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ORIGINAL PAPER

Comparative analysis of deadwood abundance and characteristics in protected versus managed forests in Northeastern Turkey

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Abstract Deadwood is essential for maintaining forest ecosystem health and biodiversity. This study investigates and compares the abundance and characteristics of deadwood in Eastern spruce (*Picea orientalis* Link. At Carr) stands located within the Velikoy Forest Management Unit (FMU) and Karagol-Sahara National Park (NP) in northeastern Turkey. A total of 476 randomly selected sampling plots were assessed —236 in Velikoy FMU and 240 in Karagol-Sahara NP—based on stand type, canopy cover, and age class. Deadwood was classified into standing deadwood, stumps, and downed deadwood, with volumes measured for each category. To model deadwood volume, we applied both fixed and mixed non-linear models alongside a Generalized Linear Mixed Model (GLMM), incorporating stand parameters, physiographic variables, and geographical factors. Model performance was evaluated using adjusted R^2 ($R^2_{_adj}$), root mean square error (RMSE), Akaike's Information Criterion (AIC), and Bayesian Information Criterion (BIC). The results showed that in Velikoy FMU, the composition of deadwood volume was 29.5% standing, 37.8% stumps, and 32.7% downed. In contrast, Karagol-Sahara NP exhibited 47.8% standing, 22.7% stumps, and 29.4% downed deadwood. Statistical analyses revealed significant positive correlations between total deadwood volume and factors such as basal area, stand density, stand volume, tree count, site index, stand age, and distance to settlements. However, physiographic variables like slope and aspect showed no clear association. The fixed-effects model yielded $R^2_{_adj} = 0.714$, RMSE = 10.376 m^3 ha^{-1}, AIC = 1584.9, and BIC = 1590.4. The mixed-effects model improved performance significantly with R^2_adj = 0.787, RMSE = 5.815 m^3 ha^{-1}, AIC = 1262.2, and BIC = 1267.4. The GLMM identified basal area, stand density, and distance to settlements as the most influential predictors of deadwood volume. The GLMM model further reduced -2LogL, AIC, and BIC to 737.7, 741.7, and 749.5, respectively, underscoring the effectiveness of incorporating random effects in modeling. These findings emphasize the value of deadwood in forest management and its relationship with structural stand attributes. The integrated modeling framework offers robust tools for informing biodiversity-oriented forest management and conservation planning. Enhancing basal area and stand density, particularly in areas distant from human settlements, can foster deadwood accumulation and support biodiversity.

Keywords Deadwood volume estimation · Fixed and mixed effect models · GLMM · Stand and physiographic parameters · Karagol-sahara national park · Velikoy forest management unit

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Introduction

Dead and decaying trees play a pivotal role in sustaining the vitality and functionality of forest ecosystems. They contribute to diversity maintainance, nutrient cycling, carbon sequestration, energyflow, natural regeneration, and hydrological balance (Siitonen 2001; Bässler et al. 2010). Among these, deadwood is especially significant as it provides essential habitat and food resources numourus species, including fungi, insects, birds, and mammals—many of which are obligate saproxylics adopted to decaying wood environments (Lassauce et al. 2011; Girona et al. 2023; Löfroth et al. 2023). Additionally, it aids in soil enrichment through decomposition (Berg and McClaugherty 2014; Harmon et al. 2004), and plays a vital role in carbon storage, thereby contributing to climate change mitigation. Deadwood also retains soil moisture and influences hydrological processes on the forest floor (Hagen-Thorn et al. 2004; Anderson and Lockaby 2011), while enhancing forest structural complexity and resilience against environmental disturbances (Jonsson et al. 2005; Lindenmayer et al. 2014).

Given its multifunctional ecological value, the conservation and management of deadwood have become essential aspects of sustainable forest management (Bauhus et al. 2009; Stokland et al. 2012). This shift in perception is reflected in the growing incorporation of biodiversity considerations into forest management regimes, highlighting deadwood's role in promoting habitat heterogeneity (Shvidenko et al. 2022; Augustynczik et al. 2024). Accordingly, guidelines have been established to support the inclusion of deadwood in forest conservation frameworks (Ferris-Kaan et al. 1993; Hodge and Peterken 1998; Humphrey et al. 2002), based on its recognized significance for biodiversity (Ratcliffe and Peterken 1995; Siitonen et al. 2023).

The quantity and diversity of deadwood in a forest ecosystem are influenced by a wide range of factors, including forest type, site characteristics (e.g., slope, aspect, elevation, proximity to roads and settlements), and stand attributes (e.g., type, age, density, development stage, crown closure). Other influential elements include vegetation zones, natural or anthropogenic disturbances, and forest management regimes and intensities (Lombardi et al. 2008; Karahalil et al. 2017; Edelmann et al. 2023; Saygili and Kahriman 2023). Particularly in unmanaged or minimally disturbed forests, many species rely on decaying wood in various forms and decay stages for survival and reproduction (Fridman and Walheim 2000; Ódor and Standovár 2001; Rock et al. 2008; Yavuz and Vatandaşlar 2018; Özdemir et al. 2023). According to Dudley and Vallauri (2004), approximately one-third of forest-dwelling species are dependent on over-mature trees and deadwood for habitat.

Deadwood is typically categorized to enhance ecological understanding and inventory precision (Löfroth et al. 2023). While a basic classification includes **standing deadwood** and **downed deadwood** (Fridman and Walheim 2000; Christensen et al. 2005), more detailed typologies identify four categories: (a) standing deadwood, (b) stumps, (c) downed logs and large branches, and (d) lying fine and coarse woody debris (Kirby et al. 1998; Schuck et al. 2004; Travaglini et al. 2007; Vítková et al. 2018). The standing deadwood refers to trees that have died but remain upright, while downed deadwood includes all woody debris that has fallen to the forest floor. These distinctions help clarify the functional roles of different deadwood types in ecosystem dynamics.

To assess deadwood dynamics and informed management, inventories are conducted in both managed and unmanaged forest stands (Mountford 2002; Saniga and Schütz 2002; Oettel et al. 2023). Modern deadwood assessments now incorporate both qualitative and quantitative measures (Edelmann et al. 2023; Özdemir et al. 2023), recognizing how factors like slope and protection status influence deadwood presence (Rahman et al. 2008; Çolak et al. 2009; Yavuz and Vatandaşlar 2018; Staniaszek-kik et al. 2019). For example, the **ICP Forests** study across 19 European countries (ICP Forests,-Level 1, 3243 sample area) reported an average of 15.8 m^3 ha^{-1} of deadwood (range: 5.6–33.1 m^3 ha^{-1}) (Puletti et al. 2019). Forest-Europe et al. (2011) further documented average deadwood volumes of 10 m^3 ha^{-1} across 21 European countries, rising to 20.5 m^3 ha^{-1} when including Russia. As of 2015, the mean deadwood volume across 28 European countries, including Turkey, was 11.5 m^3 ha^{-1}, with an average proportion of 7.1% relative to standing forest stock volume. For Turkey alone, this value reached 16.5 m^3 ha^{-1} and 22.3%, respectively (Forest-Europe 2020).

In Turkey, Eastern spruce (*Picea orientalis* Link. At Carr), Scots pine (*Pinus sylvestris* L.), and Caucasian fir (*Abies nordmanniana* (Steven) Spach. *subsp. nordmanniana*) represent ecologically and economically valuable tree species with extensive distribution across primary forests (Ercanli and Kahriman 2015; Çakir and Kahriman 2018; Özdemir et al. 2023). These species are distinguished by their growth characteristics and their contribution to timber production (Öztürk and Türker 1998, 2000). According to 2020 inventory data from the General Directorate of Forestry (GDF 2021), Eastern spruce covered 365,845 ha (1.6%), Scots pine 1,410,177 ha (6.15%), and Caucasian fir 511,703 ha (16.95%) of Turkey's total area.

Over the past three decades, increasing global awareness of environmental degradation and biodiversity loss has led to a substantial expansion in the extent and number of protected areas worldwide (Chandra and Idrisova 2011; Bruun and Heilmann–Clausen 2021; Innternational 2023; Löfroth et al. 2023). These protected zones aim to conserve ecological processes, safeguard habitats, and maintain biodiversity

across various ecosystems. However, the designations and categorization of protected areas—such as nature reserves, national parks, and environment protection areas—vary across countries and administrative frameworks (Myers et al. 2000; UNEP-WCMC and IUCN 2024). As of April 2024, protected terrestrial and inland water areas account for approximately 6.95% of Turkey's total land (UNEP-WCMC and IUCN 2024). Among these, national parks constitute around 24.7% of the country's designated protected areas (NCNP 2022).

A key focus within many protected forest ecosystems is the retention of structural elements that enhance biodiversity, such as deadwood. Particularly in Europe, forest conservation strategies increasingly emphasize the ecological significance of deadwood as a habitat for numerous species and as an indicator of forest naturalness (Jonsson et al. 2005; Oettel et al. 2023). Müller and Bütler (2010) recommend maintaining at least 20–50 m^3 ha^{-1} of deadwood in European forests to support biodiversity, although actual averages are considerably lower—approximately 20 m3 ha^{-1} in Central and Western Europe and just 8 m3 ha^{-1} in Northern Europe (Forest-Europe 2020). These discrepancies reflect differences in forest management practices, climatic conditions, and ecological history.

Despite this recognition, empirical data on deadwood quantities and distribution patterns remain limited for many forest types in Turkey, especially within Eastern spruce (*Picea orientalis*) dominated stands. Eastern spruce is a regionally important conifer species found predominantly in northeastern Turkey, where forest ecosystems range from intensively managed production units to strictly protected reserves. Understanding deadwood dynamics in such contrasting settings is essential for evaluating the effects of forest management and protection on biodiversity-related structural attributes.

This study aims to address this knowledge gap by focusing on two representative forest systems in northeastern Turkey: Karagöl-Sahara National Park (Karagöl-Sahara NP), which is strictly protected, and Veliköy Forest Management Unit (Veliköy FMU), which is subject to conventional forestry practices. The primary objectives of this research are to: (1) quantify deadwood abundance in both mixed and pure Eastern spruce forests—including stands composed of Eastern spruce with Scots pine and Caucasian fir—within the two study areas; (2) analyze the variation in deadwood volume in relation to stand characteristics, physiographic variables, and spatial factors; (3) calculate and compare the distribution of different deadwood types, including stumps, downed deadwood, standing deadwood, and total deadwood; and (4) estimate the variance in deadwood volume associated with stand characteristics, physiographic variables, and geographical factors across both managed and protected forest conditions.

By integrating quantitative field assessments with statistical modeling, this study contributes to a better understanding of deadwood dynamics in Eastern spruce ecosystems and informs evidence-based forest conservation and management strategies in Turkey.

