

Structural characteristics of old-growth forest of silver fir and beech at Biogradska Gora

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Abstract

This paper presents the results of a study on the structural characteristics of mixed old-growth silver fir (*Abies alba* Mill.) and beech (*Fagus sylvatica* L.) forests in Biogradska Gora, Montenegro, one of the last remaining primeval forests in Europe. In terms of diameter structure studied forests are characterized by a slightly lower tree density per unit area compared to created normal modes, showed a significant shortage of silver fir trees in the lowest diameter classes. However, the presence of large-diameter trees resulted in the dominance of fir in terms of height structure, as well as a higher total growing stock compared to the theoretical norms. The average growing stock of 931.5 m³ ha⁻¹ has been determined, with an annual volume increment of 10.14 m³ ha⁻¹. Understanding the fundamental characteristics of untouched forests provides an invaluable contribution to expanding knowledge about the complex nature of forests and offers a basis for close-to-nature forest management, which represents the main adaptive approach to forest management under climate change conditions. Research on such forests contributes to a better understanding of environmental changes and the conservation of biodiversity.

Keywords: Biogradska Gora; mixed forest; old-growth forest; primeval forest

Introduction

A small number of untouched forests remain in Europe, mostly in rugged montane areas of south-east of the continent or at high latitudes (Sabatini *et al.*, 2018; Parviainen *et al.*, 2020). Old-growth forests are estimated to cover 3.5 million hectares (2.0% of the European forest area) (Barredo *et al.*, 2021).

Due to their exceptional importance, the remaining old European forests are generally under a certain level of protection. However, they are most often small. Of all forest protected areas in Europe, less than 2% exceed 1,000 ha. Most strict forest reserves are less than 50 ha in size-likely too small to encompass the minimum dynamic area necessary to sustain many species (Nagel *et al.*, 2025).

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Biogradska Gora in Montenegro represents a unique reserve of primary old-growth forest, covering 1,600 ha of untouched woodland. The protection of Biogradska Gora forest dates from the end of the 19th Century when it was used as a royal hunting reserve, and in 1952, it was proclaimed as National Park (Motta *et al.*, 2015). In recent years, research on natural, undisturbed forests has gained renewed relevance due to the ongoing process of climate change. The largest European forest carbon sinks are located in the old-growth forests of the Dinaric Alps. Some recent studies suggest that the total carbon sink potential of old forests is greater than previously thought, as dominant old trees, particularly silver fir, do not exhibit the growth decline typically associated with aging (Palandrani *et al.*, 2021; Bono *et al.*, 2024).

To facilitate better adaptation of forests to climate change, forest management should be directed toward maintaining the most natural and diverse stand compositions possible. Stands that are closest to natural forest conditions (in terms of tree species, structure, canopy closure, etc.) are optimal for their site and the most resistant to various abiotic and biotic stresses. In this regard, mixed uneven-aged forests of silver fir (*Abies alba* Mill.) and European beech (*Fagus sylvatica* L.) play a critical role. These forests are floristically richer than the forests of Central Europe (Gazdić *et al.*, 2018). The high number of species present in these forests makes them unique from a biodiversity perspective (Brunet *et al.*, 2010; Bledý *et al.*, 2024). The presence of native species across different fir stands underscores the need for biodiversity-focused forest management and the importance of continuous monitoring (Solomou and Koulelis, 2025). These forests also represent the most important forest type in the Dinarides of Southeast Europe (Boncina *et al.*, 2014). Beech and silver fir form stable stands on these sites, being relatively balanced in competition, with each occupying a slightly different ecological niche.

It is of great importance to gain a deeper understanding of the structural characteristics and processes in untouched forests, especially in mixed forests such as the fir-beech stands of the Dinarides. This research aims to understand better the complex nature of mixed fir-beech forests in Biogradska Gora, Montenegro, one of the last preserved primary forests of the Dinaric Alps (Motta *et al.*, 2023). A better understanding of the fundamental characteristics of these primeval forest ecosystems provides a basis for close-to-nature forest management in the broadest sense (Larsen *et al.* 2022). Due to the absence of human impact, these ecosystems are of particular scientific interest and represent valuable research sites, as managing forests at a sufficiently high biodiversity level re-quires knowledge of the condition and processes occurring in undisturbed stands (Čurović *et al.*, 2020). Detailed insights into the structural characteristics of old mixed silver fir-beech forests, such as those found in the strict reserve of Biogradska Gora, provide a valuable foundation for planning in accordance with the principles of close-to-nature forest management.

