stumps and tree cavities offer food, nests, roosts, and forage to a variety of species, including vertebrates and invertebrates, plants, and saproxylic fungi (Boyle et al. 2008, Bütler et al. 2013).

Deadwood volume and composition depend on a variety of elements such as tree species composition, stand age, and natural tree mortality. Furthermore, macroclimatic conditions, forest management and silvicultural intervention also affect the amount and characteristics of deadwood (Přívětivý et al. 2016, Doerfler et al. 2017). Concerning deadwood volume, some authors highlighted that 40 $m^3 \cdot ha^{-1}$ of deadwood can be considered a suitable threshold for the existence of saproxylic communities in boreal forests (Martikainen et al. 2000), while other authors highlighted a deadwood threshold of 10–70 $m^3 \cdot ha^{-1}$ for saproxylic organisms in boreal spruce-pine forests (Müller and Bütler 2010). The amount of deadwood is closely related to past and current forest management strategies: generally, forests managed for timber production are characterized by the average volume of deadwood between 5 $m^3 \cdot ha^{-1}$ and 10 $m^3 \cdot ha^{-1}$ (Paletto et al. 2014, Banaś et al. 2014, Skwarek and Bijak 2015), while in unmanaged forests or protected areas deadwood volume exceeds 25 $m^3 \cdot ha^{-1}$ (Green and Peterken 1997, Bayraktar et al. 2020). Nevertheless, it is important to note that deadwood volume alone is an insufficient criterion for investigating and assessing the level of biodiversity, the naturalness of forests and the related conservation value (Kunttu et al. 2015, Oettel et al. 2020). In this sense, deadwood diversity is another crucial element due to the varying habitat requirements of different species (Brin et al. 2009).

As emphasized by several authors, quantitative but also qualitative attributes of deadwood (e.g. volume, size, components, and decay class) can strongly influence the saproxylic communities (Kraus and Krumm 2013, De Meo et al. 2022). The deadwood distribution by component (lying deadwood, standing dead trees, stumps) influences the water storage capacity of the forest ecosystems (Přívětivý and Šamonil 2021). Lying deadwood in contact with the ground is the most important component as a water reserve for organisms during the dry season, and it determines the activity of decomposers and the composition of fungal communities (Shorohova and Kapitsa 2014). Another important attribute for deadwood diversity qualification is the decay class because it affects deadwood-inhabiting fungi, bryophyte presence and diversity (Ódor and Standovár 2001). Some authors highlighted that the richness of saproxylic species is the highest in the first two decay classes of conifers and in third decay class of broadleaves (Hammond et al. 2004, Ulyshen and Hanul 2010).

Therefore, the amount of deadwood in forests must be investigated together with its diversity and the characteristics of the forest stand in order to understand the complexity of the described mechanisms and phenomena.

In literature, some indicators to assess deadwood diversity have been developed and tested in case studies (Oettel et al. 2020, De Meo et al. 2022). When using these indicators, it is important to observe that the use of various deadwood assessment methods in Europe (Kunttu et al. 2015) complicates data harmonization and comparison. Dealing with indicators which assess deadwood occurrence, and its diversity could be valuable information to support forest management and interventions aimed at nature conservation and increasing naturalness of forests. In fact, both the deadwood volume and diversity indexes are often correlated with other naturalness indicators and can be regarded as consistent measures of naturalness.

Based on the above considerations, the aim of the present study was to define and implement a set of indicators to measure deadwood diversity attributes. The set of indicators was investigated in four old-growth forests in the Pirkanmaa region in southern Finland.

MATERIALS AND METHODS

Study Area

The study area included the old-growth forests located in the Juupajoki municipality, in the Pirkanmaa region in Finland (61°51′N, 24°17′E). The Juupajoki municipality has a land area of 258.45 km^2 almost exclusively covered by forests, and a population of 1,780 inhabitants (population density 6.89 inhabitants per km^2). The main forest types are coniferous uneven-aged forests, dominated mainly by Norway spruce (*Picea abies* (L.) H. Karst.) and Scots pine (*Pinus sylvestris* L.), with some deciduous trees such as European aspen (*Populus tremula* L.) and silver birch (*Betula pendula* L.). The ground cover vegetation consists of shrubs (mainly *Vaccinium vitis-idaea* L., *Vaccinium myrtillus* L.), and several mosses and lichens typical of boreal forests (Hellén et al. 2004, Helmisaari et al. 2007).