This investigation builds upon our earlier reasearch titled "*Variation of deadwood density by decay class in pure and mixed Oriental spruce stands in Northeastern Black Sea*" (Özdemir et al. 2023), which was conducted in the same geographic region. While the previous study focused on characterizing deadwood based on decay classes, the present research expands the scope by developing multivariate regression models to quantify how deadwood volume varies as a function of key stand characteristics, physiographic factors, and spatial variables. This broader analytical approach allows for a more comprehensive evaluation of the structural and environmental drivers influencing deadwood accumulation in contrasting forest management contexts.

Materials and methods

Study site

The scope of this study encompasses the boundaries of Karagol-Sahara NP and Velikoy FMU, both of which are affiliated to Şavşat Forest Enterprise, which is situated under the territorial jurisdiction of Artvin Regional Directorate of Forestry (Fig. 1).

The Şavşat region is situated in the vicinity of the Black Sea, occupying a transitional area characterized by a blend of continental and marine climates. As a result, the spring and autumn seasons in this region are characterized by moderate temperatures and abundant precipitation, while the winters are characterized by severe cold and substantial rainfall. Conversely, the summer months in this region have relatively less rainfall. On a monthly basis, the average air temperature ranges from − 6.2 to 17.5 °C, with an annual average of 5.9 °C. The monthly minimum temperatures range from − 10.3 °C in January to 12.9 °C in August. The maximum temperature recorded is 26 °C. In the geographical area characterized by an annual mean relative humidity fluctuating between 72 and 76%, it is observed that the mean annual total precipitation amounts to 1047 mm (TSMS 2021).

One of the study areas, Velikoy FMU, has a total area of 28,951.6 ha, of which 10,520.9 ha (36.3%) is covered by forestland. The administration units have changed in Turkey in 2020 and Velikoy FMU has now been divided into two FMUs, Velikoy and Sahara. The border and area covered here represents both Velikoy and Sahara FMUs. Another research area, Karagol-Sahara NP, has a total area of 3251.0 ha, of which 1198.0 ha (36.9%) is forestland

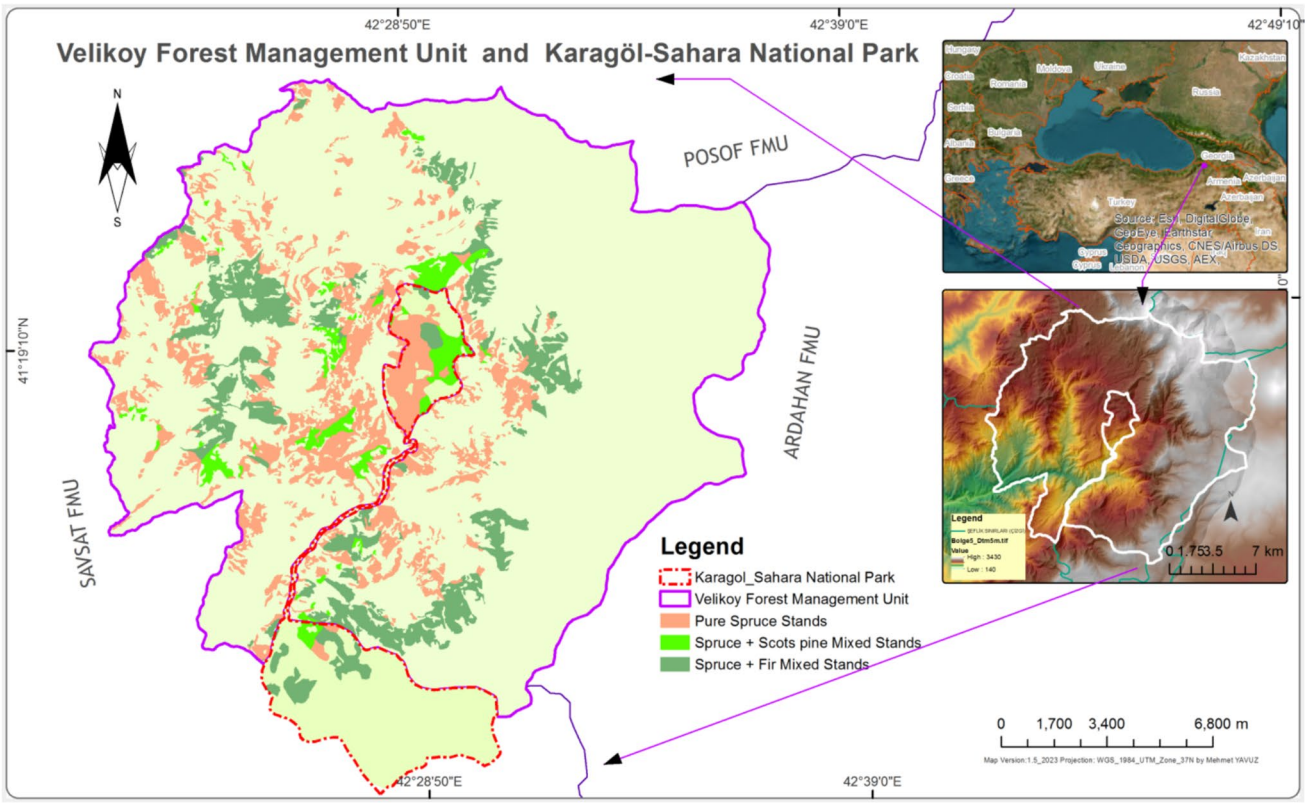


Fig. 1 Overview of the research area (insets: (a) Turkey, (b) Topographic view of Velikoy Forest Management Unit and Karagöl-Sahara National Park, and (c) Spatial distribution of pure and mixed Eastern spruce, Caucasian fir and Scots pine stands within the study area. The boundaries of the administration units have changed in Turkey since 2020. Following that, Velikoy FMU has now been divided into two FMUs, Velikoy and Sahara. The border and area covered here represents both Velikoy and Sahara FMUs

(GDF 2021). In the Karagol-Sahara NP, the area covered by stands of Eastern spruce-Scots pine, Eastern spruce-Caucasian fir, and pure Eastern spruce is 184.0, 270.0, and 405.0 ha, respectively, whereas in the Velikoy FMU, the stands are 2095.7, 479.4, and 577.2 ha. Spruce, on the other hand, is a dominant species in the study area's low altitude zones, where mixed stands of Spruce-Fir and Spruce-Fir-Scots pine can be found, however at higher altitudes, there are more Spruce-Fir mixed stands. The Velikoy FMU's elevation above sea level is between 950 and 3100 m, and the area is mainly undulating slope (GDF 2021).

Karagol-Sahara National Park, established in 1994, has a total area of 3251 ha, with the lowest elevation of 1150 m and the maximum elevation of 2600 m. This national park is divided into two sections: Karagol and Sahara. While Eastern spruce, Scots pine, and Caucasian fir tree species are common in the woods of the Karagol region, Scots pine tree species are common in the lower zones, with Eastern spruce and Caucasian fir being the most common in the Sahara section. The Caucasus hotspot, which Conservation International (Myers et al. 2000) identifies as one of the world's 35 biodiversity hotspots, is home to the Karagol-Sahara NP, which has a high level of biodiversity and natural, uneven-aged forests, according to Davis and Heywood (1994). The biogeographical aspects of this region have led to its recognition as one of the 200 globally recognized priority ecological zones by the World Wide Fund for Nature (WWF) (Olson and Dinerstein 2002).

Sampling design and field measurements

In this study, a total of 476 sample plots were systematically selected using a rigorous random sampling approach to ensure comprehensive representation of the forest stands within the Velikoy FMU and Karagol-Sahara NP. The selection process was guided by key stand characteristics, physiographic variables, and geographical factors to effectively capture the structural and ecological variability across the study areas. To reflect stand composition diversity, the sample plots were strategically distributed among different stand types, including pure Eastern spruce, Eastern spruce—Scots pine, and Eastern spruce—Caucasian fir mixtures.

Additionally, the plots were stratified according to canopy cover classes (11–40%, 41–70%, and > 70%) and age classes (21–40, 41–60, 61–80, 81–100, and > 100 years) to ensure a balanced representation of young, mature, and old-growth stands. The dimensions of the circular sampling plots were determined based on the canopy cover: 800 m^2 for canopy cover less than 40%, 600 m^2 for canopy cover between 41–70%, and 400 m^2 for canopy cover greater than 70%, following the guidelines set by the national forest inventory (GDF 2018). To eliminate subjectivity and potential bias, the selection process utilized a random number generator to assign plots within each stratum, ensuring that each plot had an equal probability of being selected. This approach allowed for a robust analysis of deadwood volume and its distribution across different forest conditions. The centers of each sampling plot locations were surveyed using Garmin Montana 650 GPS unit (Garmin 2014).

The breast height diameters (DBH) of all trees within the plots were measured (arithmetic mean of two measurements at 90˚) if they were 4 cm or more, and the heights of 10–15 trees were recorded and uniformly dispersed within every diameter class. Site index classes were assessed using the "100 trees per hectare method", with the heights of 4–8 representative trees measured within each plot. The age of each plot was determined by taking ring core samples from 2–3 representative median trees. Crown closures (CC) were visually estimated and classified into three categories: CC = 11–40% as Class 1, CC = 41–70% as Class 2, and CC > 70% as Class 3. The slope was determined for each plot using a Haglof VL3 Vertex hypsometer (Haglöf, Sweden AB). The measured slope values were categorized into six classes (0–9%: gentle slope, 10–17%: moderate slope, 18–36%: strong slope, 37–58%: very strong slope, 59–100%: steep slope, > 100%: extremely steep slope).

The slope aspect, representing the directional orientation of each plot, was classified into the cardinal directions: East, West, South, and North. The elevation above the mean sea level and the geographic coordinates of the sampling plot centers were recorded using a Garmin Montana 650 GPS unit (Garmin, Olathe, Kansas, USA). The elevations subsequently categorized into five elevation classes: < 1450 m, 1450–1650 m, 1650–1850 m, 1850–2050 m, and > 2050 m. The closest distances from each sampling plot center to the nearest road and settlement were calculated using the "Near" function within the Proximity/Analysis Toolset (ArcToolbox > Analysis Tools > Proximity > Near) in the ArcGIS10.2.1 software developed by ESRI in California, USA. The distances to roads were categorized into four groups: 0–100 m, 101–250 m, 251–500 m, and greater than 500 m. The distance to the settlements was classified into four categories: 0–500 m, 501–1000 m, 1001–1500 m, and greather than 1500. Spatial data layers, including settlement layer (point), forest roads (line feature) and highway network (line) were obtained from the Şavşat Forest Enterprise (GDF 2021). The slope and aspect data were derived from the digital elevation model provided by the Turkish General Directorate of Mapping (GDM 2019), using Spatial Analysis tool in ArcGIS 10.2.1 software (ESRI 2013). This detailed and systematic sampling approach ensured the collection of accurate and representative data, enabling robust analysis of deadwood abundance and its associated environmental and spatial factors across the study areas.