Materials and Methods

Study site

The research was conducted in the old-growth forests of the Biogradska Gora National Park in Montenegro. Institutional framework of the forestry and related sectors for nature protection governance should provide a clear division of responsibilities between institutions and organizations. National parks in Montenegro are managed by the Public Enterprise “National Parks of Montenegro,” which undertakes measures and activities aimed at implementing the established policy for the management, use, protection, development, and improvement of national parks. Accordingly, this research was carried out in cooperation with the National Parks of Montenegro, the institution responsible for implementing protection measures within the Strict Reserve, which represents the most valuable part of Biogradska Gora National Park. The locations of the sample plots were selected to represent optimal stands of mixed silver fir and beech forests at different altitudes within the Biogradska Gora Primeval Forest Reserve. Measurements were carried out on four sample plots with a total area of 1 ha (Figure 1 and Figure 2). In the sample plots, diameters at breast height and tree heights were measured for all trees with a diameter above 10 cm.



Figure 1. Position of the sample plots within the Biogradska Gora Primeval Forest Reserve (original image)



Figure 2. Old-growth Forest of silver fir and beech at Biogradska Gora (original image)

Soil characteristic and climatic conditions represent an important ecological factor influencing forest stands in this area. In the broader area of Biogradska Gora, forest stands are predominantly established on dystric brown soils developed over eruptive substrates (Fuštić and Đuretić, 2000). A more detailed insight into the soil characteristics on the sample plots was obtained through the analysis of collected samples. Soil samples were collected from all sample plots and analyzed in the laboratory of the Biotechnical Faculty of the University of Montenegro in Podgorica. The soils on the experimental plots exhibit a slightly acidic reaction. The measured pH values in the humus horizon of the profiles amount to 5.01, 5.02, 5.44, and 6.2, respectively.

From the aspect of physical properties, these soils are classified as highly skeletal. In the humus layer of all profiles, the sand fraction predominates in comparison to the silt and clay particles.

The average annual air temperature in the investigated part of Biogradska Gora varies between 2 and 3 °C, depending on altitude. The average annual precipitation in the studied area ranges from approximately 1.750 mm in the lower elevations to about 2.000 mm in the higher and eastern parts. During the vegetation period, precipitation amounts to roughly 500 mm to 700 mm (Čurović, 2010).

Data analysis

The study of developmental phases within the life cycle of a natural forest is based on criteria that consider stand structure-diameter, height, and volume structure-as well as volume increment data as the most important characteristics (Podlaski, 2004).

The balanced structure of uneven-aged forests is considered a condition close to the optimal state. In most cases, particularly when balance is determined based on the number of trees per diameter class, the balanced state is defined using mathematical models. To determine the differences between the actual condition and the functionally optimal state of the studied stands, theoretical "normal modes" were constructed. To determine the elements of the normal state, which define the distribution of the number of trees by diameter (K, D), as well as the normal volume (Vn) based on the top stand height (h_{max}), equations for fir (Susmel, 1956) and equations for beech (Colette, 1960) were used.

For silver fir:

$$K = \frac{4.3}{\sqrt[3]{H_{\max}}}, \quad D_{\max} = 2.64 \cdot H_{\max}, \quad V_n = \frac{H_{\max}^2}{3} \tag{1}$$

For beech:

$$K = \frac{4.54}{\sqrt[3]{H_{\max}}}, \quad D_{\max} = 2.33 \cdot H_{\max}, \quad V_n = \frac{H_{\max}^2}{4.23} \tag{2}$$

Where:

K - coefficient of geometric progression

H_{max} - mean height of dominant trees

D_{max} - mean diameter of dominant trees

V_n - normal volume

The obtained parameters are shown in Table 1.