From a pedological point of view, on top of homogenous bedrock the soil type at the site is Haplic podzol on glacial till. The annual mean temperature of the area is 3.5°C, and the warmest and coldest months are July (mean 16.0°C) and February (mean –7.7°C), respectively. The mean annual precipitation is 711 mm, and July (92 mm) and August (85 mm) are the wettest months of the year. The altitude is between 100 and 180 m a.s.l. (Suni et al. 2003).

Sampling and Field Measurements

The sample plots were randomly located in the old-growth forests within the boundaries of the Juupajoki municipality (Figure 1). Through a location randomization algorithm, 25 plots located in four old-growth forest areas were identified and distributed proportionally to the area: two sample plots in the Kalela's spruce forest (KA – 2.5 ha; geographical coordinate WGS84: 61.8527 N - 24.3031 E), five sample plots in the Lake Kuivajärvi old-growth forest (KU – 22.0 ha; geographical coordinate WGS84: 61.8503 N - 24.2820 E), nine sample plots in the Susimäki old-growth forest (SU – 50.0 ha; geographical coordinate WGS84: 61.8590 N - 24.2364 E), and nine sample plots in the Musturi old-growth forest (MU – 62.0 ha; geographical coordinate WGS84: 61.8719 N - 24.3691 E). It was decided to use a higher number of small plots distributed in each old-growth forest to consider the typical variability of old-growth forests.

Each sample plot is representative of an area between a minimum of 1.25 ha in the Kalela's spruce forest and a maximum of 6.9 ha in the Musturi old-growth forest. These four forests can be considered old-growth forests as they fall within the definition provided by Rouvinen et al. (2005, 22): "...a forest where the natural successional dynamics have been predominant for a period of time lasting at least for several decades and there are thus no marks of human activity in the field or in the historical documents".

The data was collected in the field using circular sampling units of 13 m radius (531 m^2) with two transects inside arranged perpendicular to each other.

In each sampling unit, the dendrometric data of standing living trees and deadwood were measured. For all standing living trees with a diameter at breast height (DBH) greater than 4.5 cm, species and DBH were recorded, while height was measured for five living trees closest to the central point of the plot. In addition, all deadwood components (logs, snags and stumps) with a diameter threshold greater than 4.5 cm were recorded and measured, while small woody debris not reaching the above-mentioned threshold was classified as litter. According to Rouvinen et al. (2005), logs are sound and rotting pieces of wood located on the ground, snags are standing dead trees with a height greater than 1.3 m, while stumps are standing dead trees truncated or cut to a height of less than 1.3 m.

All snags in the sampling unit with a height more than 1.3 m were measured by collecting two perpendicular diameters at DBH, height of standing dead trees or broken height, species, and decay class. For each stump two perpendicular diameters measured on the broken height, minimum and maximum height of the stump on the broken height, species, and decay class were recorded. Logs were measured using the Line Intersect Sampling (LIS) method based on the principles underpinning Buffon's needle problem (Warren and Olsen 1964). In this sampling method, diameter of logs is measured at the point of intersection along one (or more than one) transects of a given length. Transects are often arranged in different orientations to reduce the potential for orientation bias (Russell et al. 2015), while the total length of transects affects the precision of the estimate because the probability of sampling a woody debris piece is proportional to its length (Bell et al. 1996).

In this study, two transects of 26 m were located within the sampling unit passing through the central point: the first transect in the direction NW-SE, and the second transect in the direction NE-SW, perpendicular to the first transect. For each log intercepted by transects and with a diameter greater than 4.5 cm, the following information was recorded: two perpendicular diameters measured in the intersection point of the transect, species, decay class, and moisture measured with PCE-MMK 1 Moisture Meter.

During field measurements, the assignment of the three components to a decay class was based on the visual assessment method. Logs, snags and stumps were classified according to a 5-decay class classification system (Naesset 1999, Paletto and Tosi 2010, De Meo et al. 2017): recently dead (1st decay class), weakly decayed (2nd decay class), medium decayed (3rd decay class), very decayed (4th decay class) and almost decomposed (5th decay class). The method is built on visible morphological characteristics of deadwood, wood colour, presence of bark, and integrity of wood structure. To reduce the variability and subjectivity of the visual assessment, only one forestry technician assigned the decay classes in all 25 plots.

Data Processing

The data collected in the field were processed to estimate a set of indicators related to deadwood diversity in the old-growth forests (Table 1). As a first step, data were processed to provide the following information to characterize the forest stand: i) the number of trees per hectare (n stems·ha^{-1}), ii) stand basal area per hectare ($m^2 \cdot ha^{-1}$), iii) standing living trees volume per hectare ($m^3 \cdot ha^{-1}$), and iv) living tree biomass per hectare ($t \cdot ha^{-1}$). Subsequently, five indicators of deadwood diversity (deadwood amount, deadwood diversity by species, component, decay class, and water reservoir in logs) were calculated starting from the data collected in the field.