This research investigated three distinct categories of deadwood: (a) standing deadwood, (b) stumps, and (c) downed deadwood. Standing deadwood refers to trees with a diameter at breast height (DBH) of above 4 cm and a height over 130 cm, whether or not they have trunk wood or broken tops (Harmon et al. 2011). Stumps refer to tree roots along with stumps that are 1–130 cm in height above the ground and greater than 6 cm in diameter. The term "downed or leaned deadwood" describes woody debris that has fallen or tilted, with a diameter of 6 cm or more and a length of 15 cm or more.

The estimation of standing deadwood volume was conducted through measurements of DBH and total tree height. For stumps, diameters were measured at 30 cm above the ground for those shorter than 30 cm, and at mid-height for stumps between 30 and 130 cm in height. In the case of downed deadwood, trees shorter than 6 m in and with a DBH greater than 4 cm were measured for stump length, tip, bottom, and middle diameters, as well as segment length. Downed deadwood exceeding 6 m in length was divided into 4-m segments, with DBH measurements recorded at intervals of 4.3 m, 8.3 m, 12.3 m, and so forth along the log.

Deadwood volume estimation and data analysis

The diameter-length shape coefficient approach was employed to estimate the height, DBH, and volume of the standing deadwood (h > 1.3 m). The form of the trunk was assumed to lie between a geometric cone and a paraboloid, following established models (Eq. 1) (Sippola et al. 1998; Chmura et al. 2016; Herrero et al. 2016; Staniaszek-kik et al. 2019; Šēnhofa et al. 2020). Stumps up to 30 cm in height, volume was determined using the cylinder volume formula (Eq. 2) (Burrascano et al. 2008; Di Cosmo et al. 2013; Puletti et al. 2019) based on measurements of the cut surface diameter at 30 cm from the thin end. Stumps ranging from 30 to 130 cm in height were assessed using the Huber formula (Eq. 3) which involves measuring the diameter at the midpoint and the total length (Sippola et al. 1998; Laar and Akça 2007; Błońska et al. 2020). For downed deadwood shorter than 6 m, volume was estimated using the Newton-Riecke equation (Eq. 4), which incorporates measurements of tip, middle, and base diameters along with total length (Herrero et al. 2016). In cases where downed deadwood exceeded

6 m in length, total volume was derived by summing the volume of the stump (Eq. 5 using the cylinder volume equation at 30 cm height), segment volumes calculated via the Smalian equation (Eq. 6), and the tip section volume based on the cone formula (Eq. 7) (Kalıpsız 1984; Laar and Akça 2007), resulting in a final composite volume (Eq. 8). Following volume estimations for standing deadwood, stumps, and downed logs, deadwood volumes were determined for every sample plot and standardized to per-hectare values.

Standing deadwood

$$V = \frac{\pi}{4}.d_{1.3}^2.h.f_{1.3} \quad \left(f_{1.3} : 0.415, \text{middle of cone - paraboloid}\right) \tag{1}$$

Stumps

$$\text{height} < 0.30\text{m} \quad V = \frac{\pi}{4}.d_{0.3}^2.0.3 \tag{2}$$

$$\text{height } 0.30 - 1.30\text{m} \quad V = \frac{\pi}{4}.d_{0.5}^2.l \quad \text{(Huber Eq.)} \tag{3}$$

Downed deadwood

$$\text{length} < 6\text{m} \quad V = \frac{\pi}{4}.\frac{1}{6}.\left(d_0^2 + 4d_{0.5}^2 + d_n^2\right).l \quad \text{(Newton - Riecke Eq.)} \tag{4}$$

length > 6 m

$$\text{base section} \quad V_{base} = \frac{\pi}{4}.d_{0.3}^2.0.3 \tag{5}$$

$$\text{central section} \quad V_{central} = \frac{\pi}{4}.\frac{1}{6}.\left(d_0^2 + d_n^2\right).l \quad \text{(Smalian Eq.)} \tag{6}$$

$$\text{top section} \quad V_{top} = \frac{\pi}{4}.\frac{1}{3}.d_n^2.l \tag{7}$$

$$\text{Total} \quad V_{total} = V_{stump} + V_{central} + V_{top} \tag{8}$$

where, $d_{0.3}$ is the stump diameter, d_0 is the base diameter, $d_{0.5}$ is the middle diameter, d_n is the top diameter, h is the tree height, and l is the section length.

The volumes of individual living trees (standing live volume), within the designated sample regions were computed using the following formulas for single entry (DBH) (Eqs. 9–11) and double entry (DBH and HEIGHT) (Eqs. 12–14) allometric equations. The volume values per hectare for each stand, from which the sample areas were derived, were calculated using a conversion of the total volume values within each sample area to values per hectare. Furthermore, several stand parameters including stand age, density value, canopy, growth age, and site index were computed for each sample region.

For single entry (DBH) allometric equiations:

$$V = 0.000143d^{2.482109} \tag{9}$$

for Eastern spruce by Kahriman et al. (2023),

$$\ln V = -8.209 + 2.324 \ln d - 3.664/d \tag{10}$$

for Scots pine by Yavuz et al. (2010)

$$V = 0.0000424688d^{2.85763} \tag{11}$$

for Caucasian fir by Yazici (2019).

For double-entry (DBH and HEIGHT) allometric equiations:

$$V = d^2(0.00032505 + 0.00002453h) \tag{12}$$

for Eastern spruce by Akalp (1978),

$$\ln V = -9.769 + 1.872 \ln d + 0.987 \ln h + 5.784h^{-2} \tag{13}$$

for Scots pine by Yavuz et al. (2010),

$$V = d^2(0.000086534 + 0.0000367103h) \tag{14}$$

for Caucasion fir by Yazici (2019)

where, d is DBH, h is height, and V is the standing live volume of the stands.

Statistical methods and justification

We conducted ANOVA test (IBM-SPSS 2010) to examine the variation in deadwood volume across multiple stand and physiographic factors such as stand type, age, crown closure, site index, elevation, aspect, and distance to roads and settlements. ANOVA was chosen because it allows for the comparison of means across more than two groups, helping us to identify which specific factors significantly influence deadwood volume. Before conducting the ANOVA test, the Kolmogorov–Smirnov (K-S) test was used to evaluate the normality of the variables. The Kolmogorov–Smirnov test was chosen because of the large sample size (n = 476 > 50). A p-value over 0.05 indicates that the data conforms to a normal distribution. If a variable did not meet the normality assumption ($p < 0.05$), it was log-transformed to approximate a normal distribution. Additionally, the Tukey Honestly Significant Difference (HSD) post-hoc test was employed following ANOVA to pinpoint the exact groups where significant differences occurred, providing detailed insights into the relationships between variables.

To investigate the relationship between deadwood volume and various stand and physiographic characteristics, we performed the Pearson Correlation Analysis (Schober

et al. 2018) and a Multidimensional Scaling (MDS) analysis were conducted to assess variations in stand and site factors concerning deadwood volume (Riffenburgh 2012; Siegel 2016). This method was selected to assess the magtitude and orientaiton of linear relationships between variables. By identifying significant correlations, we could determine which factors were most closely associated with variations in deadwood volume, guiding management practices to enhance deadwood conservation.

Models for estimating deadwood volume

We developed fixed and mixed effects nonlinear models (Eq. 15) to predict total deadwood volume based on several independent variables, including basal area, density, stand volume, number of trees, site index, stand age, and distance to settlements (Mohr et al. 2022). Multiple regression model was appropriate as it allows for the estimation of the impact of multiple predictors on a single dependent variable, providing a comprehensive model of deadwood volume estimation (Siegel 2016; Mohr et al. 2022). The selection of variables was guided by their biological relevance and statistical significance, ensuring the model's robustness and applicability in forest management (Pinheiro and Bates 2000).

$$DW = e^{(\beta_0+\beta_1\cdot t+\beta_2\cdot \ln SI+\beta_3\cdot Sd+\beta_4\cdot BA+\beta_5\cdot V+\beta_6.N+\beta_7\cdot \ln (DTS))} \quad (15)$$

where, DW for deadwood volume, t for the age (year), SI for site index (m), Sd for the degree of density, BA for stand's basal area (m^2 ha^{-1}), V for stand volume, N for number of trees per ha, DTS for distance from settlements (m), $\beta 0$,..., $\beta 7$ for model parameters.

The parameters of these deadwood volume models were estimated using the PROC MODEL procedure in SAS/STAT® 9.3 software (SAS-Institute 2013). The mixed-effect model was fitted using maximum likelihood estimation in the SAS macro NLINMIX (SAS-Institute 2013). The evaluation of model performance was conducted utilizing the adjusted coefficient of determination (R^2_adj) (Eq. 16) (Draper and Smith 1998), Root Mean Square Error (RMSE) (Eq. 17) (Chai and Draxler 2014), Akaike's Information Criterion (AIC) (Eq. 18) (Akaike 1974), and Schwarz's Bayesian information criterion (BIC) (Eq. 19) (Schwarz 1978). A desirable model has an R^2_adj value close to 1, along with lower RMSE, AIC, and BIC values.

$$R^2_{adj} = 1 - \frac{(n-1)\sum_{i=1}^{n}\left(y_i-\hat{y}_i\right)^2}{(n-p)\sum_{i=1}^{n}\left(y_i-\bar{y}_i\right)^2} \quad \text{(Draper and Smith 1998)} \quad (16)$$

$$RMSE = \sqrt{\frac{\sum_{i=1}^{n}\left(y_i-\hat{y}_i\right)^2}{n-p}} \quad \text{(Chai and Draxler 2014)} \quad (17)$$

$$AIC = -2\ln(L) + 2k \quad \text{(Akaike 1974)} \quad (18)$$

$$BIC = -2\ln(L) + k.\ln(n) \quad \text{(Schwarz 1978)} \quad (19)$$

Let n represent the number of observations, p donate the number of parameters, y_i, $\hat{y}_i$ and $\bar{y}$ signify the observed, predicted, and mean values of the dependent variable, respectively. L indicates the maximum likelihood, while k refers to the total number of parameters in the model including error term.

The Generalized Linear Mixed Models (GLMM) was utilized using a gamma distribution with a log link function to estimate deadwood volume. The GLMM model, which surpasses conventional standard linear regression, accomodates a wider variety of error distributions in response variables and do not need to transformation of the answer to achieve a normal distribution (Yang et al. 2024). The model was calibrated to data gathered in northeastern Türkiye using the PROC GLM procedure available in SAS/STAT® 9.3 software (error structure = Gamma; link function = log) (SAS-Institute 2011).

Results

Field measurement results

Descriptive statistics for stand structure and site conditions in the Veliköy FMU and Karagöl-Sahara NP are presented in Table 1. On average, stands in Karagöl-Sahara NP were older (mean age: 100.5 years) than those in Veliköy FMU (mean age: 88.0 years). Site index values were slightly higher in the NP (26.9 m) compared to the FMU (24.9 m), indicating more productive growing conditions. Karagöl-Sahara NP also exhibited greater stand density (9.6 vs. 8.0) and crown closure (84.6% vs. 74.0%). The NP area was located on steeper terrain (mean slope: 65.7%) than Veliköy FMU (51.2%), though both sites had similar average altitudes (1807.8 m in the NP vs. 1795.7 m in the FMU). Distances to roads and settlements were slightly greater in Veliköy FMU, although variation was high across both sites.

