

Lack of large-diameter living trees and low structural diversity characterise managed dry-mesic oak forests in the Hungarian Carpathians

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ABSTRACT

Oaks are the dominant species of a wide range of forest types and are of great ecological, economic and cultural importance. Forest structure and composition have a major influence on forest function and biodiversity. It is a core determinant of naturalness, carbon storage and can be an important goal for forest management. We investigated the composition and structure in five age classes of dry-mesic oak forests in the Hungarian Carpathians. We collected standardised data from different stands and compared the structure (density, basal area, regeneration, dead wood, size distribution) and composition of oak forests among different age classes (40–165 years) and by management type (managed – abandoned). The effect of age class on the derived variables was analysed using general linear mixed models with age class as a fixed effect and region as a random effect. Oaks dominated all age classes in the canopy layer, with the combined relative basal area of oaks ranging from 95 % to 99 %. The composition of the understorey was very different from that of the canopy, with oak not dominating either the sapling or seedling size classes in any of the age classes. The diameter at breast height (DBH) range for age classes younger than 120 years old exceeds 28 cm on average, while in the oldest age class it reaches 45 cm. It is notable that large trees (DBH > 60 cm) are practically absent from the managed dry-mesic oak stands. The mean number of large trees per hectare was found to be 0.2 for all managed stands, while in the abandoned stands (with an age of over 120 years old) it was close to 5 trees per hectare. The diameter distribution of managed age classes exhibits a bell-shaped curve, whereas stands exceeding 120 years of age display a double-peak pattern, with the lower secondary peak occurring within the 35–40 cm diameter range. In order to facilitate the transition of dry-mesic oak forests towards a more natural state, it is crucial to ensure the preservation of intact areas and habitat trees, in addition to implementing appropriate techniques for their regeneration following felling. It is recommended that retention patches cover a percentage of the total area that is between 5 % and 25 %. Without leaving such immature patches, large trees will continue to be absent from dry-mesic oak forests in Hungary.

1. Introduction

Quercus is among the most important genera in the northern hemisphere, with at least 400 deciduous, semi-evergreen and evergreen species (e.g. Schwarz, 1964; Nixon, 1997, 2006; Menitsky, 2005). Many species grow into large trees, but there are also many shrubs and small trees, with most species found in North and Central America and East Asia. Oaks have also great ecological, economic and cultural importance. They are the dominant species of a wide range of forest types, from temperate deciduous to evergreen subtropical forests, but also occur in other vegetation types such as pine forests, temperate and

subtropical forest-grassland mosaics. Oaks are often long-lived species, living for up to 900 years (Leuschner and Ellenberg, 2017), and thus they are associated with a wide range of other organisms, primarily with consumers (Mölder et al., 2019), such as insects (Brändle and Brandl, 2001; Csóka and Szabóky, 2005), but also forest herbivores and fungi (Leuschner and Ellenberg, 2017; Nitare, 2000). Oaks are also closely linked to the material and spiritual part of human culture, their wood has been used by humans for thousands of years and their cultural significance is high (Gil-Pelegrín, 2017, Johnson et al., 2019).

In Hungary, four species of oaks are native and occupy large areas (*Q. robur*, *Q. petraea*, *Q. cerris*, *Q. pubescens*), and the native status of one

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other species (*Q. frainetto*) with a sporadic distribution is doubtful. *Q. cerris* forms dry-mesic stands together with *Q. petrae* (91M0 Pannonian-Balkan turkey oak-sessile oak forests, Bölöni et al., 2011) on the hillsides and the southern slopes of the mid-mountains at 200–700 m a.s.l. The national extent of this forest type is min. 120, 000 ha, which is 6.5 % of the national forest area, 2/3 of which is located in the Hungarian Carpathians.

The structure and composition of forests exert a significant influence on their functional capabilities and biodiversity (Oliver and Larson, 1996; Paillet et al., 2019). In this context, the role of large trees is of particular significance (Martin et al., 2001; Rambo and North, 2009; Lutz et al., 2018). These attributes are fundamental determinants of forest naturalness and natural forest conditions (Peterken, 1996; Lindenmayer et al., 2012) and capacity for carbon storage (Keeton, 2018; Keith et al., 2024), and thus could be important considerations in forest management. Examination of the structure and composition of the lower layers is particularly important for the possibility of compositional changes in the absence of disturbances that promote oaks, and it is also typical of old-growth oak stands that the relative density of oaks in the canopy and lower layers can vary considerably (Bölöni et al., 2021).