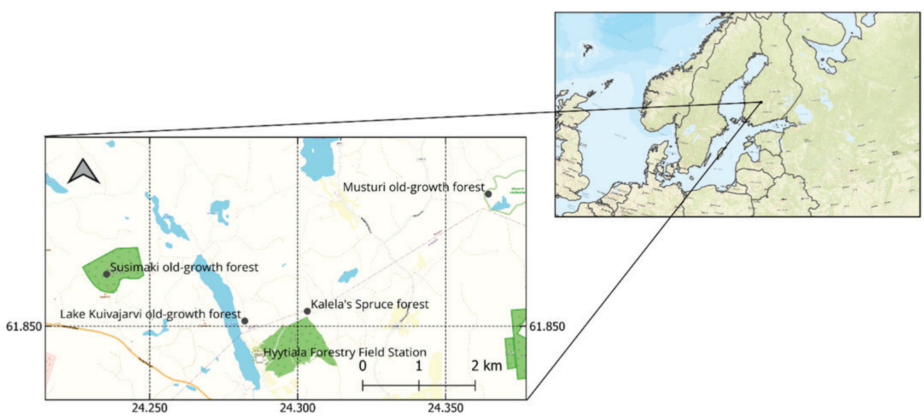

Figure 1. Location of the sample plots in the old-growth forests in the Juupajoki municipality, Finland.

Table 1. Set of indicators to assess deadwood diversity in old-growth forests.

Indicators	Description	Measure
Deadwood amount	Volume of deadwood per hectare expressed either absolutely or as ratio between deadwood and living volume (De Meo et al. 2017)	Deadwood volume per hectare ($m^3 \cdot ha^{-1}$)
Deadwood diversity by species	Deadwood species distribution distinguishing between species (Oettel et al. 2020). Deadwood species distribution is useful when associated with the tree species composition to understand stand dynamics	Shannon index for deadwood species (SH_{ds})
Deadwood diversity by component	Deadwood distribution by component (lying deadwood, standing dead trees, stumps)	Shannon index for deadwood component (SH_{dc})
Deadwood diversity by decay class	Deadwood distribution by deacy class considering the five classes used in the National Forest Invetories (Oettel et al. 2020). Deadwood distribution by decay class influences microbial communities' richness (Pastorelli et al. 2020)	Shannon index for deadwood decay class (SH_{dd})
Water reservoir in logs	Lying deadwood increases the water storage capacity of forests and provides resources for many organisms (Přívětivý and Šamonil 2021)	Potential water reservoir in logs (W_r, $kg \cdot m^{-3}$)

The data collected in the field was used to estimate deadwood volume by component and decay class. Deadwood amount was recorded as a quantitative indicator of diversity. Snags' volume was calculated considering the basal area, the snag height measured in the field, and the stem form factor of conifer species (De Meo et al. 2022), while stumps' volume was estimated using the Smalian's formula (De Meo et al. 2017). The formulas used to estimate the volumes of these two deadwood components (snags, Equation 1; stumps, Equation 2) are the following:

$$V_s = f \cdot BA \cdot h_s \quad (1)$$

$$V_{st} = \frac{\pi}{4} \cdot \left(\frac{H_{st} + h_{st}}{2}\right) \cdot \left(\frac{D_1 + D_2}{2}\right)^2 \quad (2)$$

where: V_s is the volume of snags (m^3), V_{st} is the volume of stumps (m^3), BA is basal area (m^2), f is the stem form factor as the relationship between real stem volume and cylinder volume (0.5), h_s is height obtained from the hypsometric curve (m), H_{st} is the maximum height of the stump (m), h_{st} is the minimum height of the stump (m), D_1 and D_2 are two perpendicular diameters of the stump (m).

Logs' volume was estimated using the equation proposed by Van Wagner (1968) for the LIS method (Equation 3):

$$V_l = \left(\pi^2 \sum \frac{di^2}{8L}\right) \quad (3)$$

where: V_l is the volume of lying deadwood ($m^3 \cdot ha^{-1}$), L is transect length (m) and d_i is average diameter (mean of the two diameters) of the intersection point along the transects (m).

The deadwood diversity in the old-growth forests was calculated considering the following three qualitative characteristics of deadwood: species, decay class (5-class classification system), and component (snags, logs, stumps). Another indicator of diversity was calculated using the Shannon index formula modified by Oettel et al. (2020) to consider the peculiarities of deadwood (Equation 4):

$$SH = -\sum_{i=1}^{n} p_i \log_2 p_i \quad (4)$$

where: p_i is the proportion of individuals of the i^{th} (where i can be the species, decay class, or component) divided by the total number of individuals.