Deadwood and standing live characteristics

Descriptive statistics for deadwood components and standing live volume across the two study sites are compiled in Table 2. The mean total deadwood volume was 22.5 m^3 ha^{-1} in the NP and 10.1 m^3 ha^{-1} in the FMU. Similarly, the deadwood-to-standing live volume was greater in the NP (4.2%) than in the FMU (2.5%). In Karagöl-Sahara NP, standing deadwood accounted for the largest proportion of total deadwood volume (47.8%; 10.8 m^3 ha^{-1}), followed by downed deadwood (29.4%; 6.6 m^3 ha^{-1}), and stumps (22.7; 5.1 m^3 ha^{-1}). In contrast, in Veliköy FMU, the largest

Table 1 Summary statistics of the stand and physiographic parameters used in the managed and unmanaged study areas (adapted from Özdemir et al. (2023))

Study Site	Variables	Minimum	Mean	Maximum	Std. Dev
Velikoy Forest Management Unit	Age (years)	31.1	88.0	199.0	28.4
	Site index (m)	12.9	24.9	34.4	4.0
	Stand density	2.37	8.0	15.90	3.1
	Crown closure (%)	10.1	74.0	100.0	18.5
	Slope (%)	1.0	51.2	140	28.5
	Altitude (m)	1152.0	1795.7	2410.0	234.8
	Distance to road (m)	20.0	329.2	1090.0	270.6
	Dist. to settlement (m)	45.0	913.6	2450.0	479.0
Karagöl-Sahara National Park	Age (years)	44.0	100.5	143.0	19.3
	Site index (m)	19.8	26.9	33.9	2.6
	Stand density	2.2	9.6	15.9	2.5
	Crown closure (%)	35.0	84.6	100.0	13.1
	Slope (%)	3.0	65.7	140.0	32.1
	Altitude (m)	1424.0	1807.8	2117.0	143.7
	Distance to road (m)	25.0	305.0	1080.0	210.0
	Dist. to settlement (m)	100.0	849.8	2080.0	374.4

Table 2 Basic deadwood volume statistics for deadwood types in managed and protected areas

Study sites	Variable	Min	Mean	Max	Std. Dev
Velikoy Forest Management Unit	Standing deadwood (m^3 ha^{-1})	0.0	3.0	87.1	8.4
	Stump (m^3 ha^{-1})	0.0	3.8	11.9	2.6
	Downed deadwood (m^3 ha^{-1})	0.0	3.3	31.1	5.1
	Total deadwood (m^3 ha^{-1})	0.2	10.1	96.2	11.3
	Deadwood/Standing live ratio (%)	0.0	2.6	27.5	2.7
	Standing Live Volume (m^3 ha^{-1})	63.5	412.5	1000.5	212.7
Karagöl-Sahara National Park	Standing deadwood (m^3 ha^{-1})	0.0	10.8	148.0	21.2
	Stump (m^3 ha^{-1})	0.0	5.1	18.1	3.2
	Downed deadwood (m^3 ha^{-1})	0.0	6.6	51.3	9.5
	Total deadwood (m^3 ha^{-1})	0.2	22.5	175.4	26.5
	Deadwood/Standing live Ratio (%)	0.0	4.2	33.7	5.3
	Standing live volume (m^3 ha^{-1})	61.1	589.7	1098.2	170.7
Total study area	Standing deadwood (m^3 ha^{-1})	0.0	6.9	148.0	16.6
	Stump (m^3 ha^{-1})	0.0	4.5	18.1	3.0
	Downed deadwood (m^3 ha^{-1})	0.0	5.0	51.3	7.8
	Total deadwood (m^3 ha^{-1})	0.2	16.3	175.4	21.3
	Deadwood/Standing live ratio (%)	0.0	3.4	33.7	4.3
	Standing live volume (m^3 ha^{-1})	61.1	501.8	1098.2	211.9

component was stumps (37.8%; 3.8 m^3 ha^{-1}), followed by downed deadwood (32.7%; 3.3 m^3 ha^{-1}), and standing deadwood (29.4%; 3.0 m^3 ha^{-1}) (Table 2).

The effects of the stand and site variables on deadwood volume

Multidimensional scaling analysis (MDS)

In the Multidimensional Scaling the stress value was 0.263, which shows that the analysis result is valid for a

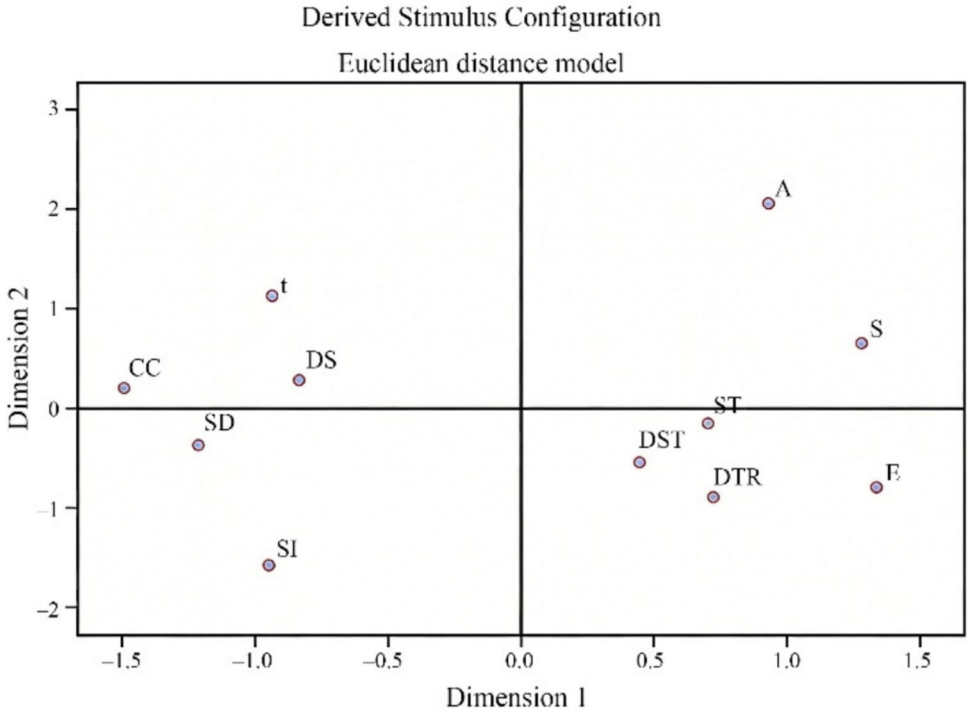


Fig. 2 Multidimensional Scaling Analysis (MDS) plot of stand and site parameters based on deadwood volume data (t: age, SI: site index, SD: stand density, BA: basal area, V: stand volume, N: tree count in ha, DTR: distance to roads, and DTS: distance to settlements)

2-dimentional ordination (Fig. 2). The taxa coded as distance to roads, distance to settlements, stand type, and elevation were separated as one group; five parameters as stand density, crown closure, site index, age, and development stage were designated as a secondary group, and the remaining two parameters as slope and age were amalgamated to become the third group (Fig. 2).

Normality testing of deadwood variables

Normality of deadwood volume components across various stand and physiographic classes was assessed using the Kolmogorov–Smirnov Z-test in both Veliköy Forest FMU and Karagöl-Sahara NP (Table S1). In general, p-values greater than 0.05 were interpreted as evidence that the data did not significantly deviate from a normal distribution.

Correlation of deadwood variables

Table 3 summarizes the Pearson correlation coefficients between stand variables and deadwood volume in two contrasting forest types. In the managed forest (Veliköy FMU), deadwood volume showed strong positive correlations ($p < 0.01$) with most stand variables, notably standing live volume ($r = 0.414$), mean height ($r = 0.395$), and basal area ($r = 0.357$). Moderate but significant associations were also found with site index, distance to settlements, distance to road, stand age, crown closure, mean diameter, and stand density.

Table 3 Correlation analysis results between stand variables and deadwood volume in managed and protected forest stands

Variables	Velikoy FMU		Karagöl-Sahara NP	
	r	*p*	*r*	*p*
Mean diameter (cm)	0.241**	0.000	0.067 ns	0.299
Mean height (m)	0.395**	0.000	0.085 ns	0.190
Age (year)	0.283**	0.000	0.107 ns	0.097
Site index (m)	0.337**	0.000	−0.024 ns	0.715
Basal area (m^2/ha)	0.357**	0.000	0.030 ns	0.647
Standing live volume (m^3 ha^{-1})	0.414**	0.000	0.060 ns	0.355
Number of trees (N/ha)	0.094 ns	0.151	−0.012 ns	0.856
Density (%)	0.351**	0.000	0.133*	0.039
Slope (%)	0.094 ns	0.150	0.105 ns	0.105
Aspect (degree)	-0.074 ns	0.254	0.136*	0.036
Elevation (m)	0.019 ns	0.774	0.165*	0.010
Crown closure (%)	0.260**	0.000	0.059 ns	0.360
Distance to road (m)	0.285**	0.000	−0.005 ns	0.936
Distance to settlement (m)	0.326**	0.000	0.206**	0.001

(**) signifant at 0.01 level, (*) significant at 0.05 level, and (ns): statistically not significant

In contrast, in the protected forest (Karagöl-Sahara NP), a few weak yet signifcant correlations emerged—specifically

Table 4 Site characteristic classes and their deadwood volume distributions (m^3 ha^{-1}) along with ANOVA and Tukey's HSD test results