Forest management has a fundamental influence on forest composition and structure (Bengtsson et al., 2000; Decocq et al., 2004, 2005; Tárrega et al., 2006; Schweitzer and Dey, 2011). In the Middle Ages and the Early Modern Period in the oak forests of Hungary the main silvicultural system was coppicing or coppicing with standard accompanied by intensive masting, grazing and firewood collection (Járás, 1997; Szabó, 2005; Johann et al., 2011). As the result of the first Forest Law introduced in Hungary in 1879 the forest use has changed to a uniform shelterwood silvicultural system and the majority of oak forests were converted into high forests. In oak management, both at the level of principles and practice, the aim was to achieve homogeneous stands of the same age. This included successive schematic cleanings every 10–20 years, followed by thinnings. The regeneration was made artificially after clear cutting or based on natural regeneration using shelterwood system, in this case the regeneration period was short (2–5 years). The most common forest management currently used in dry-mesic oak forests in the Hungarian Carpathians is shelterwood system based on one preparation and a final cutting. The typical rotation period of dry-mesic oak forests became 80–100 years, the higher cutting age is quite rare (Danszky, 1972; Savill, 2004), the forest regeneration period is 2–10 years, most often 3–5 years (Csontos, 2010).

The species composition of forests dominated by *Q. cerris* and *Q. petraea* is well documented by botanists in the Carpathian Basin (Coldea and Pop, 1996; Chytrý, 1997; Roleček, 2005, 2007), including Hungary (e.g. Borhidi et al., 2013). However, the structural and dynamic characteristics of such forests are much less well understood. The first few decades of succession of dry-mesic oak stands dominated by *Q. cerris* and *Q. petraea* under forest management have been studied by Csontos (1996), (2010). However, these studies focused on only the changes of herb layer and not on tree layers. There are no studies comparing the stand structure of these managed stands with the natural or near-natural dry-mesic oak forests from the studied region. There are studies on the natural-like dynamics of dry-mesic oak forests in Hungary in only one small area, the so-called Síkfőkút Project at the foothills of the Bükk Mountains, Heves County (Jakucs and Papp, 1974; Kotroczó et al., 2007), the research here concern only one stand in a relatively small area.

The paucity of data on the structure and dynamics of primary dry-mesic oak forests is partly due to the almost complete absence of reference stands. Such “primeval forest stands” are practically non-existent in our country and hardly found in Europe (Korpel, 1995; Saniga and Schütz, 2002; Jasfik and Polák, 2011). There is practically no forest in Europe that has not been affected by at least indirect or low-intensity human impacts (Peterken, 1996). The lack of references on the stand structure of semi-dry oak forests is well reflected in the review published in 2021 (Bölöni et al., 2021), from the 180 reference

old-growth stands only 10 was selected from Europe.

We have been studying managed and abandoned oak stands, especially the dry-mesic type, for a long time in the framework of several projects. We have previously summarized our results on dead wood (Bölöni et al., 2017) and the effect of stand structure on herb layer (Ádám et al., 2013, 2018), and now we present the most important results of our research on tree stand composition and structure. The aim is to provide a general description of the structure and composition of the dry-mesic oak forests dominated by *Q. cerris* and *Q. petraea* of the Hungarian Carpathians. We collected standardized data from different stands and compared the structure (density, basal area, regeneration, dead wood, size distribution) and composition of oak forests among different age classes (40–165 years) and by management type (managed - abandoned). It was assumed that the composition and structure of the tree stand would differ between age classes and treatment types, and that there would also be differences from natural (old-growth) stands. Our main questions focused on this:

1) Is there a detectable difference between stands of dry-mesic oak forests of different ages and management types according to key structural and compositional variables?

2) Which structural and compositional variables show the greatest differences between the studied stand types?