Higher diversity is indicated by higher SH-values. The Shannon index was applied to analyse the deadwood diversity with regard to the species (SH_{ds}), component (SH_{dc}), and decay class (SH_{dd}) in accordance with the method proposed by Oettel et al. (2020).

Finally, another key biodiversity indicator related to deadwood in forests is the accumulation of water in logs. According to Přívětivý and Šamonil (2021), logs plays an important role in increasing the water storage capacity of forests and providing resources for many organisms, increasing biodiversity. Logs can play a key role as a water reservoir for organisms due to their position whether in contact with the ground or not. This parameter can influence the moisture content in relation to the amount of contact area with the ground and, subsequently, the activity of decomposers and the composition of fungal communities (Rajala et al. 2012, Přívětivý and Šamonil 2021). In this study, the moisture (%) measured using the PCE-MMK 1 Moisture Meter for each log in the plots was used to estimate the potential water reservoir in the lying deadwood of old-growth forests using the following formula (Equation 5):

$$W_r = -\sum_{i=1}^{n} v_i \cdot dd_i \cdot mc_i \quad (5)$$

where: W_r is the potential water reservoir in the logs (kg), v_i is the volume of log i, (m^3), dd_i is the dry (or basic) density of log i ($m^3 \cdot kg^{-1}$) considering five decay classes, mc_i is the moisture content (%) of log i measured with the PCE-MMK 1 Moisture Meter, and n is the number of logs.

The Pearson correlation test was performed to evaluate the correlation between stand parameters and deadwood volume in the four old-growth forests.

Differences in the deadwood distribution by decay class (p=0.036) and deadwood component among the four forests were tested using the Chi-square (χ^2) test (p<0.05)

Finally, the Analysis of Similarities (ANOSIM), a non-parametric statistical test proposed by Clarke and Green (1988), and the Kruskal-Wallis non-parametric test were used to investigate whether there are statistically significant differences between the four old-growth forests. In particular, differences between sites were tested considering the three indicators of deadwood diversity ($SH_{ds,}$ $SH_{dc,}$ SH_{dd}). Ordination analysis was obtained using the indicators of deadwood diversity by means of non-parametric multidimensional scaling (NMDS) with Euclidean distance. NMDS is a widely used multivariate analysis technique in which a distance matrix (in this case a Euclidean distance matrix) is calculated, representing the pairwise dissimilarity between samples based on a set of multiple variables (in this case $SH_{ds,}$ $SH_{dc,}$ and SH_{dd}). This distance matrix is used by the NMDS algorithm (999 permutations) to produce a 2-dimensional view of the dissimilarity between samples, in which the position of each point on the ordination plane relates to their dissimilarity respect to all other points. The plot was then enriched by highlighting the grouping with solid lines and with dashed lines, pointing to the centroid of the group. Finally, to highlight the direction of maximum change in the variables producing this ordination, the ENVFIT procedure was used, and represented with arrows. In addition, the Multi-Response Permutation Procedure (MRPP) test was also applied to verify the significant grouping between sites. ANOSIM test, NMDS ordination and ENVFIT procedure, as well as MRPP analysis were performed in R software (v 4.2.1, R core team, 2022) using the *vegan* package (v2.6-4, Oksanen et al. 2022) with 999 permutations.

RESULTS

The characteristics of the four old-growth forests (KA, KU MU, SU) are shown in Table 2. The results show the value of stem density, basal area, volume and biomass by old-growth forest.

Concerning deadwood, the results evidenced an average deadwood volume of 85.0±27.8 $m^3 \cdot ha^{-1}$. comprised in a range between a minimum of 46.7 $m^3 \cdot ha^{-1}$ (MU) and a maximum of 113.2 m^3 ha^{-1} (KA). The average deadwood volume was thus distributed by the three components: 47.0% in logs (average volume of 40.0 $m^3 \cdot ha^{-1}$), 38.7% in snags (32.5 $m^3 \cdot ha^{-1}$), and 14.3% in stumps (12.1 $m^3 \cdot ha^{-1}$). In particular, the Susimäki old-growth forest (SU) was characterized by a prevalence of snags (42.9% of total deadwood volume), while the other three sites were characterized by a greater quantity of logs (Table 3). In all old-growth forests, there were on average 174 stumps per hectare with volumes ranging between 8 $m^3 \cdot ha^{-1}$ for KU and 16.3 $m^3 \cdot ha^{-1}$ for SU, corresponding to less than 15% of the total deadwood volume.

