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Structure and dynamics of deadwood in the mixed beech-conifers Frakto virgin forest of Greece

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Abstract Virgin forests are considered valuable reference areas for studying forest ecosystem structures and functions as they have been naturally grown with no human interventions. In the Mediterranean region there are few such areas and even scarcer data on deadwood which is a key element for multi-functional forest management. Data regarding the amount and variety of standing and lying deadwood were recorded in the core zones of the Frakto virgin forest in the central Rodopi Mountains in eight square plots of 0.25 ha each. The average deadwood volume accounted for 175.71 m^3 ha^{-1} with lying deadwood consisting mainly of conifers and representing over 60% of the total deadwood. The deadwood distribution showed a decreasing trend towards larger size classes while in terms of quality deadwood it was represented by all stages of decay, thus showing high variability. The research outcomes contribute to knowledge standards when adopting management regimes in mixed beech forests aiming at sustainable forest ecosystem management.

Keywords: coarse woody debris, snags, logs, stumps, decay stages.

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Introduction

Deadwood has a vital role in sustainable forest ecosystem management. It is a key element for enriching biodiversity in forest ecosystems as it provides habitats and food for many epiphytic and epixylic species including bryophytes, lichens and vascular plants (Dittrich et al. 2014, Staniaszek-Kik et al. 2019), vertebrates (Redolfi De Zan et al. 2017, Moreira-Arce et al. 2021, Ionescu et al. 2024) and invertebrates (Bloszyk et al. 2021, Parisi et al. 2021). Also, the presence of deadwood in forest ecosystems increases their productivity (Marra & Edmonds 1994) and enhances their natural regeneration by facilitating the establishment of the tree seedlings (Ježek 2004, Zielonka 2006, Orman & Szewczyk 2015), while the lying deadwood prevents soil erosion and surface water runoff (Stevens 1997, Kraigher et al. 2002) and provides effective protection from falling rocks and avalanches (Kupferschmidt et al. 2003).

Deadwood constitutes an important component of carbon storage and therefore the availability and structure of deadwood has also been discussed with regard to its contribution to carbon storage (Pregitzer & Euskirchen 2004). All size classes of decaying wood pieces contribute to long-term organic matter accumulation, because the lignin and humus of well-decayed wood are high in carbon content (Maser et al. 1988). However, the most important elements for carbon storage are the coarse woody debris (Paletto et al. 2014), since these act as a long-term carbon reservoir, until the decomposition process is completed. This process in particular may extend up to 1000 years in exceptional cases (Feller 2003), depending on the wood characteristics, the climate and the location on the ground (Merganicova & Merganic 2010). Biomass accumulations over long periods of time contribute to high levels of carbon storage, thus rendering virgin forests very important in relation to the global carbon cycle and climate change mitigation (Pregitzer & Euskirchen 2004).

Apart from the ecological importance of deadwood its recreational value has also been pointed out in the framework of multifunctional forest management (Edwards 2012, Pastorella et al. 2016). Tourists' perceptions and preferences have shown a tendency towards forests with a high level of naturalness, which was characterized by the presence of both standing and lying deadwood (Pastorella et al. 2016).

For the reasons described previously the quantity of deadwood expressed as the volume of standing and lying deadwood for different forest types has been included as a key indicator in the high-level policy framework of the Pan-European Indicators for Sustainable Forest Management (MCPFE 2003) under Criterion 4, concerning "Maintenance, conservation and appropriate enhancement of biological diversity in forest ecosystems".

The presence of deadwood constitutes a structural indicator which defines the level of naturalness in forest ecosystems (Rahman et al. 2008, Laarmann et al. 2009, Winter et al. 2010). It provides information on the intensity of past human influences and the extent to which they resemble virgin forests (Stokland 2001, Woodall & Nagel 2006). However, for the proper use of deadwood as an indicator for sustainable forest management, reference values attributed to the natural state are required. Such reference values can be derived from natural unmanaged forests also called virgin forests (Hahn & Christensen 2004, Humphrey et al. 2004), although such areas are rather rare (Peterken 1996, Diaci 1999, Sabatini et al. 2018). In Europe, for example, only a few scattered remnants of virgin forests have survived in mountainous areas mainly in the geographical areas of the Carpathians, the Balkans and the Alps (Leibundgut 1982, Prusa 1985, Körpel 1995, Diaci 1999, Brändli & Dowhanytsch 2003, Parviainen 2005, Hamor et al. 2008), most probably because these areas suffered minimal impacts from human activities that favoured their conservation status well before their nomination as protected areas. Therefore, deadwood studies in these types of forests are very important, because they can provide a better baseline for studying natural deadwood availability and structure levels (Körpel 1995, Standovár & Kenderes 2003).

Based on the records of the "Ancient high conservation value forest (A-HCVF)" program, which was implemented by WWF France and aimed at identifying potential sites of ancient forests in the Mediterranean ecoregion, they comprise less than 1% of the total area of the ecoregion (Mansourian et al. 2013). Specifically in Greece only one such area has been recorded through this program, the Frakto virgin forest (Mansourian et al. 2013). Considering the scarcity of this type of forests and the limited studies on deadwood attributes of mixed beech-conifer forests, the current research aims to fill this gap by:

i. analysing the deadwood profile of the strictly protected Frakto virgin forest through its quantitative and qualitative characteristics and comparing it with those of other mixed beech-fir-spruce virgin forests of Central and Southeastern Europe;

ii. identifying the deadwood diameter distribution functions, so as to obtain reference values for naturalness that help define appropriate regimes for multifunctional forest management.

Materials and Methods

Study area

The Frakto virgin forest located in the northeastern part of the Rodopi Mountain Range National Park, central Rodopi Mountains, Greece has served as the study area for the current research (Figure 1). The forest occupies 589.25 ha and it was designated as Preserved Monument of Nature by national legislation in 1980, following decades of banning any human intervention but scientific research. The altitude of the area ranges from approximately 1500 to 1953 m, the mean annual temperature is 11.4°C, while the mean annual precipitation around 694 mm.

The deadwood in the current research included the standing deadwood which comprises standing dead trees and fragmented dead trees (snags), the stumps and the lying deadwood or logs, referred to as Coarse Woody Debris (CWD). A full census of CWD on the fixed-area plot (quadrat) was conducted. In each plot, dead standing trees and snags with diameter at breast height (*dbh)* at least 5 cm and height at least 1.3 m were recorded as list. The category of stumps included all the naturally formed stumps of height less than 1.3 m, since in the study area no management practices are allowed. Downed log records included the fallen pieces of stem or branch with diameter at least 10 cm at the lower end of the log (Hochbichler et al. 2000, IPCC 2003), and length at least 2 m.