Variable	Classes	Velikoy FMU (N = 236)				Karagöl-Sahara NP (N = 240)			
		Standing deadwood	Stump	Downed deadwood	Total deadwood	Standing deadwood	Stump	Downed deadwood	Total deadwood
Stand type	S	1.3^{a}	3.1^{a}	1.9^{a}	6.3^{a}	10.5^{ab}	6.1^{b}	6.9^{a}	23.6^{a}
	S-Sp	3.4^{a}	3.4^{a}	3.3^{a}	10.0^{a}	6.4^{a}	4.1^{a}	6.3^{a}	16.7^{a}
	S-F	4.2^{a}	4.8^{b}	4.6^{b}	13.7^{b}	14.7^{b}	4.8^{a}	6.5^{a}	26.0^{a}
ANOVA	F	2.51	11.73	6.63	9.64	2.84	8.85	0.11	2.42
	p	0.084	**0.000**	**0.002**	**0.000**	**0.060**	**0.000**	0.898	0.091
Age (year)	21–40	0.8^{a}	1.6^{a}	0.5^{a}	2.9^{a}				
	41–60	0.3^{a}	2.6^{ab}	1.1^{a}	3.9^{a}	2.5^{a}	2.9^{a}	6.3^{a}	11.7^{a}
	61–80	2.3^{a}	3.6^{bc}	3.3^{ab}	9.2^{ab}	6.7^{a}	5.6^{a}	7.2^{a}	19.4^{a}
	81–100	3.0^{a}	4.3^{c}	4.5^{b}	11.7^{b}	12.0^{a}	5.0^{a}	5.2^{a}	22.3^{a}
	> 100	5.1^{a}	4.4^{c}	3.4^{ab}	12.9^{b}	11.4^{a}	5.1^{a}	7.3^{a}	23.8^{a}
ANOVA	F	2.10	6.39	3.93	5.61	0.78	0.91	0.83	0.48
	p	0.082	**0.000**	**0.004**	**0.000**	0.506	0.438	0.476	0.694
Site class (m)	30–33	6.7^{a}	5.0^{b}	6.4^{b}	18.1^{c}	11.8^{a}	5.5^{a}	7.8^{a}	25.1^{a}
	27–30	2.6^{a}	4.4^{b}	6.5^{b}	13.5^{bc}	10.4^{a}	5.2^{a}	7.4^{a}	23.0^{a}
	24–27	3.6^{a}	4.5^{b}	3.2^{a}	11.4^{b}	11.6^{a}	5.0^{a}	5.5^{a}	22.1^{a}
	21–24	2.6^{a}	4.1^{b}	2.7^{a}	9.4^{ab}	7.7^{a}	4.7^{a}	6.9^{a}	19.3^{a}
	18–21	1.47^{a}	1.6^{a}	0.7^{a}	3.9^{a}	8.6^{a}	5.8^{a}	1.8^{a}	16.2^{a}
ANOVA	F	1.48	12.49	10.75	8.21	0.18	0.31	0.69	0.19
	p	0.208	**0.000**	**0.000**	**0.000**	0.947	0.872	0.598	0.944
Density	< 6	1.4^{a}	2.6^{a}	1.9^{a}	5.8^{a}	3.6^{a}	2.8^{a}	4.8^{a}	11.2^{a}
	6–8	1.4^{a}	3.9^{ab}	2.3^{a}	7.6^{ab}	10.1^{a}	5.0^{b}	3.5^{a}	18.7^{a}
	8–10	4.1^{ab}	4.4^{b}	3.2^{a}	11.6^{abc}	10.9^{a}	5.2^{b}	6.4^{a}	22.4^{a}
	10–12	2.0^{a}	4.9^{b}	6.2^{b}	13.1^{bc}	11.3^{a}	5.1^{b}	8.7^{a}	25.1^{a}
	> 12	8.9^{b}	4.5^{b}	4.4^{ab}	17.7^{c}	13.2^{a}	6.0^{b}	7.4^{a}	26.6^{a}
ANOVA	F	4.85	7.93	5.70	7.83	0.67	3.30	1.92	1.41
	p	**0.001**	**0.000**	**0.000**	**0.000**	0.612	**0.012**	0.108	0.232
Development stages (cm)	8–20	0.5^{a}	2.3^{a}	0.7^{a}	3.5^{a}	3.3^{a}	3.9^{a}	10.4^{a}	17.6^{a}
	21–36	3.6^{a}	4.2^{b}	3.8^{ab}	11.6^{b}	10.2^{ab}	5.2^{a}	6.6^{a}	21.9^{a}
	> 36	3.5^{a}	4.6^{b}	6.1^{b}	14.2^{b}	37.1^{b}	3.7^{a}	4.5^{a}	45.3^{a}
ANOVA	F	2.56	11.10	9.09	11.18	5.06	0.83	0.38	2.35
	p	0.079	**0.000**	**0.000**	**0.000**	**0.007**	0.438	0.681	0.097
Crown closure (%)	11–40	2.0^{a}	1.8^{a}	1.6^{a}	5.3^{a}	1.6^{a}	2.3^{a}	5.6^{a}	9.4^{a}
	41–70	2.3^{a}	3.2^{b}	2.1^{ab}	7.7^{ab}	10.7^{a}	4.2^{ab}	7.5^{a}	22.3^{a}
	> 70	3.6^{a}	4.5^{b}	4.4^{b}	12.5^{b}	11.0^{a}	5.3^{b}	6.5^{a}	22.9^{a}
ANOVA	F	0.71	12.94	6.97	6.87	0.58	4.33	0.18	0.75
	p	0.493	**0.000**	**0.001**	**0.001**	0.561	**0.014**	0.836	0.473

Superscript letters (a), (b), and (ab) denote groupings based on post hoc multiple comparison (Tukey HSD) test. Means sharing at least one letter are not significantly different ($p < 0.05$), whereas means with no common letters differ significantly

Bold values indicate statistically significant ($p < 0.05$) variations

with distance to settlements ($r = 0.206$, $p < 0.01$), elevation ($r = 0.165$, $p = 0.010$), aspect ($r = 0.136$, $p = 0.036$), and density ($r = 0.133$, $p = 0.039$). Other structural stand variables including mean diameter, height, age, and basal area showed no significant relationships with deadwood volume.

Statistical comparison of deadwood volume across management types and site variables

Results of ANOVA and the Tukey's Honestly Significant Differences (HSD) test revealed significance differences ($p < 0.05$) in deadwood volumes based on various stand (Table 4) and physiographic parameters (Table 5). In both

Table 5 Physiographic parameter classes and their deadwood volume distributions (m^3 ha^{-1}) along with ANOVA and Tukey's HSD test results

Variable	Classes	Velikoy FMU (N = 236)				Karagöl-Sahara NP (N = 240)			
		Standing deadwood	Stump	Downed deadwood	Total deadwood	Standing deadwood	Stump	Downed deadwood	Total deadwood
Slope (%)	0 – 9	0.1^{a}	3.6^{a}	1.9^{a}	5.6^{a}	5.6^{a}	8.3^{a}	4.7^{a}	18.6^{a}
	10 – 17	0.4^{a}	2.2^{a}	3.5^{a}	6.1^{a}	11.8^{a}	6.1^{a}	6.9^{a}	24.8^{a}
	18 – 36	2.3^{a}	3.8^{a}	2.1^{a}	8.2^{a}	4.9^{a}	5.5^{a}	6.2^{a}	16.6^{a}
	37 – 58	4.8^{a}	4.3^{a}	4.4^{a}	13.4^{a}	4.2^{a}	5.5^{a}	5.7^{a}	15.3^{a}
	59 – 100	2.9^{a}	3.8^{a}	3.8^{a}	10.4^{a}	15.9^{a}	4.8^{a}	7.1^{a}	27.8^{a}
	> 100	7.1^{a}	3.8^{a}	2.8^{a}	13.6^{a}	11.4^{a}	4.6^{a}	7.1^{a}	23.1^{a}
ANOVA	*F*	9.31	2.91	2.41	11.47	14.44	3.53	9.82	21.17
	p	1.529	1.085	1.476	2.229	2.832	1.330	0.204	1.979
Aspect	North	3.1^{a}	4.0^{ab}	3.8^{ab}	10.9^{a}	16.7^{a}	5.8^{a}	6.1^{a}	28.6^{a}
	East	4.6^{a}	4.5^{b}	3.2^{ab}	12.2^{a}	7.2^{a}	5.8^{a}	6.6^{a}	19.5^{a}
	South	2.1^{a}	2.9^{a}	2.1^{a}	7.1^{a}	8.2^{a}	4.7^{a}	7.2^{a}	20.1^{a}
	West	2.6^{a}	4.3^{b}	4.6^{b}	11.5^{a}	14.6^{a}	4.5^{a}	6.3^{a}	25.3^{a}
ANOVA	*F*	0.87	4.91	2.96	2.75	2.61	2.98	0.16	1.30
	p	0.455	**0.003**	**0.033**	**0.044**	0.052	0.032	0.921	0.274
Elevation (m)	< 1450	3.8^{a}	3.1^{ab}	1.3^{a}	8.1^{ab}	0.1^{a}	2.2^{a}	5.6^{a}	8.0^{a}
	1450 – 1650	3.3^{a}	3.3^{b}	2.3^{ab}	8.9^{ab}	9.4^{a}	3.9^{a}	3.5^{a}	16.8^{a}
	1650 – 1850	3.9^{a}	3.9^{b}	3.0^{ab}	10.9^{b}	9.9^{a}	5.3^{a}	6.8^{a}	21.9^{a}
	1850 – 2050	2.7^{a}	4.7^{b}	4.9^{b}	12.3^{b}	12.2^{a}	5.4^{a}	6.8^{a}	24.3^{a}
	> 2050	0.3^{a}	1.7^{a}	1.2^{a}	3.2^{a}	13.3^{a}	4.8^{a}	10.7^{a}	28.7^{a}
ANOVA	*F*	0.83	7.72	5.04	3.46	0.34	1.64	1.33	0.76
	p	0.507	**0.000**	**0.001**	**0.009**	0.850	0.165	0.258	0.553
Distance to roads (m)	0 – 100	1.6^{a}	2.4^{a}	1.4^{a}	5.3^{a}	5.5^{a}	5.6^{a}	6.7^{a}	17.8^{a}
	101 – 250	2.2^{a}	4.0^{b}	3.5^{ab}	9.7^{ab}	10.9^{a}	4.8^{a}	6.9^{a}	22.6^{a}
	251 – 500	3.3^{a}	4.2^{b}	3.3^{ab}	10.8^{b}	12.0^{a}	5.1^{a}	6.2^{a}	23.3^{a}
	> 500	4.9^{a}	4.6^{b}	4.7^{b}	14.2^{b}	11.3^{a}	5.5^{a}	7.1^{a}	23.8^{a}
ANOVA	*F*	1.82	8.87	4.39	6.59	0.72	0.62	0.11	0.36
	p	0.145	**0.000**	**0.005**	**0.000**	0.540	0.602	0.953	0.784
Distance to settlements (m)	0 – 500	0.8^{a}	2.9^{a}	1.8^{a}	5.6^{a}	5.3^{a}	4.7^{a}	3.2^{a}	13.2^{a}
	501 – 1000	2.6^{ab}	3.4^{ab}	2.3^{a}	8.3^{ab}	8.5^{ab}	4.8^{a}	5.9^{ab}	19.2^{ab}
	1001 – 1500	3.3^{ab}	4.4^{bc}	4.2^{ab}	11.9^{b}	14.7^{ab}	5.7^{a}	8.7^{b}	29.1^{bc}
	> 1500	6.6^{b}	5.0^{c}	6.5^{b}	18.1^{c}	19.9^{b}	5.7^{a}	9.7^{b}	35.3^{c}
ANOVA	*F*	3.38	6.20	8.37	10.77	3.36	1.71	4.14	5.54
	p	**0.019**	**0.000**	**0.000**	**0.000**	**0.020**	0.166	**0.007**	**0.001**

Superscript letters (a), (b), and (ab) denote groupings based on post hoc multiple comparison (Tukey HSD) test. Means sharing at least one letter are not significantly different Bold values indicate statistically significant ($p < 0.05$) variations ($p < 0.05$), whereas means with no common letters differ significantly

areas, the ANOVA indicated statistically significant variations in deadwood volume by stand type, age, crown closure, and other structural stand characteristics ($p < 0.05$).