2. Study area and methods

2.1. Study area

This study was conducted on the Hungarian Carpathians, in Northern Hungary. This range is covered of various dry to mesic forest types mainly characterised by oaks, hornbeam, and beech. We examined 40–165 year old managed and abandoned oak dominated dry-mesic forest stands, which can be classified as Natura2000 91M0 Pannonian-Balkan Turkey oak-sessile oak forests dominated by *Q. petraea* and *Q. cerris* (European Commission DG Environment, 2013). This kind of dry-mesic oak forests create a forest belt between 200 and 700 m a.s.l. in the Hungarian Carpathians. Study sites are in Pilis, Börzsöny, Cserhát, Mátra and Bükk Mountain Ranges, at various aspects (Fig. 1.). The climate of this area is classified as warm summer humid continental with a mean annual precipitation of 600–700 mm. The mean annual temperature is 8–10 °C. The bedrock is mainly volcanic (andesite and andesite tufa), but limestone, sandstone, shale and loess bedrock types are also present, on which mostly leptosols and cambisols of various depth have developed (Krasilnikov et al., 2009).

2.2. Field methods

The study focused on managed dry-mesic oak forest, the inclusion criteria for the stands was, that the combined relative volume of *Q. cerris* and *Q. petraea* should be at least 80 %, and the maximum relative volume of shade tolerant tree species of mesic forests (e.g. *Carpinus betulus*, *Fagus sylvatica*, *Tilia* spp.) was less than 5 %. Forest subcompartments satisfying this criteria were selected from the National Forest Stand Database (NFK, 2022). The investigated stands were selected from this pool based on stratified random selection using age categories and geographical region as stratification criteria. Based on our previous field knowledge and the database, we also selected 8 unmanaged, abandoned stands older than 120 years (Bölöni et al., 2017). Then all the selected stands were classified according to the age of the dominant trees and management status. We defined the following managed age classes: age class 1: 40–59 years old, age class 2: 60–79 years old, age class 3: 80–99 years old, age class 4: 100–119 years old and an unmanaged age class 5: 120–165 years old. The size of the stands ranged from 5 to 50 ha. In smaller stands (5–15 ha) 2–8 sample plots, in stands larger than 15 ha at least 10 sample plots were designated to collect data on stand structure for the study. The minimum distance between the centre of sampling plots and minimum distance from roads to avoid edge effect was 50 m.