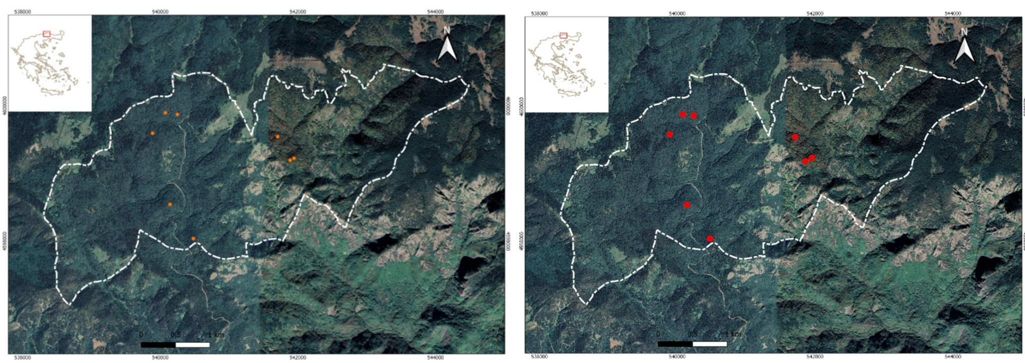

Figure 1 Location map of the study area and plot distribution.

Table 1 Decay stages of logs, snags and stumps in the Frakto virgin forest, Greece.

Decay stage	Log characteristics	Snag characteristics	Stump characteristics
1	bark fully intact, small branches present, round form, wood texture preserved, log raised on a support point;	standing dead tree with bark and most branches still attached, wood remains firm;	bark intact, wood remains solid
2	bark intact, small branches present, round form, wood texture well preserved, log elevated on support point;	dead tree with few branches remaining and loose bark, wood still firm	bark nearly fully intact, outer wood firm, inner wood decayed, texture includes large pieces
3	some bark remaining, no twigs, round shape, wood firm, texture with large fragments, log sagging close to the ground	bark absent, no twigs, wood firm	partial bark remaining, decay spread throughout most of the stump, blocky texture
4	bark completely absent, no twigs, shape from round to oval, wood firm, texture blocky, entire log resting on the ground	no bark, no twigs, wood ranging from firm to soft (soft sapwood < 70%)	back, wood soft and powdery
5	bark absent, no twigs, oval shape, wood soft and powdery texture, entire log on the ground	no bark, no twigs, wood ranging from firm to soft (soft sapwood > 70%).	-

For the dead standing trees and snags the height and diameter at breast height of those higher than 1.3 m, were measured. In the case of lying deadwood, measurements of its total length and diameter were taken at 1/2 of its length, whereas for the stumps only the diameter at 0.3 m of height was measured.

The decay stage of the logs and standing deadwood was classified according to a five-class system (Motta et al. 2006, Castagneri et al. 2010) while that of the stumps according to a four-class system (Motta et al. 2006) (Table 1).

Data analysis

The standing dead tree volume of fir and spruce was calculated according to the local yield tables of the Forest Service of Drama using breast height diameter and total height (Drama Forest District Office 1974) in concordance with that of living trees, while that of beech, according to the two-parameter (DBH, height) equation derived by Raptis et al. (2020). The volume of the broken snags was estimated in analogy to a frustum of a cone (Motta et al. 2006, Castagneri et al. 2010) while the volume of the stumps was determined in analogy to the volume of a cylinder of height equal to 0.3 m (Merganicova & Merganic 2010). The volume of the lying deadwood (logs) was calculated according to the volume of a second-degree paraboloid using the Huber's formula (Rahman et al. 2008, Merganicova & Merganic 2010):

$$v = h * g_{1/2} \qquad (1)$$

where $\boldsymbol{v}$ the volume of the log in m^3, $\boldsymbol{h}$ the length of the log in m and $\boldsymbol{g_{1/2}}$ the cross-sectional area at 1/2 length of the log in m^2.

The total volume of the coarse woody debris was determined as the sum of the volumes of standing deadwood, logs and stumps.

The deadwood diameter distribution was fit to several theoretical functions in order to test the goodness-of-fit. The theoretical functions were selected among those published as describing better the diameter distributions in old growth forests presenting an uneven-aged structure (Chivulescu et al. 2020). Thus, the Lognormal, Gamma, Weibull and Exponential probability distributions were chosen for the goodness-of-fit tests to the deadwood diameter distribution of the Frakto virgin forest.

The probability density function for the lognormal distribution is given by equation (2):

$$f(x) = \frac{exp\left[-\frac{1}{2}\left(\frac{ln(x)-\mu}{\sigma}\right)^2\right]}{x\sigma\sqrt{2\pi}} \qquad (2)$$

where $\boldsymbol{x}$ the mean of the diameter class (x>0) in centimeters, π=3.1416, $\boldsymbol{\mu}$ the location parameter, $\boldsymbol{\sigma}$ the scale parameter.

The corresponding function for the 2-parameter Gamma distribution is presented by equation 3:

$$f(x) = \frac{x^{\alpha-1} \boldsymbol{e}^{\frac{-x}{\beta}}}{\beta^{\alpha}\Gamma(\alpha)} \quad (3)$$

for $x \geq 0$, $\alpha \geq 0$, $\sigma \geq 0$.

where α the shape parameter, β the scale parameter and Γ(α) the gamma function given by equation 4.

$$\Gamma(\alpha) = \int_0^{\infty} t^{\alpha-1} e^{-t} dt \quad (4)$$

The density function for the 2-parameter Weibull distribution is shown by equation 5:

$$f(x) = \left(\frac{\gamma}{\beta}\right)\left(\frac{x}{\beta}\right)^{\gamma-1} exp\left[-\left(\frac{x}{\beta}\right)^{\gamma}\right] \quad (5)$$

where $\boldsymbol{\beta}$ the scale parameter and $\boldsymbol{\gamma}$ the shape parameter, with $\gamma \geq 0$. The cumulative distribution function (CDF) for the Weibull (2P) distribution, which facilitates the estimation of the proportion of deadwood items in diameter classes, is:

$$F(x) = 1 - \exp\left[-\left(\frac{x}{\beta}\right)^{\alpha}\right] \quad (6)$$

where $\boldsymbol{x}$, $\boldsymbol{\alpha}$ and $\boldsymbol{\beta}$ as described above.

The function for the Exponential distribution is shown by equation 7:

$$F(x) = \lambda e^{(-\lambda x)} \quad (7)$$

where $\boldsymbol{\lambda}$ the scale parameter.

The maximum likelihood estimation (MLE) was used in order to estimate the model parameters while the goodness of fit was checked by using the Kolmogorov–Smirnov (KS), the Anderson–Darling (AD) and the Cramer-von Mises (CvM) test (D'Agostino & Stephens 1986). A significant level of a = 0.05 was used. Three tests were used to check the goodness of fit as each one of them alone highlights another aspect of the goodness of fit. Thus, the combined application of the three tests ensures finding the best fitting performance of the distributions to meet various requirements of goodness of fit providing therefore a comprehensive evaluation.