Observing the data for old-growth-forests, the results highlighted that that higher values of living tree volume correspond to higher values of total deadwood volume. However, the Pearson correlation test showed a non-significant correlation between living trees' volume and deadwood volume (r=0.161, p=0.442), as well as between basal area and deadwood volume (r=0.294, p=0.154).

Observing the data by decay class, the results showed that deadwood volume was distributed quite uniformly among the five decay classes: 26.4% in the 1st decay class, 14.9% in the 2nd decay class, 27.1% in the 3rd decay class, 19.2% in the 4th decay class, and 12.4% in the 5th decay class. In addition, it is important to emphasize that 60.7% of stumps' volume was concentrated in the 5th decay class. Conversely, the volume of snags and logs was mainly in the two least decomposed classes (1st and 2nd decay classes): 91.2% for snags and 56.0% for logs.

The results of the Chi-square (χ^2) test showed significant differences among the four sites both regarding deadwood distribution by decay class (p=0.036) and deadwood component (p<0.0001). In particular, SU old-growth forest was characterized by a higher deadwood volume in the more decomposed decay classes (4th and 5th) compared to the less decomposed, while KA and KU old-growth forests were characterized by higher deadwood volumes in the 1st decay class. In the SU old-growth forest, a high quantity of deadwood was concentrated in the snags in respect to the other components (stumps and logs), while in the other three old-growth forests the logs were the component with highest volumes.

The results regarding the diameter distribution of living trees (Figure 2) highlighted that the majority of Norway spruce stems have a diameter between 10 and 25 cm (18.8% of total stems have a diameter between 10 and 15 cm, 23.8% between 16 and 20 cm; 21.9% between 21 and 25 cm), while birch and Scots pine have a diameter distribution more shifted towards the upper classes. It is interesting that 33.6% of Scots pine stems have a diameter greater than 40 cm.

Table 2. Stand characteristics by old-growth forest (mean±SD).

Stand characteristics	Plot			
	KA	KU	MU	SU
Stem density ($n \cdot ha^{-1}$)	583.80±159.80	538.61±97.49	578.42±133.92	897.11±117.99
Basal area ($m^2 \cdot ha^{-1}$)	41.99±0.81	39.11±0.30	31.13±0.47	42.90±0.39
Volume ($m^3 \cdot ha^{-1}$)	471.47±80.86	494.76±162.62	339.00±111.30	477.29±99.26
Biomass ($t \cdot ha^{-1}$)	179.67±31.99	189.84±62.61	127.90±40.27	177.11±35.43

NOTE: Kalela's spruce forest (KA), Lake Kuivajärvi old-growth forest (KU), Musturi old-growth forest (MU) and Susimäki old-growth forest (SU).

Table 3. Deadwood volume distribution by component and decay class ($m^3 \cdot ha^{-1}$) by old-growth forest (mean±SD).

Deadwood characteristics	Plot			
	KA	KU	MU	SU
Decay class				
1st	9.55±13.51	32.78±58.85	4.78±7.44	6.05±4.60
2nd	16.56±2.95	9.28±11.50	7.79±14.99	2.31±2.45
3rd	26.92±17.07	15.16±13.36	5.45±5.28	11.19±10.38
4th	5.37±7.26	7.38±16.08	4.52±10.45	11.51±13.75
5th	0.46±0.06	6.63±7.09	1.49±2.54	8.06±7.92
Component				
Snags	40.99±20.54	36.66±41.17	10.95±11.58	42.87±35.68
Stumps	16.31±3.12	8.00±3.11	12.64±4.83	11.53±5.65
Logs	55.94±0.39	44.68±22.61	23.08±34.68	36.14±21.58

NOTE: Kalela's spruce forest (KA), Lake Kuivajärvi old-growth forest (KU), Musturi old-growth forest (MU) and Susimäki old-growth forest (SU).

With regard to the deadwood diameter distribution, the results showed that for Norway spruce an average value of 87 standing dead trees, 167 stumps and 115 logs per hectare was estimated.

Deadwood of Scots pine was almost exclusively characterized by standing dead trees – approximately 24 standing dead trees per hectare compared to eight stumps and three logs – with a diameter between 31 and 40 cm (40.6% of total Scots pine standing dead trees).

With regard to birch, an average number of nine logs, eight standing dead trees and 17 stumps per hectare were estimated.