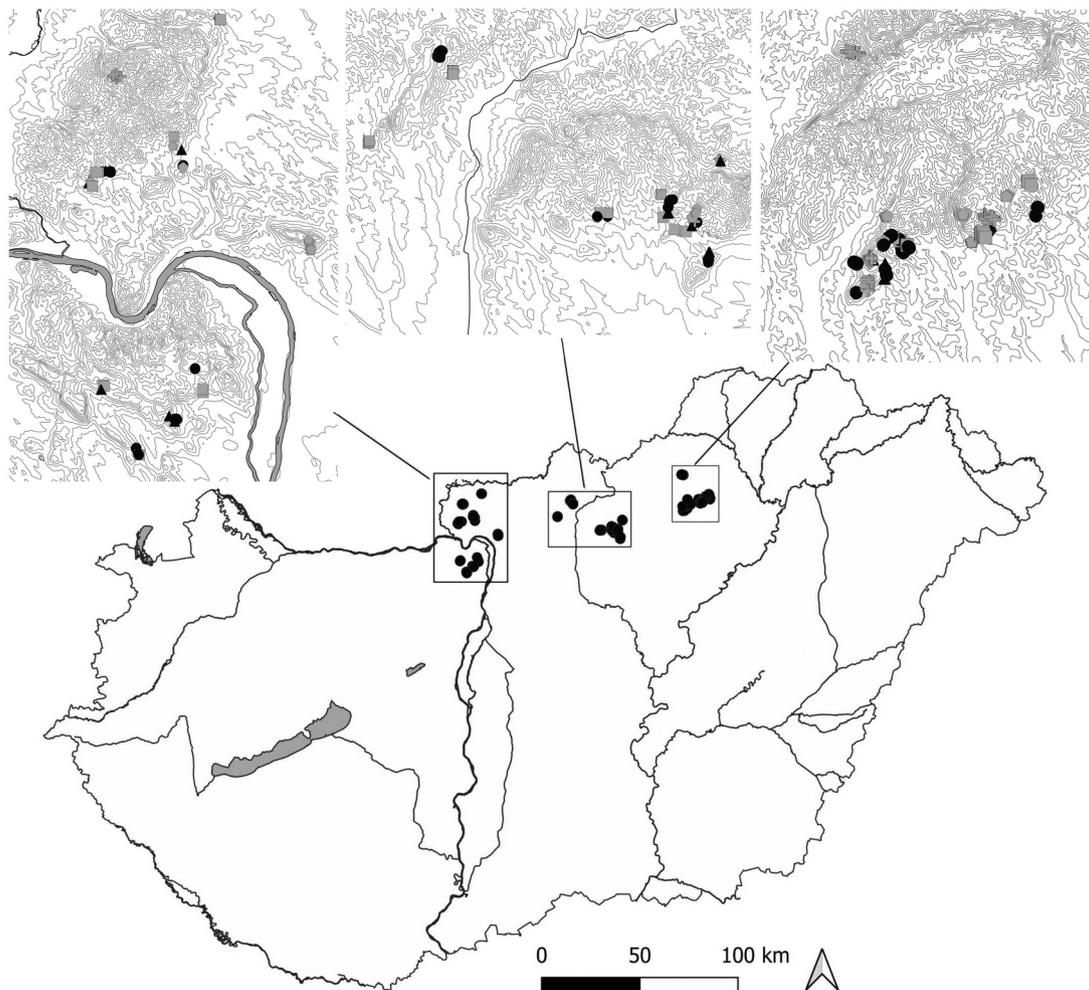


Fig. 1. Study sites in three regions of the northern Hungarian Carpathian Mountains (1 – Pilis – Börzsöny; 2 – Cserhát – Mátra; 3 – Bükk). Legend: Black triangle = age class 1, black dots = age class 2, grey squares = age class 3, grey pentagons = age class 4, grey crosses = age class 5.

Finally, in total of 378 managed (age class 1–4) and 160 abandoned (age class 5) sample plots were recorded between 2009 and 2020 (Table 1). The sampling plots were geographically separated in three regions, but almost all categories were represented with similar stand number in each region (Fig. 1). This approximately balanced design was not possible for abandoned stands because of their limited number in most regions, they showed an aggregated pattern and became therefore over-represented in one region.

The survey method of canopy layer (DBH – diameter at breast height larger than 5 cm) varied within the study, because we use data from different projects. However, in each protocol the density of trees in different tree species and DBH categories were converted to the same unit (individual/hectare). The field surveys were the followings: 1) All trees were measured within a circle of the same radius where the radius (R) was 12.62 m or 15.96 m, which varied according to tree density

(stand age); 2) Combined sampling used in the Hungarian Forest Reserve Programme (Horváth et al., 2012), where a circle of R= 9 m was used to survey trees with DBH< 25 cm, then in the case of larger trees a point relascope method with a factor 2 prism relascope was used to identify trees added to the sample. 3) Concentric circle sampling method used in the LIFE4Oak Forests project (<https://www.life4oakforests.eu/>), in that trees with DBH between 5 and 40 cm were surveyed in circular plots with R= 9 m or R= 13 m (depending on tree density and stand age), while trees with DBH> 40 cm were added to the sample based on a 20 m radius circle. Both dead and living trees were measured in each sampling plot. For each individual living and dead trees, species and DBH of all trees were recorded. The downed dead wood was surveyed according to the line intercept sampling method (Ståhl et al., 2001) along 3 lines of 16/20 m length, with the lines oriented at 0, 120 and 240 degrees. Species and diameter of downed dead wood (diameter min. 5 cm, length min. 50 cm) were recorded in each intersection point. The decay stage of dead wood were also evaluated on an ordinal scale (I-V, Spetich et al., 1999).

The species and densities of DBH< 5 cm and height > 1.3 m woody understory trees and shrubs were recorded using circular plots (R=6 m) nested within the basic plots. Four additional circular plots of 2 m² size were located 6 m from the centre along the cardinal compass directions to survey the low understory layer (height 0.5–1.3 m), where seedlings were counted.

Table 1
Distribution of sampling plots by regions and age classes.