The KS, the AD and the CvM tests were calculated with the following functions 8, 9 and 10:

$$KS = max\{D^+, D^-\} \quad (8)$$

where $D^+ = max_{i=1,\ldots,n}(\frac{1}{n} - F_i)$

and $D^- = max_{i=1,\ldots,n}(F_i - \frac{i-1}{n})$

$$AD = -n - \sum_{i=1}^{n}(2i-1)\frac{\log\left(F_i(1-F_{n+1-i})\right)}{n} \quad (9)$$

$$CvM = \frac{1}{12n}\sum_{i=1}^{n}\left\{F_i - \frac{(i-0.5)}{n}\right\}^2 \quad (10)$$

where $\boldsymbol{F_i} \triangleq \boldsymbol{F(x_i)}$, with F the fitted cumulative distribution function, $\boldsymbol{F_n}$ the empirical distribution function, $\boldsymbol{x_i}$ the n observations of a continuous variable X in ascending order. The lower the value of the tests, the better the fit. Two goodness-of-fit criteria, the Akaike Information Criterion (AIC) and the Bayesian Information Criterion (BIC) were also used for the comparison of the models. The statistical analysis regarding the distribution parameters and the goodness-of-fit test was performed using the fitdistrplus R package (Delignette-Muller & Dutang 2015) from R software.

Results

Deadwood quantity

The mean CWD volume was calculated equal to 175.71 m^3 ha^{-1} reaching 31.0% of the total volume of the living trees. The volume of logs made up 65.3% of the total CWD volume exceeding that of standing deadwood (32.1%) and stumps (2.6%).

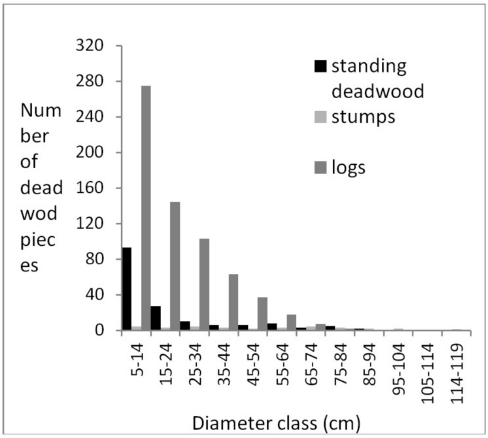

Figure 2 Distribution of all deadwood pieces sampled on all plots (2 ha) by diameter class (cm).

Regarding the classification of tree species an additional category of "not specified" deadwood was added as it was difficult with no considerable error to identify deadwood mostly in the advanced decay classes. However, the deadwood consisted mainly of conifers. In terms of volume, Norway spruce was dominant in the snags while the stumps originated mainly from beech.

The mean density of snags was 80 trees ha^{-1} with beech accounting for 48 trees ha^{-1} corresponding to 60.0% of the snags followed by spruce (27.5%) and fir (12.5%). Despite their greater abundance the beech snags were mostly concentrated at small diameters < 20 cm (85.0%) while conifers presented a more uniform distribution. Snags were dominating in small diameter classes while logs were also concentrated mostly in smaller sizes with over 90.0% found in diameter classes up to 50 cm. Stumps were almost equally distributed, being also present in the largest diameter classes (diameter > 100 cm) (Figure 2).

The diameter distribution for the standing and lying deadwood of the Frakto virgin forest with the fitted curves of the four models, Lognormal, Gamma, Weibull and Exponential are shown in Figure 3, while the corresponding probability distributions are shown in Table 3.

Goodness-of-fit statistics and criteria showed that the Lognormal probability distribution described better the distribution of standing as well as lying deadwood followed by the Weibull distribution as far as standing deadwood is concerned and the Gamma distribution for lying deadwood. The exponential distribution showed the lowest fit performance for both standing and lying deadwood in the Frakto virgin forest.

Table 2 Deadwood volume (total, lying and standing dead wood) and number of snags per species (mean ± standard error, minimum, maximum, median and range values) in the Frakto virgin forest, Greece.

	CWD parts	Beech	Silver fir	Norway spruce	Not specified	Total deadwood
Volume (m^3 ha^{-1})	Snags	13.79 ± 3.46	13.11 ± 6.54	29.34 ± 9.93	0.26 ± 0.26	56.50 ± 8.28
	min-max	1.64-31.10	0.00-45.33	1.56-77.93	0.00-2.11	19.89-95.97
	Logs	23.65 ± 6.22	18.00 ± 11.37	12.51 ± 12.51	60.56 ± 18.62	114.72 ± 18.45
	min-max	2.12-60.52	0.00-90.21	0.00-100.09	11.99-171.87	43.27-200.11
	Total deadwood	39.49 ± 4.60	31.86 ± 17.05	42.00 ± 18.32	62.36 ± 19.23	175.71 ± 19.34
	min-max	20.30-62.16	0.00-130.10	1.56-151.87	12.49-174.30	91.01-265.14
Density (N ha^{-1})	Snags	48 ± 9.83	10 ± 3.46	22 ± 7.33	-	80 ± 13.73
	min-max	12-100	0-24	0-24	-	40-132

Table 3 Parameters and statistics of probability distribution fitted for standing and lying deadwood in the Frakto virgin forest, Greece.

Distribution	Parameters (St. error)							Goodness-of-fit statistics		Goodness of fit criteria	
	α	β	γ	λ	σ	μ	KS	AD	CVM	AIC	BIC
Standing deadwood											
Lognormal	-	-	-	-	0.79 (0.04)	2.71 (0.06)	0.13	4.36	0.69770	1249.0	1255.1
Gamma	1.59 (0.16)	0.075 (0.01)	-	-	-	-	0.17	7.75	1.37	1283.9	1290.1
Weibull	-	22.83 (1.60)	1.20 (0.07)	-	-	-	0.16	7.50	1.29	1293.1	1299.2
Exponential	-	-	-	0.05 (0.00)	-	-	0.21	7.80	1.23	1300.3	1303.4
Lying deadwood											
Lognormal	-	-	-	-	0.72 (0.02)	2.89 (0.03)	0.09	5.94	0.89	5404.9	5413.9
Gamma	2.12 (0.11)	0.09 (0.01)	-	-	-	-	0.10	8.25	1.23	5455.4	5464.4
Weibull	-	25.72 (0.72)	1.46 (0.04)	-	-	-	0.10	9.02	1.23	5494.0	5503.1
Exponential	-	-	-	0.04 (0.00)	-	-	0.22	31.36	4.69	5633.8	5638.3

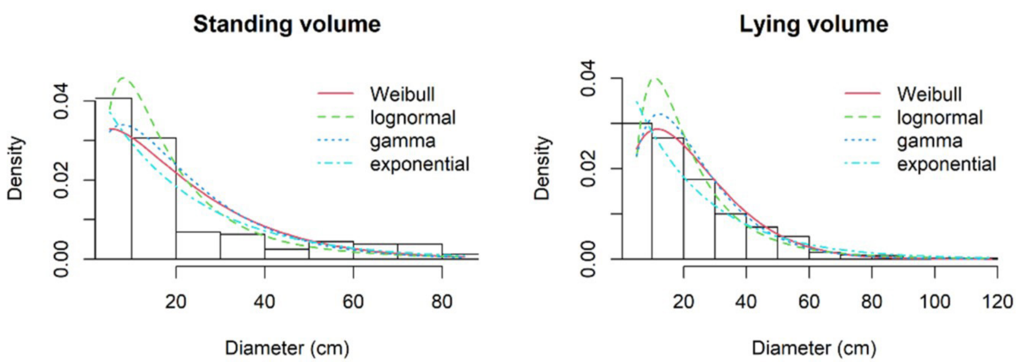

Figure 3 Fitted curves of probability density functions for standing and lying deadwood.