Table 1. Values of parameters K, D_{max}, and V_n

Species	H _{max}	K	V _n	D _{max}
	(m)		(m ³ /ha)	(cm)
Silver fir	38.70	1.27	499.23	102
Beech	32.50	1.42	249.70	76

Timber volume (V) was calculated using volume tables according to the formula:

$$V = n_1v_1 + n_2v_2 + \dots + n_iv_i \tag{3}$$

Where n₁, n₂..., n_i are the number of trees per diameter class, and v₁, v₂...v_i are the volumes of the average trees in each class. The volumes of average trees were calculated using the Schumacher and Hall (1930) function:

$$V = a d^b h^c \tag{4}$$

The coefficient values (a, b, c) for beech, silver fir, and spruce in Montenegro are:

Silver fir: a=0.34388, b=1.89391, c=0.996429

Beech: a=0.32037037, b=1.93358, c=1.0261000

Height curves were generated using the Statgraphics Centurion XV software package, in which several heights-diameter functions were tested. Based on regression and correlation statistical indicators, as well as statistical significance tests of differences between fitted and empirical heights, the optimal function for each case was selected.

For increment determination, due to the strict protection regime, wood samples were taken from fallen trees. Trees of different diameter classes were selected. Due to the small sample size, increment results should be considered indicative. For smoothing diameter increment data in uneven-aged forests, it was used a second-degree parabolic equation. After numerical smoothing using Statgraphics Centurion XV the following equations for diameter increment were obtained:

Silver fir: $id = -0.544361 + 0.162511*d - 0.00158468*d^2$

Beech: $id = 2.85619 - 0.0182725*d + 0.000308783*d^2$

Results

Diameter structure

The distribution of trees by diameter classes is conventionally used to describe stand structure, including unmanaged forests (Keeton, 2006). In mixed beech-silver fir forests at Biogradska Gora, the distribution of trees by diameter (Diameter at Breast Height - DBH) classes are characterized by large variation ranges and the occurrence of several peaks (Table 2).

Table 2. Diameter structure - distribution of trees by DBH classes

DBH	Number of trees/ha		
	Beech	Silver fir	Total
12.5	42.8	9.4	52.2
17.5	27.1	11.5	38.6
22.5	32.4	19.8	52.2
27.5	19.8	14.6	34.4
32.5	24.0	18.8	42.8
37.5	19.8	12.5	32.4
42.5	11.5	7.3	18.8
47.5	14.6	6.3	20.9
52.5	13.6	11.5	25.0
57.5	7.3	5.2	12.5
62.5	6.3	5.2	11.5
67.5	3.1	5.2	8.3
72.5	1.0	4.2	5.2
77.5	2.1	10.4	12.5
82.5	1.0	13.6	14.6
87.5	0.0	5.2	5.2
92.5	0.0	6.3	6.3
97.5	0.0	3.1	3.1
>100	0.0	3.1	3.1
Sum and percent	226.5 (56.7%)	173.2 (43.3%)	399.7 (100.0%)

DBH: Diameter at Breast Height

Such a distribution is typical of stands that have developed naturally and differs from the “J-shaped” distribution characteristic of managed uneven-aged forests.

The distribution of tree numbers shows a low proportion of silver fir in the smallest diameter classes. The total number of trees recorded was 399.7 per hectare, with silver fir accounting for 43.3%.

For a more complex analysis of the current diameter distribution, a comparison was made with a constructed balanced model of tree diameter distributions (Table 3). The theoretical (normal) distribution of the number of trees per diameter classes was determined for the both species separately and for total number of trees.