The Shannon index showed high diversity values both for the component and the decay class, with an average value of the index equal to 0.932 (SD=0.323) for the component and 1.286 (SD=0.366) for the decay class. Considering the four sites, the Shannon index values for the species was comprised in a range between a minimum of 0.115 (SD=0.157) for the Musturi old-growth forest (MU) and a maximum of 0.691 (SD=0.176) for the Lake Kuivajärvi old-growth forest (KU). The indices for the decay class were in a narrow range from 1.449 for SU and 1.003 for MU. Also, regarding the Shannon index for the component the lowest values were found for the Musturi old-growth forest (MU) with an average value of 0.626 (SD=0.506), while the other three sites showed similar values (1.044 for KA, 1.058 for KU, and 1.050 for SU). However, the Kruskal-Wallis non-parametric test (α=0.05) showed statistically significant differences among the four sites for two of the three indices: SH_{ds} (p=0.003) and SH_{dd} (p=0.042).

The results regarding the last diversity indicator, the potential water reservoir in logs, showed a total average value of 78.87±32.87 kg of water · m^{-3} of lying deadwood and the following average values by old-growth forests: 49.65±38.26 kg·m^{-3} for MU old-growth forest; 83.16±29.96 kg·m^{-3} for KU old-growth forest; 92.22±13.97 kg·m^{-3} for KA old-growth forest; and 93.09±21.73 kg· m^{-3} for SU old-growth forest.

The results of the ANOSIM test show statistically significant differences among the four old-growth forests (R=0.3004, p=0.003). Ordination analysis and Envfit testing, as shown in Figure 3, suggests that the Susimäki old-growth forest (SU) was characterized by a high deadwood species diversity (SH_{ds}), as-well-as a medium-low component and decay class diversity (SH_{dc}, SH_{dd}). Conversely, the Kalela's spruce forest (KU) was characterized by a high decay class and component diversity and slightly lower species diversity, while the Musturi old-growth forest (MU) was the one that had the lowest values of all deadwood diversity indicators, as well as higher intra-group heterogeneity (higher dispersion in the ordination plot). In addition, the results of the MRPP test (A=0.217, p=0.003) confirmed that there is a statistically significant difference among groups, and additionally that the Musturi old-growth forest (MU) was characterized by a higher intra-group variability (MU, A=2.728) in comparison to the other groups (KA, A=0.7183; KU, A=1.232; SU, A=1.178).

DISCUSSION

Our results showed that in the Juupajoki old-growth forests the average deadwood volume is equal to approximately 80 $m^3 \cdot ha^{-1}$. In literature, Lõhmus and Kraut (2010) estimated an average deadwood volume between 140 and 200 $m^3 \cdot ha^{-1}$ in four old-growth forests in Estonia, while Tyrrell and Crow (1994) found deadwood volumes between 150 and 200 $m^3 \cdot ha^{-1}$ in old-growth hemlock-hardwood forests of hemiboreal North America. Burrascano et al. (2013) in a global review of 93 papers found median deadwood volumes for old-growth forests of 157.3 $m^3 \cdot ha^{-1}$. In addition, as highlighted in the literature on boreal forests, the values of the present study showed that the deadwood volumes of old-growth forests are significantly higher than those of managed mature and over-mature forests. In fact, Siitonen et al. (2000) found

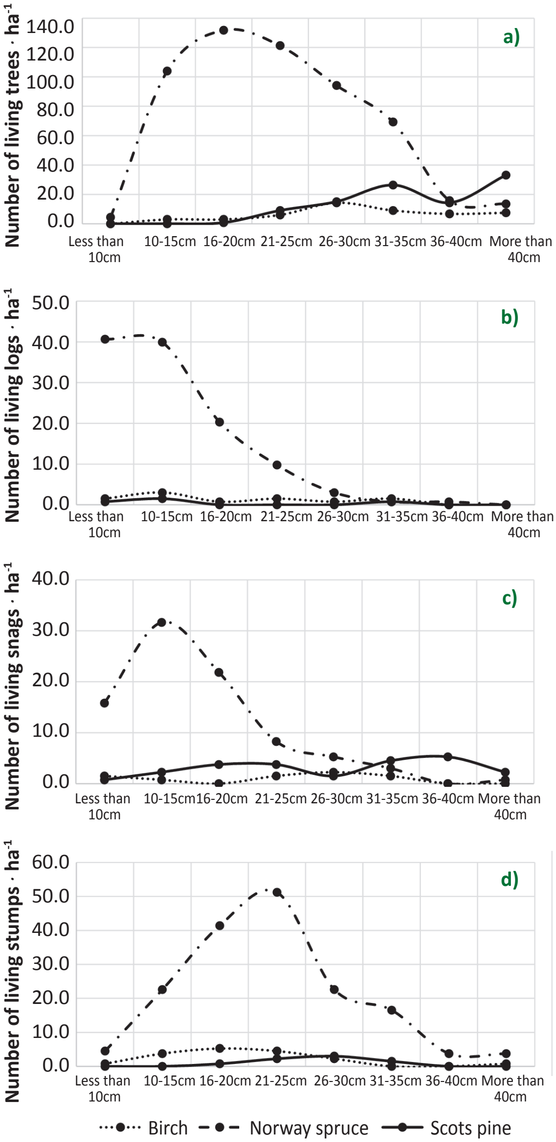

Figure 2. Diameter distribution by species: **a)** living trees; **b)** logs; **c)** snags; **d)** stumps.