Deadwood quantity

In terms of the deadwood quality all decay classes were represented, but deadwood was classified mostly in the most decayed class (34.3%) followed by classes 3 (26.2%), 2 (20.2%), 4 (15.9%) and 1 which represented forest, Greece only 3.4% of the total volume of CWD. While almost half of the snags (49.1%) were found in class 3, stumps and logs showed a more advanced decay representing 47.4% and 62.4% in classes 5 and 4 respectively. Thus, highly decayed deadwood comprised the largest proportion of the lying and total deadwood.

Table 4 Deadwood volume of snags, logs, stumps by species and decay classes (m^3 ha^{-1}) in the Frakto virgin.

Decay class	1	2	3	4	5	Total deadwood
Standing deadwood (m^3ha^{-1})	5.52 ± 3.09	12.57 ± 6.60	27.76 ± 5.84	4.78 ± 1.64	5.87 ± 4.44	56.50 ± 8.28
Beech	3.37 ± 2.74	1.57 ± 1.07	6.35 ± 2.43	2.43 ± 0.92	0.07 ± 0.05	13.79 ± 3.46
Silver fir	0.37 ± 0.37	2.23 ± 1.63	5.02 ±3.60	1.50 ± 1.45	3.99 ± 3.99	13.11 ± 6.54
Norway spruce	1.74 ± 1.33	8.75 ± 6.93	16.29 ± 6.76	0.75 ± 0.54	1.81 ± 1.36	29.34 ± 9.93
Not specified	0.04 ± 0.04	0.02 ± 0.02	0.10 ± 0.10	0.10 ± 0.10	0	0.26 ± 0.26
Logs (m^3ha^{-1})	0.53 ± 0.40	22.79 ± 5.08	16.65 ± 4.26	20.38 ± 7.93	54.37 ± 7.49	114,72 ± 8.76
Beech	0.34 ± 0.26	6.14 ± 2.17	5.37 ± 2.43	3.06 ± 1.00	8.75 ± 3.38	23.65 ± 6.22
Silver fir	0	4.75 ± 4.22	3.39 ±1.97	2.54 ± 1.89	7.32 ± 4.56	18.00 ± 11.37
Norway spruce	0	2.77 ± 2.77	0.91 ± 0.91	2.17 ± 2.17	6.65 ± 6.65	12.51 ± 12.51
Not specified	0.19 ± 0.14	9.13 ± 3.33	6.98 ± 3.29	12.61 ± 7.92	31.65 ± 7.43	60.56 ± 18.62
Stumps (m^3ha^{-1})	0	0.08 ± 0.08	1.61 ± 1.60	2.80 ± 1.26	-	4.49 ± 0.67
Beech	0	0	1.60 ± 1.60	0.45 ± 0.43	-	2.05 ± 1.49
Silver fir	0	0	0	0.75 ± 0.21	-	0.75 ± 0.55
Norway spruce	0	0.08 ± 0.08	0	0.07 ± 0.07	-	0.15 ± 0.09
Not specified	0	0	0.01 ± 0.01	1.53 ± 0.87	-	1.54 ± 0.82
Total deadwood	6.05 ± 3.10	35.44 ± 6.36	46.02 ± 6.12	27.96 ± 7.68	60.24 ± 10.68	175.71 ± 9.07
Beech	3.71 ± 2.69	7.71 ± 2.57	13.32 ± 3.24	5.94 ± 1.25	8.82 ± 3.42	39.49 ± 4.60
Silver fir	0.37 ± 0.37	6.98 ± 4.65	8.41 ± 5.44	4.79 ± 3.45	11.31 ± 6.45	31.86 ± 17.05
Norway spruce	1.74 ± 1.33	11.60	17.20 ± 7.36	2.99 ± 2.28	8.46 ± 6.53	42.00 ± 18.32
Not specified	0.23 ± 0.15	9.15 ± 3.34	7.09 ± 3.34	14.24 ± 8.03	31.65 ± 7.43	62.36 ± 19.12

Discussion

The average deadwood which was estimated in the current research was 175.71 ± 19.34 m^3/ha. The findings of the current research are consistent with those of an earlier study in the Frakto virgin forest carried out by Grigoriadis et al. (2012), who estimated the overall deadwood quantity between a range of 52.8 to 226.1 m^3/ha based on measurements from 5 plots.

The estimated values of the current research also lie within the value range reported for other mixed beech-conifer (spruce-fir) virgin forests, specifically in the western Carpathians and the Dinaric Alps, varying between 91 and 420 m3/ha (Saniga & Schütz 2001, Nagel & Diaci 2006, Paluch 2007, Holeksa et al. 2009, Kral et al. 2010, Motta et al. 2011, 2015; Kucbel et al. 2012, Keren & Diaci 2018).

Moreover, the proportion of deadwood to the total volume of living trees reached 31.0 ± 9.9% and is at the same level as the average of 36.0 ± 21.0%, which resulted from the study of Christensen et al. (2005) in the 16 reserves of mixed beech forests, including virgin beech-spruce-fir forests. Motta et al. (2011, 2024) reported a much higher deadwood volume (383 m^3/ha) in the Lom forest reserve as well as other sites in Bosnia-Herzegovina representing old growth mixed beech-fir-spruce forests. However, its proportion in relation to the volume of living trees amounted to similar of the current research estimates (33.3%).

The average deadwood quantity lies far above the 13.46 m^3/ha value reported for managed beech stands within the Rodopi Mountain Range National Park (Kechagioglou et al. 2022). Although a direct comparison between pure beech forests and mixed beech–conifer forests is difficult to attempt, since spruce and fir have a longer time frame to decompose (Oheimb et al. 2007), it can still be noted that beech deadwood (39.49 ± 4.60 m^3 ha^{-1}) was found twice as higher in the current study. Comparisons between managed and unmanaged forests have shown that managed forests contain far less deadwood quantities than unmanaged forests (Ódor & Standovár 2002, Keren & Diaci 2018, (Braga et al. 2023). Such variations have been attributed at a country level in Europe to the different management regimes that affect accumulation of the deadwood based on the main European Forest Inventories (Paletto et al. 2012). At a local level potential deadwood volume as well as their qualitative features are probably being altered due to either timber extraction or sanitation fellings (Paletto et al. 2012).

The volume of lying deadwood (65.3%) is greater than the volume of standing dead trees (32.1%), as it has been observed in other virgin forests (Motta et al. 2011, 2015; Petritan et al. 2015). The proportion of lying and standing deadwood is to a large extent determined by the species composition of the stand as well as the mortality causes (Bujoczek et al. 2018). While a high proportion of standing deadwood is attributed to disturbances, such as insect outbreaks and fire events, in several studies (Pedlar et al. 2002, Taylor & MacLean 2007) this pattern has not been confirmed at a small-scale disturbance regime. Furthermore, dead conifers remain standing for longer periods of time (Rozenbergar et al. 2003), which can contribute to a higher representation of standing deadwood when conifers are present. Low fall rates have been reported for spruce snags in a subalpine Norway spruce forest in the Carpathian Mountains, which referred both to older and smaller snags (Holeksa et al. 2008).