In the Velikköy FMU, deadwood volume varied by stand type, averaging 6.3 m^3 ha^{-1} in pure Spruce (S), 10.0 m^3 ha^{-1} in Spruce-Scots Pine mixed stands (S-SP), and 13.7 m^3 ha^{-1} in Spruce- Fir mixed stands (S-F) while corresponding values in Karagöl-Sahara NP notably higher (23.6, 16.7, and 26.0 m^3 ha^{-1}, respectively; Table 4).

Deadwood volume also increased with stand age —from 2.9 m^3 ha^{-1} in 21–40 year-old stands to 12.0 m^3 ha^{-1} in stands older than 100 years in Velikköy FMU, and from 0.0 to 23.8 m^3 ha^{-1} (Table 4) in Karagöl-Sahara NP. Across stand density classes, volumes ranged from 11.2 to 26.6 m^3 ha^{-1} in Velikköy FMU and 5.8–17.7 m^3 ha^{-1} in Karagöl-Sahara NP (Table 4). By diameter class, values were in Velikköy FMU were 3.5, 11.6, and 14.2 m^3 ha^{-1} (8–20, 20–36, and > 36 cm), whereas Karagöl-Sahara NP had much higher levels—17.6, 21.9, and 45.3 m^3 ha^{-1}, respectively (Table 4).

When grouped by crown closure, deadwood volumes in Veliköy FMU were 5.3 m^3 ha^{-1} in open (11%–40%), 7.7 m^3 ha^{-1} in moderately closed (41%–70%), and 12.5 m^3 ha^{-1} in dense (> 70%) stands. Corresponding values In Karagöl-Sahara NP were higher—9.4, 22.3, and 22.9 m^3 ha^{-1}, respectively (Table 4).

Deadwood volume patterns by spatial factors

In Veliköy FMU, stands located farthest from settlements had the highest standing deadwood volume (6.6 m^3 ha^{-1}). Stump volumes were similar aspects—4.5 m^3 ha^{-1}in east and 4.3 m^3 ha^{-1} in west—and increase with elevation from 3.3 m^3 ha^{-1} at 1450–1650 m to 4.7 m^3 ha^{-1} at 1850–2050 m; Table 5). Stands farther from roads and settlements also showed higher stump volumes (4.0–5.0 m^3 ha^{-1}; Table 5).

For downed deadwood, the west aspect and higher elevations (1850–2050 m) had the greatest volumes (4.6 and 4.9 m^3 ha^{-1}, respectively), with distance stands showing 4.7–6.5 m^3 ha^{-1} (Table 5).

Overall, total deadwood peaked at mid- to high elevations (10.9–12.3 m^3 ha^{-1}) and increased with distance from roads and settlements, reaching 14.2 m^3 ha^{-1} beyond 500 m from roads and 18.1 m^3 ha^{-1} in the most remote areas (Table 5).

In Karagöl-Sahara NP, standing deadwood volume increased markedly with remoteness and elevation. The highest total volume (35.3 m^3 ha^{-1}) occurred in stands more than 1500 m from human settlements, with similar increases observed with distance from roads (17.8–23.8 m^3 ha^{-1} from 0–100 m to > 500 m). Downed deadwood volumes were also rose consistently with elevation, from 8.0 m^3 ha^{-1} below 1450 m to 28.7 m^3 ha^{-1} above 2050 m. Steep slopes (89%–100%) supported the greatest volumes (27.8 m^3 ha^{-1}), and north-facing aspects showed the highest accumulation (28.6 m^3 ha^{-1}; Table 5).

In the Veliköy FMU, similar but weaker patterns were observed. Total deadwood volume increased with both elevation (3.2–12.3 m^3 ha^{-1}) and distance from roads (5.3–14.2 m^3 ha^{-1}). The most remote stands (> 1500 m from settlements) contained 18.1 m^3 ha^{-1} of deadwood. The highest values were recorded on steep slopes (> 100%, 13.6 m^3 ha^{-1}) and east-facing aspects (12.2 m^3 ha^{-1}; Table 5).

Estimating deadwood volume with the fixed and mixed nonlinear regression models

The nonlinear regression analyses aimed at predicting total deadwood volume yielded statistically significant models for both the fixed and mixed-effect approaches (Table 6). Residuals were plotted versus the predicted deadwood volume to evaluate the homogeneity of variance (Fig. 3a–c for the fixed model and Fig. 3d–e for the mixed model). The residuals appeared randomly scattered, indicating that the variance of residuals was approximately constant across fitted values. The inclusion of a random effect parameter (b_1) in the mixed-effects model improved the homogeneity of variance and addressed the issue of autocorrelation in the errors.

Table 6 Estimated parameters of fixed and mixed nonlinear regression models for predicting deadwood volume

Parameters	Fixed model				Mixed effect model			
	Estimates	Std. err	Std. Est. value	*p*-value	Estimates	Std. err	Std. Est. value	*p*-value
b_0	−3.2780	1.6652		0.0437	−5.3196	1.4826		0.0170
b_1	0.0058	0.0020	0.151	0.0040	0.0131	0.0021	0.341	0.0102
b_2	1.2596	0.4499	0.217	0.0054	1.3323	0.3831	0.230	0.0178
b_3	0.9620	0.0238	2.876	< .0001	1.1488	0.0402	3.435	0.0223
b_4	−0.2341	0.0150	−3.827	< .0001	−0.2606	0.0150	−4.260	0.0367
b_5	0.0073	0.0010	1.589	< .0001	0.0063	0.0009	1.377	0.0346
b_6	−0.0018	0.0002	−0.614	< .0001	−0.0020	0.0001	−0.700	0.0433
b_7	0.1701	0.0670	0.112	0.0115	0.3485	0.0592	0.230	0.0107
σ_u^2	–	–			1.051E–6	0.0055		< .0001
σ^2	–	–			33.2401	2.4352		0.0416
R^2	0.714				0.787			
RMSE	10.376				5.815			
AIC	1584.9				1262.2			
BIC	1590.4				1267.4			

Parameters b_1 to b_7 represent fixed effects; (σ_u^2) indicates the variance of the random effects; and (σ^2) represents the residual variance. All parameters were statistically significant at the 0.05 level

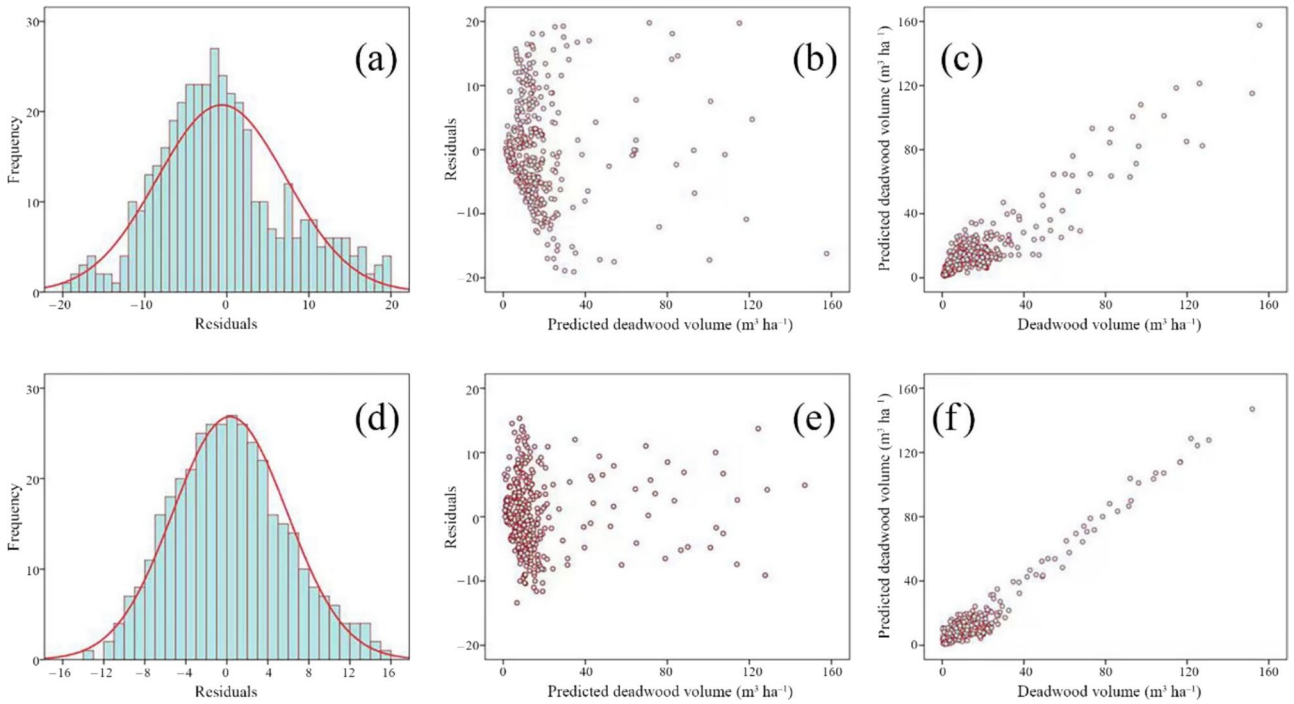


Fig. 3 Diagnostics plots for fixed and mixed nonlinear regression models predicting deadwood volume: **a**, **d** residual histograms for fixed and mixed models, respectively; **b**, **e** residuals versus predicted values; and **c**, **f** predicted versus observed deadwood volume

Table 7 Parameter estimates, *t*-values, and *p*-values of fixed effects from the Generalized Linear Mixed Model (GLMM) for deadwood volume, fitted with a gamma distribution and log link function. Results are presented for Veliköy FMU, Karagöl-Sahara NP, and the combined study area

Variables	Total study area			Velikoy FMU			Karagöl–Sahara NP		
	Estimate	*t*	*p*	Estimate	*t*	*p*	Estimate	*t*	*p*
1/T	108.000	5.08	< 0.001	1054.84	3.45	0.001	16,077.78	3.53	0.001
Ln (T)	2.268	5.98	< 0.001	24.202	4.35	< 0.001	216.134	4.55	< 0.001
1/SI	− 31.727	− 4.26	< 0.001	–	–	–	− 5571.38	− 3.86	< 0.001
Ln (SI)	–	–	–	12.301	2.37	0.019	− 147.706	− 2.72	0.007
SD	1.205	7.68	< 0.001	5.281	7.16	< 0.001	18.47	8.27	< 0.001
SD^2	− 0.030	− 5.36	< 0.001	–	–	–	–	–	–
1/BA	− 57.647	− 3.67	< 0.001	− 1334.54	− 4.56	< 0.001	− 1654.04	− 4.09	< 0.001
Ln (BA)	− 8.484	− 8.18	< 0.001	− 100.512	− 6.49	< 0.001	− 139.087	− 5.81	< 0.001
V^2	–	–	–	–	–	–	− 0.00001	− 3.27	0.001
1/V	186.470	2.05	0.041	3983.73	2.84	0.005	–	–	–
Ln (V)	2.805	4.72	< 0.001	32.343	3.72	< 0.001	–	–	–
N	− 0.001	− 4.14	< 0.001	–	–	–	− 0.046	− 6.66	< 0.001
DTS	0.001	6.33	< 0.001	0.006	4.61	< 0.001	0.007	2.55	0.012
− 2LogL	737.7	1406.6	1254.7						
AIC	741.7	1408.6	1256.7						
BIC	749.5	1411.9	1259.7						

(T: age, SI: site index, SD: stand density, BA: basal area, V: stand volume, N: tree count in ha, DTS: distance to settlements)

In the fixed-effect model, all seven predictor variables (b_1–b_7) were significant at the 0.05 level, with standardized coefficients ranging from 0.112 to 2.876. The variable with the greatest standardized effect was b_3 (stand volume) (Std. Est. = 2.876), followed by b_5 (stand density) (Std. Est. = 1.589), and b_1 (basal area) (Std. Est. = 0.151). The model explained 71.4% of the variance ($R2 = 0.714$), with a Root Mean Square Error (RMSE) of 10.376 m^3 ha^{-1},

and AIC and BIC values of 1584.9 and 1590.4, respectively (Table 6).