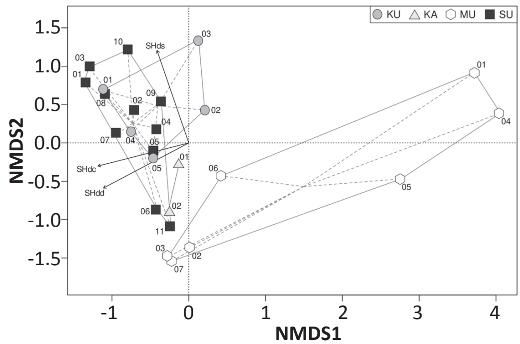

Figure 3. Non-Metric Multidimensional Scaling (NMDS) considering SH_{ds}, SH_{dd} and SH_{dc} index values. The position on the ordination plane of each point represents the values of the three indices in a sample, and distances between samples relate to differences in index values (calculated with Euclidean distance). Vectors represent the result of ENVFIT analysis with the same variables used to obtain ordination, to highlight the direction of their variation in the graph. Grouping of samples based on four old-growth forests is highlighted by different shapes (Circle = KU, Triangle = KA, Hexagon = MU, Square = SU) as well as by solid line connecting samples in a group, and dotted lines connecting the group centroid.

NOTE: Kalela's spruce forest (KA), Lake Kuivajärvi old-growth forest (KU), Susimäki old-growth forest (SU) and Musturi old-growth forest (MU).

that the mean deadwood volume in mature managed Norway spruce-dominated stands in southern Finland (age 95-120 years) is 14 m³·ha⁻¹, while in over-mature stands (more than 120 years) it is 22 m³·ha⁻¹. Always referring to Finland, Uotila et al. (2001) estimated a deadwood volume of 70 m³·ha⁻¹ in mature stands and 47 m³·ha⁻¹ in over-mature stands. Therefore, compared to literature values, our four forests have intermediate deadwood volume values between boreal old-growth forests and over-mature forests. Observing living trees, the results of this study estimated an average living tree volume of 456 m³·ha⁻¹ for the four Juupajoki old-growth forests (from 495 m³·ha⁻¹ of the Lake Kuivajärvi old-growth forest to 339 m³·ha⁻¹ of the Musturi old-growth forest). These results are comparable with those estimated by other authors in south-Finnish old-growth forests: Lilja and Kuuluvainen (2005) estimated an average living tree volume equal to 333 m³·ha⁻¹ in a dry pine stand, while Siitonen et al. (2000) quantified 396 m³·ha⁻¹ of average living tree volume in a mesic spruce stand. Besides, Penttilä et al. (2004) evidenced an average living tree volume comprised in a range between 244 m³·ha⁻¹ and 531 m³·ha⁻¹ in a study considering six old-growth spruce-dominated forests in southwestern Finland, while 381 m³·ha⁻¹ was the volume of living trees in a Norway spruce and Scots pine dominant state-owned old-growth forest as highlighted by Martikainen et al. (2000).

In managed forests the amount of deadwood is mostly affected by the intensity of management, while in unmanaged (i.e. old-growth forests) it is mostly the history of natural disturbances which influences the volume and distribution of deadwood throughout the forest (Garbarino et al. 2015, Bujoczek et al. 2018). Otherwise, there are also other factors influencing deadwood quantity such as site conditions, stand age, forest type and the volume and basal area of living trees (Castagneri et al. 2010, Banaś et al. 2014). Old-growth forests include a wide variety of changing forest structures and deadwood amount significantly varies from one structure to another. Our results evidenced that higher volume of living trees corresponds to higher volumes of deadwood. This is evident in the Musturi old-growth forest, which shows the lowest values of volume of living trees and the lowest amount of deadwood (46.7 m³·ha⁻¹). Deadwood amount in the Musturi old-growth forest is about half of that present in the other three old-growth forests.