Table 3. Actual and theoretical distribution of trees by diameter classes

Diameter class (cm)	Beech			Silver fir			Total		
	Actual trees/ha	Theor. trees /ha	Difference	Actual trees/ha	Theor. trees /ha	Difference	Actual trees/ha	Theor. trees /ha	Difference
12.5	42.80	35.48	7.32	9.40	55.97	-46.57	52.20	91.45	-39.25
17.5	27.10	24.94	2.16	11.50	44.04	-32.54	38.60	68.98	-30.38
22.5	32.40	17.53	14.87	19.80	34.65	-14.85	52.20	52.18	0.02
27.5	19.80	12.32	7.48	14.60	27.26	-12.66	34.40	39.58	-5.18
32.5	24.00	8.66	15.34	18.80	21.45	-2.65	42.80	30.11	12.69
37.5	19.80	6.09	13.71	12.50	16.87	-4.37	32.30	22.96	9.34
42.5	11.50	4.28	7.22	7.30	13.27	-5.97	18.80	17.55	1.25
47.5	14.60	3.01	11.59	6.30	10.44	-4.14	20.90	13.45	7.45
52.5	13.60	2.12	11.48	11.50	8.22	3.28	25.10	10.34	14.76
57.5	7.30	1.49	5.81	5.20	6.47	-1.27	12.50	7.96	4.54
62.5	6.30	1.05	5.25	5.20	5.09	0.11	11.50	6.14	5.36
67.5	3.10	0.73	2.37	5.20	4.00	1.20	8.30	4.73	3.57
72.5	1.00	0.52	0.48	4.20	3.15	1.05	5.20	3.67	1.53
77.5	2.10	0.36	1.74	10.40	2.48	7.92	12.50	2.84	9.66
82.5	1.00	0.00	1.00	13.60	1.95	11.65	14.60	1.95	12.65
87.5	-	-	-	5.20	1.53	3.67	5.20	1.53	3.67
92.5	-	-	-	6.30	1.21	5.09	6.30	1.21	5.09
97.5	-	-	-	3.10	0.95	2.15	3.10	0.95	2.15
>100	-	-	-	3.10	0.75		3.10	0.75	2.35
Total	226.40	118.58	107.82	173.20	259.75	-88.90	399.60	378.33	21.27

For the theoretical normal modes in mixed beech–fir forests, the projected ratio was 30% beech and 70% silver fir. The calculated balanced volume for the studied stands was 424.37 m³ ha⁻¹. Figures 3-5 illustrate the comparison between actual tree numbers and the constructed balanced model. The data indicate a pronounced shortage of fir in the smallest diameter classes, disappearing in the mid-diameter classes, and replaced by a surplus of very large trees (>55 cm DBH).

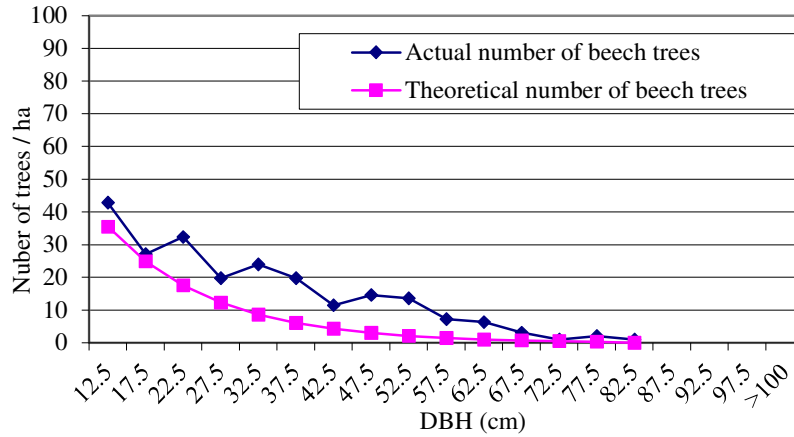


Figure 3. The lines of the current and theoretically normal distribution of beech trees by the diameter at breast height (DBH) classes

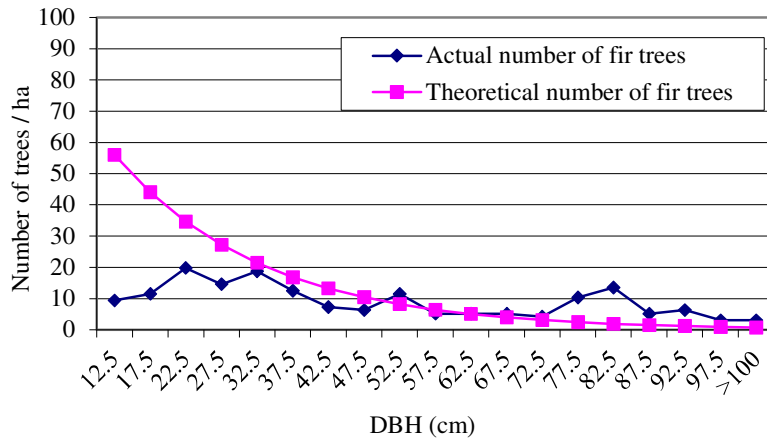


Figure 4. The lines of the current and theoretically normal distribution of silver fir trees by the diameter at breast height (DBH) classes