About 22.5% of dead wood was identified as of beech origin, 42.0% of the dead wood of conifer origin, while the remaining 35.5% of the deadwood it was not possible to determine in terms of species origin. Prevalence of conifer deadwood in relation to deadwood from deciduous trees has been reported in virgin mountain mixed forests in the southern Carpathians (Petritan et al. 2015, Chivulescu et al. 2022) and western Bosnia (Višnjic et al. 2013). Possible differences in the degree of decay of beech and conifers are likely to have influenced the ratio of deadwood between beech and conifers. Beech species decompose faster than conifers, which results in smaller amounts of deadwood in beech compared to conifers (Rozenbergar et al. 2003). Přívětivý et al. (2017) studied deadwood density and moisture variation in a natural temperate spruce-fir-beech forest and concluded that beech had the shortest total decomposition time (39 years), followed by fir (58 years) and spruce (86 years). However, although analyses of deadwood of beech and spruce in the Apennine Mountains in Italy showed that the two species have a similar degree of decomposition (Lombardi et al. 2013), this is influenced by many factors, such as the tree mortality as well as the size and position of the dead standing or lying wood. Beech trees are often colonized by fungi (Fomes fomentarius) before necrosis occurs (Muller-Using & Bartsch 2009), which accelerates the decay of beech wood as compared to conifers, thus leading to under-representation in the percentage of deadwood. Also, a possible reason for the faster decay of beech can be the fact that beech trees usually break and decompose on the ground, where the decay processes are more intensive, while conifers remain standing, which results in the drying of the wood and slow decay (Rozenbergar et al. 2003). Additionally, it has been documented that gymnosperm wood consistently decomposes slower than angiosperm wood due to clear divergence in chemical composition and other wood traits between the two groups (Weedon et al. 2009). Furthermore, the large proportion of conifer deadwood may indicate increased conifer mortality in recent decades, which is consistent with the declining trend of conifer participation in various virgin forests of central and southeastern Europe (Šamonil & Vrška 2007, Diaci et al. 2010, 2011; Ficko et al. 2011, Petritan et al. 2015). On the other hand, the participation of beech by 84.0% in the composition of the overstorey (Papadopoulou et al. 2023) confirms the long- term predominance of beech.

All degrees of decay were represented, with the degree of decay 5 prevailing with 34.3%, followed by 3, 2, 4 and 1. Similarly the deadwood amount recorded in the Sinca virgin forest in Romania was concentrated in the most advanced decay classes (Braga et al. 2023). The presence of all degrees of decay is a characteristic of natural forests, which in addition to the large volumes of deadwood (Harmon et al. 1986, Spies & Franklin 1988) and their co-occurrence indicates deadwood heterogeneity, as well as abundance of available ecological niches (Badalamenti et al. 2017). According to Lachat et al. (2013) the survival of saproxylic species depends, apart from the quantity, on quality parameters such as the decay stage, while the role of deadwood diversity has been recognized as a far more decisive indicator rather than the deadwood quantity.

Quantity and quality of deadwood can provide an insight on the mortality processes and the disturbance regime of the forest (Castagneri et al. 2010). Mixed temperate southern European forests are subject mainly to single tree mortality or small-scale disturbances with large scale disturbances being rare (Nagel & Diaci 2006, Firm et al. 2009, Kenderes et al. 2009). Thus, the snags appear more abundant in smaller size classes, as it is shown by the decreasing trend of the deadwood diameter distribution in the current research due to the density-dependent mortality. On the other hand, the small percentage of recent deadwood (decomposition grade 1) amounted to 3.0% of the total volume of deadwood, indicating that large and medium-scale disturbances have not occurred in the Frakto virgin forest at least during the last decade.

Implications for sustainable management can be drawn based either on the size or the volume of both standing and lying deadwood in unmanaged forests (Keren & Diaci 2018, Chivulescu et al. 2022). Especially knowledge of the deadwood diameter structure in forests such as the Frakto virgin forest can provide reference values for naturalness regarding standing and lying deadwood which can serve designing appropriate management regimes for multifunctional management as it has also been demonstrated in recent studies (Keren & Diaci 2018). Furthermore, the fitting of the diameter distribution to theoretical distributions can generate a standard to be pursued in the field towards achieving forest management sustainability.

Conclusions

Through the current research deadwood volume in the virgin forest of Frakto was estimated to 175.71 ± 19.34 m^3/ha, while the proportion of deadwood to the total living volume 31.0 ± 9.9%. Both values lie within the value range reported for other natural mixed beech-coniferous forests in Europe and are far higher than those of the adjacent managed forests.

Deadwood was composed to a great extent of dead conifer wood which can be attributed either to the higher decomposition rate of beech affected also by the size and position of the dead standing or lying wood as well as possible decline of conifers in the study area similar to other virgin forests of central and southeastern Europe.

All degrees of decay were identified with more advanced decayed wood prevailing, which indicates deadwood heterogeneity and availability of ecological niches.

Furthermore, both quantitative and qualitative characteristics showed a small-scale disturbance regime as standing deadwood was mostly concentrated in small diameters declining towards greater diameter classes, while fresh deadwood was almost absent.

The decreasing trend of the diameter structure fitting theoretical distributions such as the lognormal confirmed this pattern and it could serve as a standard for adopting suitable management regimes towards close to nature forest management.

Conflict of interest

The authors declare no financial or personal interests could influence the work presented in this paper.

References

Badalamenti E., La Mantia T., La Mantia G., Cairone A., La Mela Veca D.S., 2017. Living and Dead Aboveground Biomass in Mediterranean Forests: Evidence of Old-Growth Traits in a *Quercus pubescens* Willd. s.l. Stand. Forests 8(6): 187. https://doi.org/10.3390/f8060187

Błoszyk J., Rutkowski T., Napierała A., Konwerski S., Zacharyasiewicz M., 2021. Dead Wood as an Element Enriching Biodiversity of Forest Ecosystems: A Case Study Based on Mites from the Suborder Uropodina (Acari: Parasitiformes). Diversity 13(10): 476. https://doi.org/10.3390/d13100476

Braga C.I., Crisan V.E., Petritan I.C., Scarlatescu V., Vasile D., Lazar G., Petritan A.M., 2023. Short-Term Effects of Anthropogenic Disturbances on Stand Structure, Soil Properties, and Vegetation Diversity in a Former Virgin Mixed Forest. Forests 14: 742. https:// doi.org/10.3390/f14040742

Brändli U.-B., Dowhanytsch J., 2003. Urwälder im Zentrum Europas. Ein Naturführer durch das Karpaten-Biosphärenreservat in der Ukraine. Birmensdorf, Eidg. Forschungsanstalt WSL; Rachiw, Karpaten-Biosphärenreservat. Bern, Stuttgart, Wien, Haupt. 192 pp.