Our results are confirmed in the study by Oettel et al. (2020), examining data from 28 unmanaged natural forest reserves in Austria to analyze the patterns and drivers of the volume and diversity of deadwood. Those authors confirmed that when investigating forests belonging to the same forest type and developed in similar ecological and climatic conditions, like those of our study, deadwood proportion is mainly influenced by living stand volume and the proportion of deadwood increases slightly with diameter. Furthermore, in six beech-dominated old-growth forests in the Italian Apennines Lombardi et al. (2015) observed that the growing stock and deadwood volume show a nearly identical trend across different forests.

Concerning deadwood diversity, the Shannon index highlights a quite high deadwood diversification in terms of decay class (SH_{dd}=1.286) and component (SH_{dc}=0.932), but a low value per species (SH_{ds}=0.488). As with deadwood volumes, there are also differences between the four sites regarding Shannon indices: Musturi old-growth forest is characterized by the lowest values for all three indices (SH_{dc}=0.626, SH_{ds}=0.115, SH_{dd}=1.003), while the other three sites have significantly higher values. The lower deadwood diversity of the Musturi old-growth forest compared to the other three both in terms of species, component and decay class implies a potential lower availability of microhabitats and conditions favourable to saproxylic organisms. In fact, deadwood volume and diversity are key factors for saproxylic species as highlighted by Bujoczek and Bujoczek (2022).

In literature, in four old-growth forests in Estonia representing four groups of forest site types arranged along soil richness and moisture gradients, Lõhmus and Kraut (2010) evidenced a Shannon index of species diversity between 0.4 and 1.18. The first was evidenced in dry boreal forests, while the second in eutrophic boreo-nemoral forests. Furthermore, Martin et al. (2021b) estimated a Shannon index of snag decay classes between 0.52 and 1.02 and a Shannon index of log decay classes between 0.34 and 1.32 for a boreal old-growth forests in Quebec (Canada). Pesklevits (2007) found values of Shannon index of snag decay classes between 0.5 and 1.3 and a Shannon index of log decay classes between 0.6 and 1.5 in different sites of a conifer dominated old-growth forest in Nova Scotia (Canada).

Concerning the role of logs as a potential water reservoir, our results showed an average value of approximately 80 kg of water · m^{-3} of logs in the four old-growth forests of the Juupajoki municipality with a range from 50 kg·m^{-3} to 90 kg·m^{-3}. As emphasized by Rajala et al. (2012) and Přívětivý and Šamonil (2021), logs play a key role in increasing the water storage capacity of forest ecosystems and in providing resources for organisms. Therefore, this indicator should be carefully considered in the studies focused on biodiversity in forest ecosystems.

From a methodological point of view, the main strength of the study is that it provided a synthesis of deadwood-related biodiversity indicators for boreal and sub-boreal old-growth forests.

A second strength is that the indicators used are reliable and quickly measured. Obviously, different indicators can have advantages and disadvantages.

Conversely, the main weakness is the exclusion of microhabitat trees (e.g. rot holes, cavities, large nests, mould, fruiting bodies) in the set of indicators which represent a key aspect for saproxylic organisms.

In addition, it is important to remark that the efficiency of a considered indicator is dependent on several factors, and above all that data harmonizing is not straightforward due to the diversity of deadwood assessment methods from country to country.

CONCLUSIONS

The study highlighted that the four old-growth forests of the Juupajoki municipality are characterized by intermediate deadwood volume values between boreal old-growth forests and over-mature forests. Deadwood volume is evenly distributed by decay class and between logs and snags, while the stumps are few, of medium-large size and of advanced decay class as expected for old-growth forests. The high number and volume of logs is an important water reserve available for water-related organisms, while the high number and volume of large size snags is a key factor for the availability of tree-microhabitats for saproxylic species.

Deadwood diversity in terms of species, composition, and decay classes did not differ from one old-growth forest to another because diversity indicators were not employed on different forest types. In fact, the four old-growth forests of the Juupajoki municipality belong to the same forest type (i.e. Norway spruce and Scots pine-dominated stands).

Since deadwood diversity is strongly linked to biodiversity and since certain species depend on high structural diversity to meet their life history requirements, shaping the compositional structure of deadwood in managed forests should be addressed. A major challenge could be to employ this kind of indicators in interdisciplinary research that matches deadwood diversity measures with forest biodiversity measures at different levels.

Author Contributions

IDM and AP conceived and designed the research, IDM, RP and AP carried out the field measurements, RP performed laboratory analysis, FV and RP processed the data and performed the statistical analysis, IDM secured the research funding, supervised the research and helped to draft the manuscript, IDM, RP, FV and AP wrote the manuscript.

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Conflicts of Interest

The authors declare no conflict of interest.

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