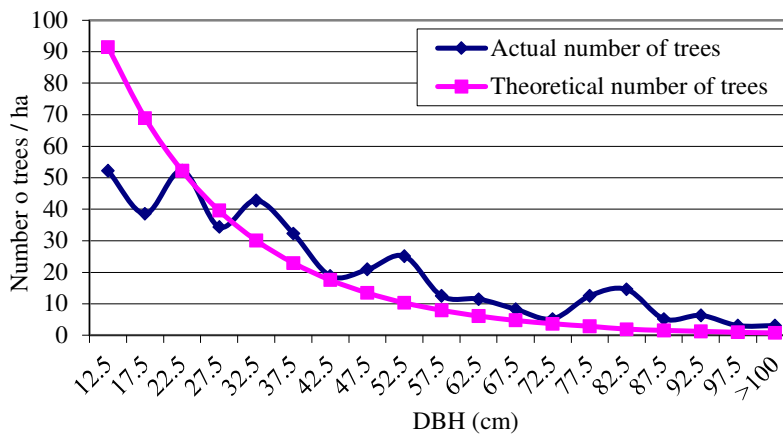


Figure 5. The lines of the current and theoretically normal distribution of trees by the diameter at breast height (DBH) classes

Height structure

The height structure of the stand is represented by the relative distribution of trees across height classes (h), expressed as the percentage of trees within each class (N). The vertical composition – height structure, shows that in addition to two pronounced beech height peaks, the height curve for silver fir is notably jagged, indicating a pronounced multi-layered structure (Figure 6). This suggests the species' tolerance of stratification and its ability to occupy different social and spatial positions due to uneven-aged stand structure.

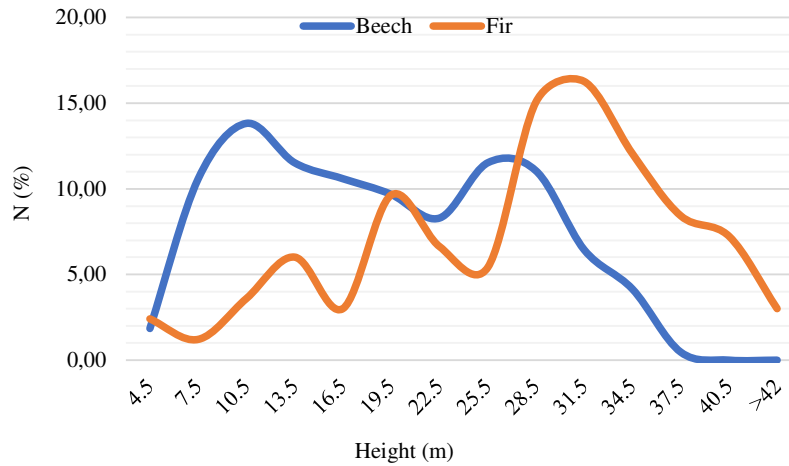


Figure 6. Height structure – the relative distribution of trees across height classes (h), based on the share of the number of trees (N)

This characteristic is valuable in practical forest management when determining the intensity of selective felling for particular diameter steps or classes.

The first dominant upper layer consists mainly of fir, with minimal beech presence, while the second layer contains both species in roughly equal proportions. Among smaller-diameter trees, beech shows clear height dominance, while fir dominates in terms of maximum attained height.

The diameter–height relationship (height curve) represents the functional relationship between tree height (h) and stem diameter at breast height (DBH). This relationship reflects stand structure, site quality, and competition conditions. The ratio of breast diameter to height - height curve (Figure 7), is most often used to determine the habitat index or as an indicator of the development phase of a stand.