In comparison, the mixed-effects model, which accounted for random variability, demonstrated improved model performance. The inclusion of a random intercept significantly enhanced the explanatory power, increasing $R2$ to 0.787 and reducing the RMSE to 5.815 m3 ha^{-1}. Furthermore, the AIC (1262.2) and BIC (1267.4) values were notably lower than those of the fixed model, indicating superior model fit. Among the predictors, b_3 (stand volume) continued to exhibit the highest standardized effect (Std. Est. = 3.435), followed by b_5 (stand density), b_2 (tree number), and b_1 (basal area), all of which had standardized values greater than 0.2. The estimated variance of the random effect ($\sigma_u 2$) was 1.051×10^{-6} ($p < 0.0001$), and the residual variance ($\sigma 2$) was 33.2401 ($p = 0.0416$), confirming the contribution of random variability in improving model accuracy (Table 6).

Deadwood volume estimation using generalized Linear Mixed Effects Models (GLMM) model

The Generalized Linear Mixed Model (GLMM), fitted with a log link function and gamma distribution, revealed significant relationships ($p < 0.05$) between deadwood volume and various stand and physiographic variables across the Veliköy Forest FMU, Karagöl-Sahara NP, and the combined study area (Table 7).

In the combined model, the most influential variables were stand density (SD), tree age (1/T and ln(T)), basal area (1/BA and ln(BA)), and distance to settlements (DTS). Stand density had a significant positive effect on deadwood volume (Estimate = 1.205, $t = 7.68$, $p < 0.001$), while the quadratic term SD2 was negatively associated ($t = -5.36$, $p < 0.001$), indicating a nonlinear correlation. Similarly, the inverse of basal area (1/BA) and its logarithmic transformation (ln(BA)) had strong negative effects ($p < 0.001$), suggesting that larger basal areas corresponded with reduced deadwood volumes under the model assumptions. Positive effects were also observed for distance to settlements (DTS) and stand volume (ln(V)) (Table 7).

For Veliköy FMU, stand density again emerged as the strongest positive predictor (Estimate = 5.281, $t = 7.16$, $p < 0.001$), followed by tree age, basal area, and site index (ln(SI)). Distance to settlements (DTS) also showed a significant positive effect (*Estimate* = 0.006, $t = 4.61$, $p < 0.001$). The model fit statistics indicated moderate performance (−2LogL = 1406.6; AIC = 1408.6) (Table 7).

In Karagöl-Sahara NP, deadwood volume was significantly associated with site index (1/SI and ln(SI)), tree count (N), and stand density. The inverse of site index (1/SI) and the logarithmic form of basal area (ln(BA)) were negatively associated with deadwood volume. Unlike Veliköy FMU, a quadratic term of stand volume (V2) was significant but with a small negative estimate ($p = 0.001$), indicating a diminishing effect of stand volume at higher levels. The model demonstrated a better fit (−2LogL = 1254.7; AIC = 1256.7) compared to Veliköy FMU (Table 7).

Discussion

This study compared deadwood quantities—categorized into standing, downed, and stump components—their ratio to standing live volume, and total deadwood volumes across managed (Veliköy FMU) and protected (Karagöl-Sahara NP) forests, drawing comporisons with values reported in previous research (Table 8). The total deadwood volume obtained in Velikoy FMU (10.1 m^3 ha^{-1}, 2.5% of standing live volume) was lower than both global and European averages previously reported (Sippola et al. 1998; Motta et al. 2006; Atici et al. 2008; Çolak et al. 2009; De Meo et al. 2017; Keren and Diaci 2018; Bayraktar et al. 2020). In contrast, the total volume in Karagol-Sahara NP (22.5 m^3 ha^{-1}, 4.2%) was comparable to or exceeded these benchmarks, aligning more closely with values from protected or unmanaged forest (Karahalil et al. 2017; Topaçoğlu et al. 2017; Puletti et al. 2019; Pala 2020). The higher accumulation in the national park can be attributed to the absence of active silvicultural interventions, allowing natural tree mortality and decomposition processes to proceed uninterrupted.

Downed deadwood showed considerable variability depending on forest type and disturbance history. Studies have reported high volumes in diverse settings, from urban pine forest (De Meo et al. 2017) to mixed historical Beech-Fir-Spruce stands (Keren and Diaci 2018). In the present study, downed deadwood constituted a substantial portion of the total deadwood volume, particularly in the protected Karagöl-Sahara National Park (29.4%; 6.6 m^3 ha^{-1}). In contrast, the managed Veliköy FMU displayed a slightly higher proportional share (32.7%) but with a markedly lower absolute volume(3.3 m^3 ha^{-1}). These values are notably lower than those reported in similar forest ecosystems. For instance, Bayraktar et al. (2020) recorded 13.44 m^3 ha^{-1} of downed deadwood (81.5% of total deadwood) in unmanaged oak-beech stands in Istanbul, while Paletto et al. (2021) reported 16.9 m^3 ha^{-1} (71%) in mountain birch (*Betula pubescens subsp. czerepanovii*) forests of the Khibiny Mountains, Russia. Similarly, Błońska et al. (2020) found 30.1 m^3 ha^{-1} (55.2%) in managed Polish forests. Much higher values have been also observed in certain ecosystems—Keren and Diaci (2018) reported 272 m^3 ha^{-1} (76%) in mixed historical beech-fir-spruce forests, while De Meo et al. (2017) documented 59.91 m^3 ha^{-1} (80%) in urban Calabrian pine forests (Table 8).

Table 8 Comparison of deadwood volume across different deadwood classes as reported in numerous research studies conducted globally

Study reference	Tree	Location, country	Management type	SDW		DDW		Stump		CWD		Snag		TDW	DWP
				$m^3\ ha^{-1}$	%	$m^3\ ha^{-1}$	%	$m^3\ ha^{-1}$	%	$m^3\ ha^{-1}$	%	$m^3\ ha^{-1}$	%	$m^3\ ha^{-1}$	%
This study	S-F-SP	Artvin-velikoy FMU	Managed	3	30	3.3	33	3.8	38	–	–	–	–	10.1	2.6
		Karagöl-Sahara NP	Protected	10.8	48	6.6	29	5.1	23	–	–	–	–	22.5	4.2
Bayraktar et al. (2020)	OK-BE	İstanbul- Türkiye	Protected	2.7	16	13.4	82	0.4	2.1	–	–	–	–	16.5	5.6
Pala (2020)	SP	Giresun- Kelkit	Managed	1.3	54	0.9	38	0.2	8	–	–	–	–	2.5	1.3
Paletto et al. (2021)	BI	Russia	Managed	2.3	9	16.9	71	4.7	20	–	–	–	–	–	–
Puletti et al. (2019)	-	19 European Countries	Managed	4.1	26	0.7	5	2.5	16	6.4	41	1.8	12	15.8	–
Błońska et al. (2020)	B	Poland	Protected	21.3	39	30.1	55	1.7	3	–	–	1.5	3	54.6	–
Keren and Diaci (2018)	BE-F-S	SE Europe	Protected	76	21	272	76	10	3	–	–	–	–	357	27
Keren and Diaci (2018)	BE-F-S	SE Europe	Managed	2.5	3,6	46.5	67	20	30	–	–	–	–	69	19.4
Topacoğlu et al. (2017)	F	Kastamonu-Türkiye	Managed	2.2	25	5.3	61	–	–	–	–	1.2	14	8.9	3.2
Karahalil et al. (2017)	CP	Köprülü Kanyon NP	Protected	0.5	13	3.1	82	0.2	5.3	–	–	–	–	3.8	2.4
De Meo et al. (2017)	C-B	Italy	Protected	13.9	18	59.9	80	1.3	2	–	–	–	–	75.1	12.6
Motta et al. (2006)	BE-F-S	Romania	Managed	114	27	–	–	6.2	2	300	71	–	–	420.4	40.8
Paletto et al. (2014)	OK	Matera- Italy	Managed	3.4	44	2.7	35	1.6	21	–	–	–	–	7.64	–
Di Cosmo et al. (2013)	C-B	Italy	Managed	5.4	61	1.9	22	1.5	17	–	–	–	–	–	–
Du Cros and Lopez (2009)	C-B	France	Managed	6.9	22	22.8	73	1.6	5	–	–	–	–	–	–
Burrascano et al. (2008)	BE	Italy	Protected	10.3	23	19	42	4.2	9	11.5	26	–	–	45	11.7
Atici et al. (2008)	BE	Northern Türkiye	Managed	3.4	15	4.1	18	–	–	5.5	24	9.87	43	22.9	4.8
Motta et al. (2006)	S	Valbona-Italy	Managed	7.5	32	9	39	6.8	29	–	–	–	–	23.3	4.8
Staniaszek-kik et al. (2019)	F	Poland	Managed	130	–	–	43	–	53	70	–	–	–	–	–
Staniaszek-kik et al. (2019)	F	Poland	Protected	150	–	–	57	–	47	114	–	–	–	–	–
De Meo et al. (2017)	C-B	Greece	Protected	1.6	17	3.1	34	4.3	49	–	–	–	–	9.2	2.3
Burrascano et al. (2008)	BE	Italy	Managed	0.3	2	3.1	26	8.5	70	0.1	1	–	–	12.1	3.2
Lee et al., 1997	AS	Alberta, Canada	Managed (young)	19.1	54	–	–	–	–	48.5	79	–	–	–	–
Lee et al., 1997	AS	Alberta, Canada	Managed (mature)	3.8	5.8	–	–	–	–	50.4	66	–	–	–	–

SDW: Standing deadwood, DDW: Downed deadwood, CWD: Coarse woody debris, TDW: Total deadwood DWP: Deadwood proportion of total volume, FMU: Forest Management Unit, NP: National Park, S: Spruce, F: Fir, SP: Scots pine, OK: Oak, BE: Beech, CP: Calabrian pine BI: Birch, C: Conifers, B: Broadleaves, AS: Aspen

Compared to these studies, the relatively low downed deadwood volumes in both study areas—especially in the Veliköy FMU—likely reflect the combined effects of forest management practices such as salvage logging, fuelwood removal, and the prioritization of stand productivity. In contrast, the moderately higher values in the Karagöl-Sahara NP support previous findings that protected areas generally retain more structural components essential to ecosystem functioning, including downed deadwood (Table 8).