Region	Pilis - Börzsöny	Cserhát - Mátra	Bükk	Total
Age, years				
40–59	14	15	13	42
60–79	16	68	51	135
80–99	17	37	56	110
100–119	37	21	33	91
120–165	27	15	118	160
Total	111	156	271	538

2.3. Data analysis

In the evaluation, trees with DBH > 10 cm were considered as overstorey, this DBH threshold is the most widely used in other studies focused on the structure of oak dominated forests. Trees smaller than this DBH are classified as understorey, in two size classes. Trees and shrubs with DBH < 10 cm but height > 1.3 m were treated as sapling layer. Trees and shrubs 0.5–1.3 m tall were considered as seedlings. Overstorey and understorey layer were analysed using standard variables. For the overstorey we calculated density (number of stems/ha), relative density of tree species (contribution to total trees), basal area (m²/ha), relative basal area. The density of large trees (DBH > 60 cm) were also analysed. For the understorey we calculated density and relative density of tree species. DBH range (max. – min. DBH) and Gini coefficient (Gini, 1912) were also trained to evaluate canopy structures. The Gini coefficient, expressing tree size diversity, was found superior with comparing the DBH structures of different stands (Lexerød and Eid, 2006). We computed Gini coefficient at both plot and age class level from the corresponding DBH distribution. The DBH range and Gini coefficient were used on plot-by-plot basis to describe the structural heterogeneity of each plot, and the aggregated Gini coefficient was used for the comparison of age classes. The species composition was compared using species richness and exponential Shannon-Weaver diversity index (Shannon and Weaver, 1949). For understorey layer we calculated density, relative density and species richness.

The sample plots were represented by their centre points. The measurement of variables was sampled by different methods, yet all data were referenced to the plot centre. Plots were utilised as the basis for analysis and evaluation. The potential for bias in the results due to variations in the size of the sampling areas was considered, but this was deemed negligible on account of the minimal discrepancy in area and the observation of a homogeneous structure. The analysed derived variables and their units are listed in Tables 2, 3 and 4. The effect of age class on the derived variables was analysed by general linear mixed models (Faraway, 2006) using age class as a fixed and region as a random effect. Three Regions were used (1 - Pilis – Börzsöny, 2 - Cserhát – Mátra, 3 – Bükk, Fig. 1.), which were geographically based, with a region containing all mountain ranges with similar bedrock structure within 25 km. The normality and variance homogeneity of the model residuals were checked, for some dependent variables “ln” or square root transformation were used to fulfil the normality criteria of the residuals. Gaussian error structure was used for the models, except for large tree (DBH > 60) density (negative binomial) and for species richness variables (Poisson). The significance of the fixed factor was tested by maximum likelihood method, and the random factor by restricted likelihood method using chi-square tests (Faraway, 2006; Zuur et al., 2009). In case of significant fixed (age class) effects the differences between the age classes were analysed by Tukey HSD multiple comparisons (Faraway, 2006). The analyses were carried out in R 4.2.2 statistical environment (R Core Team, 2022) using the “lattice” (Sarkar, 2008), “multcomp” (Hothorn et al., 2008), “emmeans” (Lenth, 2023), “lme4” (Bates et al., 2015) and “nlme” (Pinheiro et al., 2015) packages. Nomenclature follows Tutin et al. (1964–1993).

3. Results

3.1. Overstorey structure and composition

3.1.1. Structure of the overstorey by plot level

The average density of overstorey trees clearly decreases with age (Table 2.), reaching more than 1100 stems per hectare in the age class 1 and barely more than 300 stems per hectare on average in the age class 5. The average basal area varies between 26.31 and 29.13 m²/ha across the age classes, it is marginally significant (only age class 4 and 5 differed), without any trend among age classes. All the characteristics describing the stand structure suggest that the structural diversity

Table 2 Structural characteristics of overstorey trees (DBH > 10 cm) by age classes in dry-mesic oak forests of the Hungarian Carpathians and the statistics (F or Chi² and p values) of the general linear mixed models. Values are means ± standard deviations. Different letters indicate significant differences based on multiple comparisons between age classes. BA = basal area; GINI = Gini coefficient calculated based on DBH > 10 cm trees; TDW = total dead wood.