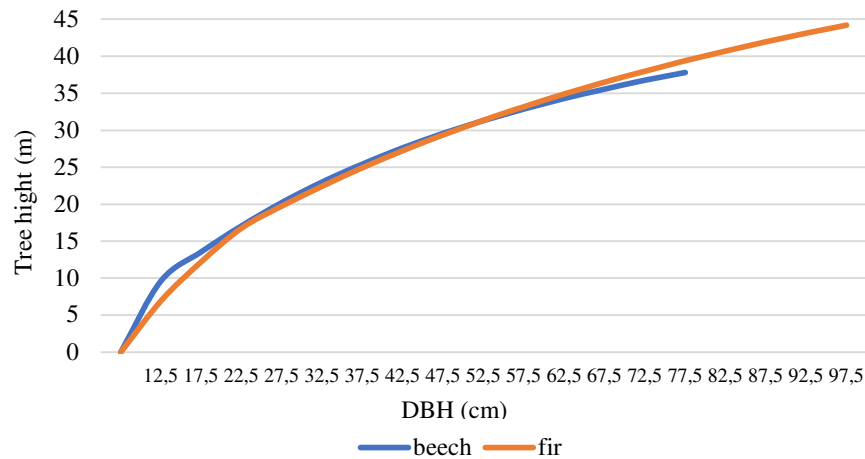


Figure 7. Diameter at breast height (DBH) and tree height relationship - height curve

Volume structure

Volume structure - distribution of the total growing stock by diameter classes and species provides insight into the stand's productive potential, developmental stage, but also carbon sequestration. Timber volume, reflecting the achieved diameters, heights, and stand density, is one of the most important structural elements for assessing the condition of forests and their productivity. On the selected sample plots, timber volumes ranged from 538.28 to 1270.87 m³ ha⁻¹, with an average of 931.5 m³ ha⁻¹. The average proportion of beech in the total volume was 29.4% (Table 4).

Table 4. Volume structure - distribution of the total growing stock by diameter classes and species

DBH (cm)	Volume (m ³ ha ⁻¹)		
	Beech	Silver fir	Total
12.5	2.66	0.53	3.19
17.5	4.07	2.42	6.49
22.5	10.09	7.97	18.06
27.5	10.70	9.88	20.58
32.5	20.41	20.48	40.89
37.5	25.13	21.7	46.83
42.5	21.12	13.96	35.08
47.5	34.86	15.59	50.45
52.5	41.13	35.42	76.55
57.5	24.84	15.16	40.00
62.5	28.23	24.39	52.62
67.5	17.45	27.75	45.20
72.5	6.81	19.33	26.14
77.5	17.16	87.49	104.65
82.5	9.00	122.09	131.09
87.5	0.00	54.84	54.84
92.5	0.00	72.7	72.70
97.5	0.00	44.8	44.80
>100	0.00	61.35	61.35
Sum and percent	273.65 (29.38%)	657.85 (70.62%)	931.50 (100.0%)

DBH: Diameter at Breast Height

Volume increment

Although the limited number of samples may affect accuracy, the values obtained of the volume increment still provide insight into the current productivity of the researched forest. Determined annual volume increment for the mixed fir-beech forests is 10.14 m³ ha⁻¹. The annual volume increment can indicate both, productivity and the developmental stage of the stands studied. The increment of wood biomass is also directly related to carbon sequestration, which represents a measure of exceptional importance for climate change mitigation.

Discussion

The number and distribution of trees by thickness, as well as the ratio of mixed species to wood volume, represent basic structural parameters. In the typological study of forests in Croatia for the ecological-management type *Abieti-Fagetum illyricum* on brown soil, rendzina, and leached rendzina, similar to the studied stands, an optimal beech share of only 30% of total tree numbers was recommended, with harvesting

diameters of 50 cm for beech and 60 cm for fir. The optimal stand volume for this eco-logical unit is 435 m³ ha⁻¹ with a mixture ratio of 70:30% in favour of conifers (Cestar *et al.*, 1986).

Unmanaged forests are characterized by a high number of large and very large trees (Braga *et al.*, 2023). Large trees in old-growth forests are vital for biodiversity, carbon sequestration, and maintaining a healthy ecosystem. They provide unique habitat structures, support diverse species, and contribute significantly to carbon storage, acting as crucial regulators of the global carbon cycle. Protecting these trees is essential for preserving the ecological integrity and resilience of old-growth forests (Lutz *et al.*, 2018).

In the smallest diameter classes, beech fills the gap left by fir and exhibits a more regular distribution. Overall, due to the clear surplus of large fir trees, there is also a surplus of total trees in the largest diameter classes compared to the expected distribution.