Regarding stump deadwood, our study recorded a maximum of 3.8 m^3 ha^{-1} (37.8%) in Velikoy FMU, a proportion considerably higher than typically reported in the literature, where stumps generally constitute the smallest fraction of deadwood (Motta et al. 2006; Di Cosmo et al. 2013; Puletti et al. 2019; Staniaszek-kik et al. 2019; Paletto et al. 2021). This elevated stump volume in managed stands likely reflects the combined effects of regular silvicultural operations and potentially unauthorized tree harvesting. The prominence of downed and stump wood over standing deadwood in Veliköy FMU further supports this interpretation. In contrast, the high standing deadwood volume (10.8 m^3 ha^{-1}, 47.8%), observed in Karagol-Sahara NP suggests lower disturbance intensity, consistent with restricted access and conservation-driven management, thereby highlighting the importance of protection status in maintaining structural complexity and indicating favorable preservation conditions (Di Cosmo et al. 2013; Paletto et al. 2014).

Our findings indicate that in Karagöl-Sahara NP, deadwood volume tends to increase across different developmental stages due to the absence of both planned silvicultural interventions and illegal harvesting activities, thereby allowing for uninterrupted natural mortality and drying processes. This contrasts with the managed context of Veliköy FMU, where anthropogenic disturbances likely disrupt these natural accumulation cycles. The observed correlation between stand density and deadwood volume is also noteworthy. While Næsset (1999) reported a negative relationship between these variables, Herrero et al. (2016) found that deadwood volume followed an "inverted J" distribution across development stages, with peaks at intermediate ages. Similarly, Karahalil et al. (2017) documented a comparable trend in Calabrian pine forests of Antalya, Turkey, where deadwood volume increased during stand maturation but declined following regeneration phases. These findings further emphasize the influence of stand structure and disturbance history on deadwood dynamics in protected forest systems.

To quantify these complex relationships and capture plot-level variability, we employed both fixed and mixed-effects nonlinear regression models. The results reveal that the mixed-effects nonlinear regression model outperformed the fixed-effect model in predicting deadwood volume, as indicated by higher R2 and lower RMSE, AIC, and BIC values. This suggests that accounting for unmeasured variability—potentially arising from site-specific or spatial heterogeneity—enhances model precision and robustness. Similar outcomes have been reported in forest structural modeling, where the inclusion of random effects significantly reduces residual errors and improves parameter estimation (Pretzsch 2009; Keränen et al. 2015).

Stand volume (b_3) emerged as the most influential variable in both models, consistent with the literature indicating that larger stand volumes are often associated with higher deadwood accumulation due to natural mortality and competitive thinning (Harmon et al. 2011; Lachat et al. 2013). Stand density (b_5) and basal area (b_1) also showed notable positive effects, emphasizing the role of stand crowding and growth intensity in deadwood dynamics.

Interestingly, the negative coefficients of crown closure (b_4) and site index (b_6) imply that higher productivity sites with denser canopies may have less accumulated deadwood, possibly due to more active decomposition and lower mortality in well-growing stands (Mäkinen et al. 2006). The positive effect of elevation (b_7) aligns with findings from montane forest ecosystems, where colder, less disturbed environments promote deadwood persistence (Gairola et al. 2011; Siitonen et al. 2023).

The inclusion of a random intercept in the mixed model captured variability not explained by the fixed parameters alone, likely attributable to plot-specific or environmental factors not directly measured (Pinheiro and Bates 2006; Zuur et al. 2009). This reinforces the necessity of hierarchical modeling frameworks when dealing with ecological data from heterogeneous forest landscapes (Bolker et al. 2009; Schielzeth and Nakagawa 2013).

This study's findings are consistent with earlier research that has highlighted the predictive value of stand and site attributes for deadwood volume using regression-based approaches. For instance, in forests that strictly protected, pristine, and primeval in Poland, Bujoczek et al. (2018) demonstrated that elevation and stand volume were significant independent predictors of deadwood volume in a linear regression model with an adjusted R2 of 63.54%. Similarly, Vlad et al. (2019) employed mixed linear and nonlinear models to assess the influence of stand age, altitude, human impact, and site productivity on deadwood volume, achieving a reduced RMSE of 47.6 m^3 ha^{-1} for the best-performing model.

Overall, the study supports the use of mixed-effect models for improving the estimation of deadwood volume, especially in structurally complex forest ecosystems. The identification of key drivers such as stand volume, density, and basal area provides a solid foundation for deadwood management and biodiversity-oriented forestry planning.

The GLMM results highlight that structural stand attributes—particularly stand density, basal area, age, and site

index—play crucial roles in determining deadwood volume, albeit with variation across management contexts.

In both the total and site-specific models, stand density (SD) showed a consistently strong and positive association with deadwood volume. This is consistent with earlier studies (Siitonen et al. 2000; Müller-Using and Bartsch 2009; Harmon et al. 2011), which reported that denser stands tend to accumulate more deadwood due to higher self-thinning and competition-induced mortality. The presence of a significant quadratic term (SD2) in the total model suggests a saturation effect, where beyond a certain threshold, increasing stand density does not proportionally increase deadwood accumulation (Spetich et al. 1997; Fraver et al. 2002).

The basal area (BA), expressed both as 1/BA and ln(BA), was negatively associated with deadwood volume across all models. This inverse relationship may be ascribed to the fact that stands with very high basal areas are typically managed intensively, resulting in less accumulation of deadwood (Linder and Östlund 1998; Siitonen 2001; Topaçoğlu et al. 2017). In contrast, stands with moderate basal areas may experience more mortality and less biomass removal, leading to higher deadwood stocks (Fridman and Walheim 2000; Harmon et al. 2004).

Tree age was another significant predictor, especially in the total model and Veliköy FMU, with both inverse and logarithmic forms contributing positively to deadwood volume. Older stands are generally associated with greater structural complexity and longer accumulation timeframes for deadwood, in agreement with findings from previous research (Fridman and Walheim 2000; Christensen et al. 2005; Lachat et al. 2013). These studies emphasize that aging forests, particularly those under low-intensity management or in protected areas, tend to support higher volumes of standing and downed deadwood due to natural mortality and decay processes over time.

Site index (SI) exhibited opposite trends in the two protected areas: it was positively associated with deadwood in Veliköy FMU (ln(SI)), whereas a negative effect (1/SI) was detected in Karagöl-Sahara NP. This contrast may reflect different site productivity and disturbance histories between the actively managed and protected forest types. In protected areas like Karagöl-Sahara NP, high site productivity may lead to competitive exclusion and more self-thinning, resulting in higher natural deadwood inputs (Fridman and Walheim 2000; Siitonen et al. 2000). Conversely, in managed forests such as Veliköy FMU, productivity might be positively linked to harvesting intensity, which can influence the remaining deadwood stock depending on management goals and retention strategies (Grove and Meggs 2003; Karahalil et al. 2017).

Interestingly, distance to settlements (DTS) had a consistently positive effect, supporting the idea that plots further away from anthropogenic disturbance zones tend to retain more deadwood. This aligns with studies highlighting the negative impact of proximity to human activities on deadwood persistence due to wood removal or firewood collection (Fridman and Walheim 2000; Putz et al. 2012; Gauthier et al. 2015; Karahalil et al. 2017). Forests closer to settlements are often more accessible and subject to higher management intensity, informal harvesting, or sanitary logging, all of which reduce the volume and structural diversity of deadwood (Stokland et al. 2012; Siitonen et al. 2023).

Lastly, tree count (N) was a significant negative predictor in Karagöl-Sahara NP, which may reflect that higher tree densities per hectare are often characteristic of younger or more intensively managed stands, where deadwood accumulation is lower due to reduced mortality and frequent thinning (Fridman and Walheim 2000; Siitonen et al. 2023). In contrast, older or less disturbed stands typically exhibit lower stem densities but higher levels of structural complexity and deadwood, as self-thinning and natural mortality processes advance over time (Runkle 1985; Næsset 1999; Müller and Bütler 2010).

Expanding on this approach, Augustynczik et al. (2024) developed a more comprehensive model that integrated four classes of predictors: forest attributes (e.g., age, biomass, mortality rate, disturbance history), climatic factors (temperature and precipitation), topological features (elevation and slope), and socio-economic factors (such as accessibility, ownership, and protection status). Their work emphasizes the multi-dimensional nature of deadwood dynamics. Moreover, Bouget and Cours (2025) demonstrated that a GLMM incorporating average dieback over the preceding five years, time elapsed since the last disturbance peak, elevation, stand age, and predominant tree species provided the best explanation for total deadwood volume. Collectively, these findings emphasize the utility of GLMM in capturing both linear and nonlinear relationships between deadwood and its potential drivers. They also reinforce the necessity of considering stand structure and landscape context in deadwood accumulation and management strategies, and highlight the robustness of mixed modeling frameworks in capturing this complexity.

Conclusion

This study employed both nonlinear regression and generalized linear mixed modeling approaches to predict deadwood volume and identify its key driving factors across different forest management regimes. The nonlinear regression models (Table 6) demonstrated that stand volume, basal area, and stand density were the most influential predictors of deadwood volume. The mixed-effects model notably outperformed the fixed model by incorporating random variability,

yielding higher explanatory power and better predictive accuracy. These findings underscore the advantages of hierarchical modeling frameworks in accounting for spatial and ecological heterogeneity in forest ecosystems.

The generalized linear mixed model (GLMM) results (Table 7) further validated the significance of site and stand variables—particularly stand age (1/T and ln(T)) and site productivity (1/SI)—in explaining variation in deadwood volume across the Veliköy FMU and the Karagöl-Sahara NP. The orientation and intensity of relationships varied between managed and protected areas, highlighting the influence of management practices and environmental gradients on deadwood accumulation.

Collectively, the results from both modeling approaches suggest that deadwood volume is strongly influenced by structural stand attributes and site conditions, and that protection status plays a significant role in modulating these effects. The integration of mixed-effects modeling and GLMM provides a comprehensive framework for understanding and predicting deadwood dynamics, supporting more effective conservation planning and forest biodiversity management. Future studies should aim to incorporate temporal data and explore species-specific decay dynamics to enhance model robustness and ecological interpretation. Addressing potential nonlinearities and ecological thresholds will further strengthen the predictive capacity of deadwood models in diverse forest ecosystems.

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Data availability Upon acceptance, data will be stored in Figshare.

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