Stand type	1		2		3		4		5		transform	F	Chi ²	p
	40-59	60-79	80-99	100-119	120-165	160								
Number of plots	42	135	110	91	91	160	312	157	312	27.01	Gaussian	126	82.7	<0.0001
Density, stem/ha	1157	584	428	359	359	157	312	157	312	27.01	Gaussian	126	82.7	<0.0001
BA, m ² /ha	26.31	27.18	28.27	29.13	29.13	6.91	27.01	6.91	27.01	6.32	Gaussian	2.8	0.0275	0.0275
DBH mean, cm	17.1	24.7	28.8	32.6	32.6	4.6	32.7	4.6	32.7	7.4	Gaussian	102	<0.0001	<0.0001
DBH range	14.6	20.6	26.7	27.3	27.3	8.6	45.0	8.6	45.0	19.8	Gaussian	110	<0.0001	<0.0001
DBH max	26	42	43	48	48	7.5	63	7.5	63	18.4	Gaussian	206	<0.0001	<0.0001
DBH absolute max	40	64	69	79	79	2.5	4.70	2.5	4.70	7.8	Negative binomial	41	<0.0001	<0.0001
Density DBH > 60 cm, stem/ha	0	0.05	0.22	0.61	0.61	0.07	0.35	0.07	0.35	0.14	Gaussian	17	<0.0001	<0.0001
GINI	0.22	0.06	0.24	0.22	0.22	27.3	45.1	27.3	45.1	53.1	Gaussian	17	<0.0001	<0.0001
TDW volume, m ³ /ha	16.2	9.1	12.2	17.0	17.0	18.4	25.4	18.4	25.4	53.1	Gaussian	17	<0.0001	<0.0001

Table 3
Compositional characteristics of overstorey trees (DBH>10 cm) by age classes in dry-mesic oak forests of the Hungarian Carpathians and the statistics (F or Chi² indices and their p values) of the general linear mixed models. Values are means ± standard deviations. Different letters indicate significant differences based on multiple comparisons between age classes. H exp= exponential Shannon-Weaver diversity index; BA=basal area. Number of species is based on the field sampling directly, while other variables are converted to 1 ha sized plots.

Stand type	1		2		3		4		5		F	Chi2	p											
	40-59	42	60-79	135	80-99	110	100-119	91	120-165	160														
Number of tree species	2.62	ab	1.54	1.94	a	±	1.00	2.41	ab	±	1.15	1.99	a	±	1.02	2.80	b	±	1.70	Poisson	ln	18.4	0.001	
H exp tree species	1.73	ab	0.80	1.51	a	±	0.68	1.81	ab	±	0.75	1.58	a	±	0.67	2.21	b	±	1.19	Gaussian	ln	7.6	<0.0001	
Oak relative density, %	95.8	a	±	9.1	96.2	a	±	9.5	92.8	a	±	11.6	95.2	a	±	9.2	84.5	b	±	19.8	Gaussian	ln	14	<0.0001
Oak relative BA, %	96.1	ab	±	8.3	98.6	a	±	5.7	97.8	a	±	4.7	98.8	a	±	2.5	94.8	b	±	7.1	Gaussian	-	9	<0.0001

Table 4
Characteristics of understorey trees and shrubs (DBH<10 cm and height>50 cm) by age classes in dry-mesic oak forests of the Hungarian Carpathians and the statistics (F and Chi² indices and p values) of the general linear mixed models. Values are means ± standard deviations. Different letters indicate significant differences based on multiple comparisons between age classes.

Stand type	1		2		3		4		5		F	Chi2	p											
	40-59	42	60-79	135	80-99	110	100-119	91	120-165	160														
Sapling density, stem/ha	1873	a	±	1622	1843	ab	±	1955	2087	a	±	1978	1263	b	±	2043	1937	a	±	1748	Gaussian	sqrt	4.168	0.0025
Seedling density, stem/ha	5507	ab	±	5131	3957	ac	±	4968	4774	ac	±	6097	2457	c	±	2853	6962	b	±	6784	Gaussian	sqrt	10.212	<0.0001
Species number, saplings	4.71	a	±	2.61	3.84	b	±	2.93	4.80	a	±	2.82	2.48	c	±	2.52	3.98	b	±	3	Poisson	ln	60.377	<0.0001
Species number, seedlings	3.55	a	±	2.38	2.58	b	±	2.19	2.67	b	±	2.52	1.87	c	±	1.73	3.78	a	±	2	Poisson	ln	73.110	<0.0001
Oak relative density, saplings	27.9	a	±	31.3	10.4	b	±	23.7	10.8	b	±	24.6	7.7	b	±	21.6	11.5	b	±	23	Gaussian	sqrt	9.895	<0.0001
Oak relative density, seedlings	14.4	a	±	28.7	12.6	a	±	26.9	8.3	a	±	22.7	11.8	a	±	23.5	7.9	a	±	19	Gaussian	-	0.782	0.537