The stability of these stands is reflected in the ability of beech to fill canopy gaps caused by tree mortality and the remarkable shade tolerance of silver fir, which can persist for centuries in suppressed conditions, up to 330 years (Pantić *et al.*, 2015). Some analysis showed that beech has significantly larger microhabitat values compared to fir, which indicates the importance of all tree species present in the stands, as well as their structure for biodiversity preservation (Martać *et al.*, 2025). Studies of old-growth forests are also important for better understanding environmental changes such as a synchronous silver fir decline. The lack of young fir recruitment suggests a gradual shift toward beech dominance; a trend observed in other old-growth beech-fir forests across the Dinarides and Carpathians (Vrška *et al.*, 2009; Diaci *et al.*, 2011; Diaci *et al.*, 2022; Bilić *et al.*, 2025).

When it comes to elements of the height structure the principle of site class determination based on tree heights is difficult to apply in the study area because old-growth forests usually have a multi-layered structure (Govedar *et al.*, 2018). The site index based on the height-diameter relationship in uneven-aged old forests is not a reliable indicator of site potential. In this context, knowledge of multiple structural characteristics provides a more complex and reliable measure of site quality and productivity.

For comparison of volume structure, in beech-fir communities in Slovenia, the average timber volume is 336 m³ ha⁻¹, with a high share of large-diameter trees (>50 cm DBH) (Boncina *et al.*, 2002). In Gorski Kotar, Croatia, volumes range from 405-445 m³ ha⁻¹, with a surplus of large-diameter trees and a notable shortage of small-diameter fir trees (Cavlovic *et al.*, 2021).

In the Southern Carpathians' virgin fir-beech forests, average volume is 893.1 m³ ha⁻¹ (Braga *et al.*, 2023), while in the Western Carpathians, values above 660 m³ ha⁻¹ are common (Parobekova *et al.*, 2018). In Bosnia and Herzegovina, old mixed beech-conifer forests show volumes ranging from 747-1201 m³ ha⁻¹ (Motta *et al.*, 2024), confirming the high growing stock potential of such forests in the Dinarides.

Examples of exceptional annual increment for this forest type are numerous. In Croatia, projections for normal stands range from 6.7-13.1 m³ ha⁻¹ depending on species composition (Cestar *et al.*, 1986). On Mountain Goč, in Serbia values range from 10.2-14.4 m³ ha⁻¹ (Obradović *et al.*, 2018). Exceptional productivity is also recorded in Serbia in National Park "Tara", where with an average of 456 trees per ha, the average volume is 709 m³ ha⁻¹, and the current increment is 15.9 m³ ha⁻¹ (Medarević, 2005).

All of the above data indicate that old-growth forests of silver fir and beech in the Dinaric region represent extremely valuable forest objects that should receive special attention in the coming period. Information related to the structural characteristics of primary mixed forests can be very important from the aspect of stability and resilience to climate change. Monitoring the state and processes in intact forests such as Biogradska Gora will undoubtedly provide significant inputs for creation of closer to nature forest management models.

Conclusions

This study provides a unique overview of the structural characteristics of old-growth silver fir-beech forests in Biogradska Gora, one of the last remaining untouched forests in Europe. The structural characteristics of old-growth forests provide a robust reference framework for the implementation of sustainable, close-to-nature forest management practices.

In terms of diameter structure, the mixed montane old-growth forests of the Biogradska Gora are characterized by a slightly low number of trees per unit area. Beech shows a relatively regular J-shaped diameter distribution matching the theoretical normal curves, while fir is underrepresented in the smallest diameter classes. In the height structure, stratification is pronounced, with fir dominating in maximum height attainment. The lack of fir in tree numbers is not reflected in the volume structure, due to the presence of large-diameter fir trees. Analysis of the current volume increment and its comparison with similar stands confirms the exceptional carbon sink potential of Biogradska Gora's Forest ecosystems. The study provides good base for further research into the development processes of these globally valuable and unique forest communities. Future research should focus on long-term monitoring of structural dynamics and regeneration processes to better understand the natural development trajectories of these forests under changing environmental conditions.

Authors' Contributions

Conceptualization: MC, MM; Field work: MC, MM, RM; Methodology: MM.; Data analyses and manuscript writing: MC, MM, DB, MG; Visualization MC, DB; Supervision and editing: RM; Resources: MC, MG.

All authors read and approved the final manuscript.

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Conflict of Interests

The authors declare that there are no conflicts of interest related to this article.

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