Bujoczek L., Szewczyk J., Bujoczek M., 2018. Deadwood volume in strictly protected, natural, and primeval forests in Poland. European Journal of Forest Research 137: 401-418. https://doi.org/10.1007/s10342-018-1124-1

Castagneri D., Garbarino M., Berretti R., Motta R., 2010. Site and stand effects on coarse woody debris in montane mixed forests of Eastern Italian Alps. Forest Ecology and Management 260(9): 1592-1598. https://doi.org/10.1016/j.foreco.2010.08.008

Chivulescu Ș., Ciceu A., Leca Ș., Apostol B., Popescu O., Badea O., 2020. Development phases and structural characteristics of the Penteleu-Viforâta virgin forest in the Curvature Carpathians. iForest-Biogeosciences and Forestry 13(5): 389-395. https://doi.org/10.3832/ifor3094-013

Chivulescu Ș., Pitar D., Apostol B., Leca Ș., Badea O., 2022. Importance of Dead Wood in Virgin Forest Ecosystem Functioning in Southern Carpathians. Forests 13(3): 409 https://doi.org/10.3390/f13030409

Christensen M., Hahn K., Mountford E.P., Odor P., Standovár T., Rozenbergar D., Diaci J., Wijdeven S., Meyer P., Winter S., Vrska T., 2005. Dead wood in European beech (*Fagus sylvatica*) forest reserves. Forest Ecology and Management 210(1-3): 267-282. https://doi.org/10.1016/j.foreco.2005.02.032

D' Agostino R.B., Stephens M.A., 1986. Goodness-of-fit Techniques. Marcel Dekker, New York.

Delignette-Muller M. L., Dutang C., 2015. fitdistrplus: An R package for fitting distributions. Journal of Statistical Software 64(4): 1–34 https://doi.org/10.18637/jss.v064.i04

Diaci, J. (ed), 1999. Virgin Forests and Forest Reserves in Central and East European Countries. Proceedings of the Invited Lecturers' reports presented at the COST E4 Management Committee and Working Group meeting in Ljubljana, Slovenia 25–28, April 1998. University of Ljubljana [includes country reports on Bosnia and Herzegovina, Croatia, Czech Republic, Poland, Romania, Slovenia and Switzerland]. 171 pp.

Diaci J., Rozenbergar D., Boncina A., 2010. Stand dynamics of Dinaric old-growth forest in Slovenia: are indirect human influences relevant? Plant Biosystems 144(1): 194–201. https://doi.org/10.1080/11263500903560785

Diaci J., Rozenbergar D., Anic I., Mikac S., Saniga M., Kucbel S., Visnjic C., Ballian. D., 2011. Structural dynamics and synchronous silver fir decline in mixed old-growth mountain forests in Eastern and Southeastern Europe. Forestry 84(5): 479–491. https://doi.org/10.1093/forestry/cpr030

Dittrich S., Jacob M., Bade C., Leuschner C., Hauck M., 2014 The significance of deadwood for total bryophyte, lichen, and vascular plant diversity in an old-growth spruce forest. Plant Ecology 215(10): 1123–1137. https://doi.org/10.1007/s11258-014-0371-6

Drama Forest District Office, 1974. Local Forest Tree Yield Tables, Ministry of Agriculture (in Greek)

Edwards D.M., Jay M., Jensen F.S., Lucas B., Marzano M., Montagné C., Peace A., Weiss G., 2012. Public preferences across Europe for different forest stand types as sites for recreation. Ecology and Society 17(1): 27-37. https://doi.org/10.5751/ES-04520-170127

Feller M.C., 2003. Coarse woody debris in the old growth forests of British Columbia. Environmental Reviews 11(1): 135–157. https://doi.org/10.1139/a03-008

Ficko A., Poljanec A., Boncina A., 2011. Do changes in spatial distribution, structure and abundance of silver fir (*Abies alba* Mill.) indicate its decline? Forest Ecology and Management 261(4): 844–854. https://doi.org/10.1016/j.foreco.2010.12.014

Firm D., Nagel T. A., Diaci J., 2009. Disturbance history and dynamics of an old-growth mixed species mountain forest in the Slovenian Alps. Forest Ecology and Management 257(9): 1893-1901. https://doi.org/10.1016/j.foreco.2008.09.034

Grigoriadis N., Petermann J., Schroeder E., Spyroglou G., 2012. Contribution to the assessment of the conservation status of spruce forests in Greece. Journal of Biological Research 17: 57-67.

Hahn K.,Christensen M., 2004. Dead wood in European Forest Reserves - A Reference for Forest Management. EFI-Proceedings 51:181-191.

Hamor F., Dovhanych Y., Pokynch ereda V., Sukh aryuk D., Bundzyak Y., Berkela Y., Voloshchuk M., Hodovanets B., Kabal M., 2008. Virgin forests of Transcarpathia. Inventory and management. Carpathian Biosphere Reserve, Royal Dutch Society for Nature Conservation, Rakhiv. 79 p.

Harmon M.E., Franklin J.F., Swanson F.J., Sollins P., Gregory S.V., Lattin J.D., Anderson N.H., Cline S.P., Aumen N.G, Sedell J.R., Lienkaemper G.W., Cromack K., Cummins K.W., 1986. Ecology of coarse woody debris in temperate ecosystems. Advances in Ecological Research 15:133–302.

Hochbichler E., O'Sullivan, A., van Hees A., Vandekerkhove K., 2000. WG2 Recommendations for Data Collection in Forest Reserves, with an Emphasis on Regeneration and Stand Structure. COST Action E4 Forest Reserve Research Network. Office for Official Publications of the European Communities, Luxembourg, 135-181.

Holeksa J., Zielonka T., Żywiec M., 2008. Modeling the decay of coarse woody debris in a subalpine Norway spruce forest of the West Carpathians, Poland. Canadian Journal of Forest Research 38(3): 415-428. https://doi.org/10.1139/X07-139

Holeksa J., Saniga M., Szwagrzyk J., Czerniak M., Staszyńska K., Kapusta P., 2009. A giant tree stand in the West Carpathians – An exception or a relic of formerly widespread mountain European forests? Forest Ecology and Management 257(7): 1577–1585. https://doi.org/10.1016/j.foreco.2009.01.008

Humphrey J.W., Sippola A.L., Lemperiere G., Dodelin B., Alexander K.N.A., Butler J.E., 2004. Deadwood as an indicator of biodiversity in European forests: from theory to operational guidance. EFI-Proceedings 5: 193-206.

Ionescu D.T., Hodor C.V., Petrițan I.C., Baltag E.Ș., 2024. The importance of standing deadwood in white-backed woodpecker (*Dendrocopos leucotos*) habitat from deciduous forests in central Romania. Annals of Forest Research 67(2): 121-134.

IPCC (Intergovernmental Panel on Climate Change), 2003. Good practice guidance for land use, land-use change and forestry. Institute for Global Environmental Strategies (IGES), Hayama, Japan.

Ježek K., 2004. Contribution of regeneration on dead wood to the spontaneous regeneration of a mountain forest. Journal of Forest Science 50(9): 405-414.

Kechagioglou S., Papadopoulou D., Tsitsoni T., 2022. Determining structure and volume of the European beech (*Fagus sylvatica* L.) deadwood in managed stands in the Rodopi Mountain Range National Park, Greece. Folia Oecologica 49(2):122-129. https://doi.org/10.2478/foecol-2022-0014

Kenderes K., Král K., Vrška T., Standovár T., 2009. Natural gap dynamics in a Central European mixed beech—spruce—fir old-growth forest. Ecoscience 16(1): 39-47. https://doi.org/10.2980/16-1-3178

Keren S., Diaci J., 2018. Comparing the quantity and structure of deadwood in selection managed and old-growth forests in South-East Europe. Forests 9(2): 76. https://doi.org/10.3390/f9020076

Körpel S., 1995. Die Urwälder der Westkarpaten. Gustav Fischer Verlag. Stuttgart, Jena, New York, 310 p.