increased with age. The average DBH is 17 cm in age class 1, and close to 33 cm in the two age classes over 100. The average DBH range is smallest in age class 1 and largest in age class 5 - while in age class 1–4 it never exceeds 28 cm on average, in age class 5 it reaches 45 cm. The average and absolute DBH of the largest tree also follows this trend. Density of large trees (DBH > 60 cm) show a strongly increasing trend with age, it never exceeds 1 tree/ha in class 1–4, while in age class 5 it is close to 5 trees/ha. Average of the Gini index for the diversity of diameter classes is below 0.25 in the age classes 1–4, while it is significantly higher (0.35) in age class 5. Total deadwood volume also increases with age, averaging 25 m³/ha in age class 4 and 45 m³/ha in abandoned stands (age class 5).

3.1.2. Structure of the overstorey by age classes

The increasing structural variation with age is also reflected in the DBH distribution of age classes and the resulting aggregate Gini coefficient (Fig. 2.). Age classes 1–4 have a bell-shaped diameter distribution, while age class 5 has a double peak, with the lower second peak occurring in the 35–40 cm diameter class. The aggregate Gini coefficient ranges from 0.27 to 0.31 in the managed age classes (1–4) and 0.45 in the age class 5. In the smaller size classes (between 10 and 20 cm), the densities clearly decreases with stand age in age class 1–4, while in age class 5 the density of this size category is high again. However, the total density of DBH above 20 cm varies in a bell-shaped pattern, being lowest in the age class 1 and age class 5 (Fig. 2.).

3.1.3. Overstorey composition

A total of 31 species were found in the overstorey layer. The average number of species varied between 1.9 and 2.8, with the highest in the age class 5 and the lowest in age classes 2 and 4 (Table 3). Shannon-Wiener diversity index showed a similar trend than tree species richness. In general, oaks dominated all age classes, the combined relative basal area of *Q. cerris* and *Q. petraea* is between 93 % and 98 %, and the combined relative basal area of all oaks is between 95 % and 99 %. Of

the other tree species, *Acer campestre*, *Sorbus torminalis*, *Carpinus betulus*, *Fraxinus excelsior*, *F. ornus* have a higher proportion in some age classes, but none of them reaches 9 % relative density and 2 % relative basal area (App.). Thus, the aggregate relative density and basal area of the admixed tree species are low, but both are significantly higher in age class 5 than in age class 1–4 (Table 3). In the DBH distribution, oaks dominate the size classes larger than 20 cm, while the majority of the admixed trees are concentrated in the thin size classes of 10–20 cm (Fig. 2). Only in age class 5, there are relatively large numbers of admixed tree species over 20 cm in DBH.

3.1.4. Understorey density and composition

The density of saplings is similar in the age classes (1800–2100 stems/ha), except for age class 4, where it is slightly lower, not reaching 1300 stems/ha on average (Table 4). The pattern is very similar for the seedlings, only the mean densities are higher, around 2500 stems/ha in the age class 4, and between 4000 and 7000 stems/ha in the others. Species numbers are similar in the sapling and seedling size classes, with the exception of age class 4 (100–119 years old), where species numbers are lower than for all other age classes (Table 4). The composition of the understorey layer differs considerably from the overstorey. Oaks do not dominate in either sapling or seedling size classes in any age class, and the relative density of oaks only reaches 20 % in the sapling layer of the age class 1. A total of 37 species were found in the understorey (App.). In the saplings layer, *A. campestre*, *Crataegus* spp., *Ligustrum vulgare*, *Cornus mas* and *F. ornus* have a relative density higher than 10 %. At the seedling level, the most common species are *L. vulgare* and *F. ornus*, but other shrub species (*C. mas*, *Crataegus* spp., *Rosa canina*) and *A. campestre* also play a significant role.