Kraigher H., Jurc D., Kalan P., Kutnar L., Levanic T., Rupel M., Smolej I., 2002. Beech coarse woody debris characteristics in two virgin forest reserves in southern Slovenia. Forestry Wood Science Technology 69: 91-134.

Král K., Vrška T., Hort L., Adam D., Samonil P., 2010. Developmental phases in a temperate natural spruce–fir–beech forest: Determination by a supervised classification method. European Journal of Forest Research 129(3): 339–351. https://doi.org/10.1007/s10342-009-0340-0

Kucbel S., Saniga M., Jaloviar P., Vencurik J., 2012. Stand structure and temporal variability in old-growth beech-dominated forests of the northwestern Carpathians: a 40-years perspective. Forest Ecology and Management 264: 125–133. https://doi.org/10.1016/j.foreco.2011.10.011

Kupferschmidt A.D., Brang P., Schönenberger W., Bugmann H., 2003. Decay of *Picea abies* snags stands on steep mountain slopes. The Forestry Chronicle 79(2): 247-252. https://doi.org/10.5558/tfc79247-2

Laarmann D., Korjus H., Sims A., Stanturf J.A., Kiviste A., Koester K., 2009. Analysis of forest naturalness and tree mortality patterns in Estonia. Forest Ecology and Management 258: 5187-5195. https://doi.org/10.1016/j.foreco.2009.07.014

Lachat T., Bouget C., Bütler R., Müller J., 2013. Deadwood: quantitative and qualitative requirements for the conservation of saproxylic biodiversity. Integrative approaches as an opportunity for the conservation of forest biodiversity. In D. Kraus and F. Krumm (eds.), Integrative approaches as an opportunity for the conservation of forest biodiversity. European Forest Institute, Freiburg, pp. 92-102.

Leibundgut H., 1982: Europäische Urwälder der Bergstufe, dargestellt für Forstleute, Naturwissenschaftler und Freunde des Waldes. Paul Haupt Verlag, Bern/Stuttgart, 306 p.

Lombardi F., Cherubini P., Tognetti R., Cocozza C., Lasserre B., Marchetti M., 2013. Investigating biochemical processes to assess deadwood decay of beech and silver fir in Mediterranean mountain forests. Annals of Forest Science 70: 101–111. https://doi.org/10.1007/s13595-012-0230-3

Mansourian S., Rossi M., Vallauri D., 2013. Ancient Forests in the Northern Mediterranean: Neglected High Conservation Value Areas. WWF France, Marseille, 80 p.

Marra J. L., Edmonds R. L., 1994. Coarse woody debris and forest floor respiration in an old-growth coniferous forest on the Olympic Peninsula, Washington, USA. Canadian Journal of Forest Research 24(9): 1811-1817. https://doi.org/10.1139/x94-234

Maser C.M., Cline S.P., K. Cormack J.R., Trappe J.M., Hansen E., 1988. What we know about large trees that fall to the forest floor. In Maser C.M., Tarrant R.F., Trappe J.M., Franklin J.F. (eds.). From the forest to the sea: A story of fallen trees. USDA Forest Service. Gen. Tech. Rep. PNW-229, Portland, pp. 25-45.

Merganičová K., Merganič J., 2010. Coarse woody debris carbon stocks in natural spruce forests of Babia hora. Journal of Forest Science 56(9): 397-405. https://doi.org/10.17221/11/2010-jfs

Moreira-Arce D., Vergara P.M., Fierro A., Pincheira E., Crespin S.J., Alaniz A., Carvajal M.A., 2021. Standing dead trees as indicators of vertebrate diversity: Bringing continuity to the ecological role of senescent trees in austral temperate forests. Ecological Indicators 129: 107878. https://doi.org/10.1016/j.ecolind.2021.107878

Motta R., Berretti R., Lingua E., Piussi P., 2006. Coarse woody debris, forest structure and regeneration in the Valbona Forest Reserve, Paneveggio, Italian Alps. Forest Ecology and Management 235(1-3): 155-163. https://doi.org/10.1016/j.foreco.2006.08.007

Motta R., Berretti R., Castagneri D., Dukic V., Garbarino M., Govedar Z., Lingua E., Maunaga Z., Meloni F., 2011. Toward a definition of the range of variability of central European mixed *Fagus-Abies-Picea* forests: The nearly steady-state forest of Lom (Bosnia and Herzegovina). Canadian Journal of Forest Research 41(9): 1871–1884. https://doi.org/10.1139/x11-098

Motta R., Garbarino M., Berretti R., Meloni F., Vacchiano G., 2015. Development of old-growth characteristics in uneven-aged forests of the Italian Alps. European Journal of Forest Research 134: 19–31. https://doi.org/10.1007/s10342-014-0830-6

Motta R., Alberti G., Ascoli D., Berretti R., Bilic S., Bono A., Milic C., Vojislav D., Finsinger W., Garbarino M., Govedar Z., Keren S., Meloni F., Ruffinatto F., Nola P., 2024. Old-growth forests in the Dinaric Alps of Bosnia-Herzegovina and Montenegro: a continental hot-spot for research and biodiversity. Frontiers in Forests and Global Change 7:1371144. https://doi.org/10.3389/ffgc.2024.1371144

Muller-Using S., Bartsch N., 2009. Decay dynamic of coarse and fine woody debris of a beech (*Fagus sylvatica* L.) forest in Central Germany. European Journal of Forest Research 128(3): 287–296. https://doi.org/10.1007/s10342-009-0264-8

Nagel T.A., Diaci J., 2006. Intermediate wind disturbance in an old-growth beech–fir forest in southeastern Slovenia. Canadian Journal of Forest Research 36(3): 629–638. https://doi.org/10.1139/x05-263

Ódor P., Standovár T., 2001. Richness of bryophyte vegetation in near-natural and managed beech stands: The effects of management-induced differences in dead wood. Ecological Bulletins 49: 219–229.

Oheimb G., Westphal C., Härdtle W., 2007. Diversity and spatio-temporal dynamics of dead wood in a temperate near-natural beech forest (*Fagus sylvatica*). European Journal of Forest Research 126: 359–370. https://doi.org/10.1007/s10342-006-0152-4

Orman O., Szewczyk J., 2015. European beech, silver fir, and Norway spruce differ in establishment, height growth, and mortality rates on coarse woody debris and forest floor—a study from a mixed beech forest in the Western Carpathians. Annals of Forest Science 72(7): 955–965. https://doi.org/10.1007/s13595-015-0492-7

Papadopoulou D., Raptis D., Kazana V., Tsitsoni T., 2023. Exploring Texture Diversity of Beech-Spruce-Fir Stands through Development Phase Analysis in the Frakto Virgin Forest of Greece. Diversity 15(2): 278. https://doi.org/10.3390/d15020278

Paletto A., Ferretti F., De Meo I., Cantiani P., Focacci M., 2012. Ecological and environmental role of deadwood in managed and unmanaged forests. In: Diez J.J (Ed.) Sustainable Forest Management–Current Research. InTech, pp. 219-238. https://doi.org/10.5772/24894

Paletto A., De Meo I., Cantiani P., Ferretti F., 2014. Effects of forest management on the amount of deadwood in Mediterranean oak ecosystems. Annals of Forest Science 71: 791-800. https://doi.org/10.1007/s13595-014-0377-1

Paluch J.G., 2007. The spatial pattern of a natural European beech (*Fagus sylvatica* L.)-silver fir (*Abies alba* Mill.) forest: a patchmosaic perspective. Forest Ecology and Management 253(1-3): 161–170. https://doi.org/10.1016/j.foreco.2007.07.013

Parisi F., Innangi M., Tognetti R., Lombardi F., Chirici G., Marchetti M., 2021. Forest stand structure and coarse woody debris determine the biodiversity of beetle communities in Mediterranean mountain beech forests. Global Ecology and Conservation 28: e01637. https://doi.org/10.1016/j.gecco.2021.e01637

Parviainen J., 2005. Virgin and natural forests in the temperate zone of Europe. Forest Snow and Landscape Research 79(1/2): 9–18.

Pastorella F., Avdagić A., Čabaravdić A., Mraković A., Osmanović M., Paletto A., 2016. Tourists' perception of deadwood in mountain forests. Annals of Forest Research 59(2): 311-326. https://doi.org/10.15287/afr.2016.482

Pedlar J.H., Pearce J.L., Venier L.A., McKenney D.W., 2002. Coarse woody debris in relation to disturbance and forest type in boreal Canada. Forest Ecology and Management 158 (1-3):189–194. https://doi.org/10.1016/S0378-1127(00)00711-8

Peterken G.F., 1996. Natural woodland: Ecology and conservation in northern temperate regions. Cambridge University Press, Cambridge, 522 p.

Petritan I.C., Commarmot B., Hobi M.L., Petritan A.M., Bigler C., Abrudan I.V., Rigling A., 2015. Structural patterns of beech and silver fir suggest stability and resilience of the virgin forest Sinca in the Southern Carpathians, Romania. Forest Ecology and Management 356: 184–195. https://doi.org/10.1016/j.foreco.2015.07.015

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

Přívětivý T., Baldrian P., Šamonil P., Vrška T., 2017 Deadwood Density and Moisture Variation in a Natural Temperate Spruce-Fir-Beech Forest. Preprints. https://doi: 10.20944/preprints201705.0215.v1

Rahman M.M., Frank G., Ruprecht H., Vacik H., 2008. Structure of coarse woody debris in Lange-Leitn Natural Forest Reserve, Austria. Journal of Forest Science 54(4): 161-169. https://doi.org/10.17221/3102-JFS

Raptis, D. I., Kazana, V., Kazaklis, A., Stamatiou, C., 2020. Development and testing of volume models for *Pinus nigra* Arn., *Fagus sylvatica* L., and *Quercus pubescens* Willd. Southern Forests: a Journal of Forest Science 82(4): 331-341. https://doi.org/10.2989/20702620.2020.1733768

Raptis D.I., Kazana V., Kechagioglou S., Kazaklis A., Stamatiou C., Papadopoulou D., Tsitsoni T., 2022. Nonlinear Quantile Mixed-Effects Models for Prediction of the Maximum CrownWidth of *Fagus sylvatica* L., *Pinus nigra* Arn. and *Pinus brutia* Ten. Forests 13(4): 499. https://doi.org/10.3390/f13040499

Redolfi De Zan L., Rossi de Gasperis S., Fiore L., Battisti C., Carpaneto G. M., 2017. The importance of dead wood for hole-nesting birds: a two years study in three beech forests of central Italy. Israel Journal of Ecology and Evolution 63(1): 19-27. https://doi.org/10.1080/15659801.2016.1191168

Rozenbergar D., Konecnik K., Zaplotnik V., Diaci J., 2003. Stand structure, gap formation, and regeneration in virgin forest remnant Strmec—Slovenia. The NatMan Project. Working Report 17. p. 16.

Sabatini F.M., Burrascano S., Keeton W.S., Levers C., Lindner M., Pötzschner F. et al., 2018. Where are Europe's last primary forests? Diversity and distributions 24(10): 1426-1439. https://doi.org/10.1111/ddi.12778

Šamonil P., Vrška T., 2007. Trends and cyclical changes in natural fir–beech forests at the north–western edge of the Carpathians. Folia Geobotanica 42: 337-361. https://doi.org/10.1007/BF02861699

Saniga M., Schütz J.P., 2001. Dynamics of changes in dead wood share in selected beech virgin forests in Slovakia within their development cycle. Journal of Forest Science 47: 557–565. https://doi.org/10.17221/11920-JFS.

Standovár T., Kenderes K., 2003. A review on natural stand dynamics in beechwoods of East Central Europe. Applied Ecology and Environmental Research 1(1-2): 19-46. https://doi.org/10.15666/aeer/01019046

Staniaszek-Kik M., Chmura D., Żarnowiec J., 2019 What factors influence colonization of lichens, liverworts, mosses and vascular plants on snags? Biologia 74: 375–384. https://doi.org/10.2478/s11756-019-00191-5

Stephens MA, 1979. Tests of fit for the logistic distribution based on the empirical distribution function. Biometrika 66 (3): 591-595. https://doi.org/10.1093/biomet/66.3.591

Stevens V., 1997. The ecological role of coarse woody debris: an overview of the ecological importance of CWD in BC forests. Working Paper 30. B.C. Ministry of Forests, Victoria, 16 p.

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.

Spies T.A., Franklin J.F., 1988. Old-growth and forest dynamics in the Douglas-fir region of western Oregon and Washington. Natural Areas Journal 8(3):190–201.

Taylor S. L., MacLean D.A., 2007. Dead wood dynamics in declining balsam fir and spruce stands in New Brunswick, Canada. Canadian Journal of Forest Research 37(4): 750–762. https://doi.org/10.1139/X06-272.

Višnjić C´., Solaković S., Mekić F., Balić B., Vojniković S., Dautbašić M., Gurda S., Ioras F., Ratnasingam J., Abrudan I.V., 2013. Comparison of Structure, Regeneration and Dead Wood in Virgin Forest Remnant and Managed Forest on Grmeč Mountain in Western Bosnia. Plant Biosystems 147(4):913-922 https://doi.org/10.1080/11263504.2012.751064

Winter S., Fischer H.S., Fischer A., 2010. Relative quantitative reference approach for naturalness assessments of forests. Forest Ecology and Management 259: 1624-1632. https://doi.org/10.1016/j.foreco.2010.01.040

Woodall C.W., Nagel L.M., 2006. Coarse woody type, a new method for analyzing coarse woody debris and forest change. Forest Ecology and Management 227 (1–2): 115–121. https://doi.org/10.1016/j.foreco.2006.02.032

Zielonka T., 2006. When does dead wood turn into a substrate for spruce replacement? Journal of Vegetation Science 17(6): 739-746. https://doi.org/10.1111/j.1654-1103.2006.tb02497.x