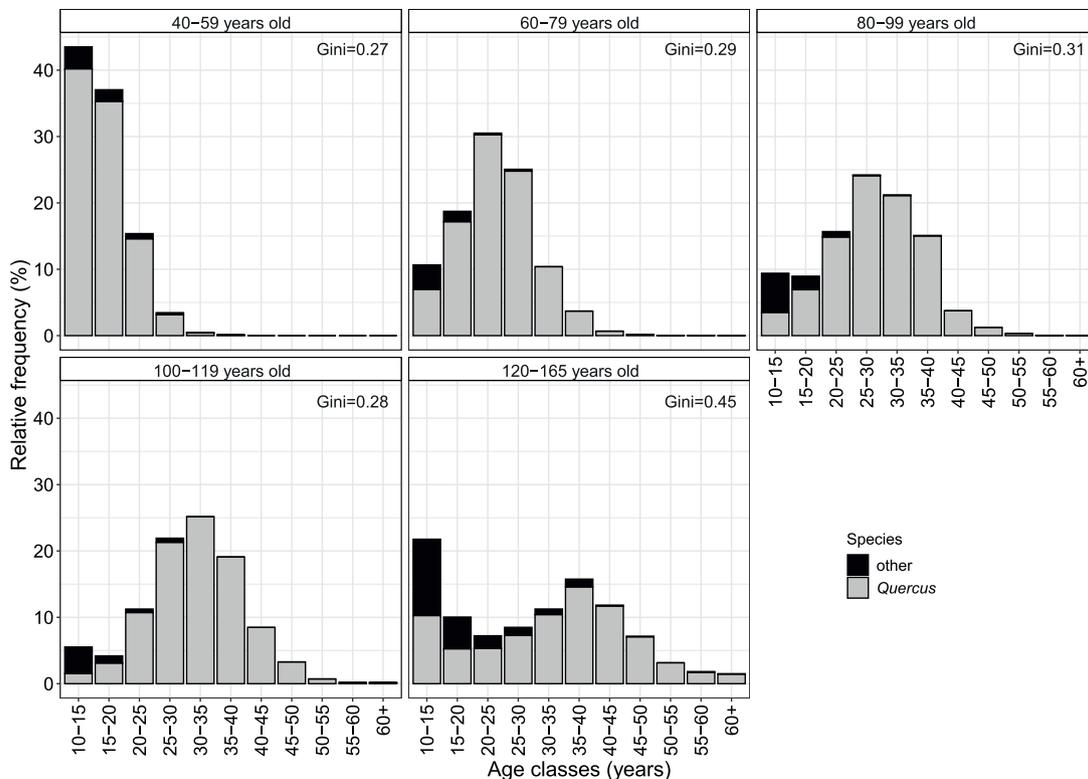


Fig. 2. Relative density (%) of living overstorey trees (DBH > 10 cm) and aggregate Gini coefficient in different age classes in dry-mesic oak forests of the Hungarian Carpathians. Grey and black colour indicate oaks and other tree species, respectively.

4. Discussion

4.1. Large trees

The most striking difference between the age classes in the dry-mesic oak stands in the study areas was the density of large trees with DBH > 60 cm. Such large trees were conspicuously rare in the stands studied. Large trees are practically absent from the dry-mesic oak stands in the managed upland-hills. We found an average of 0–0.6 large trees/ha per age class, which is 0.2 trees/ha for all managed stands. Out of 378 plots, a total of 10 plots were found with at least one tree with DBH > 60 cm. In the studied unmanaged dry-mesic oak stands (age class 5), 40 % of the 160 plots have large tree or trees, with an average number of large trees much higher than in managed stands, approaching 5 trees/ha.

There is no complete consensus on what is considered a large tree. In cold, continental forests, a large-diameter tree may only be 20 cm DBH (Baltzer et al., 2014). In productive tropical or first of all temperate forests, a large-diameter tree may be DBH > 100 cm (Lutz et al., 2012, 2013). In the present work, we considered trees with DBH > 60 cm as large trees, based on Lutz et al. (2018), because this was the best way to compare our data with other stands.

Density of large trees is related to productivity, and in more favourable site conditions, the density of large trees is usually higher in natural referenced forests. Thus, under natural conditions, relatively fewer large trees per hectare can be expected in dry-mesic oak forests than in mesic ones. But the mean density of 0.6 or even 5 trees/ha found in our study is much lower than the mean density of large trees in temperate deciduous old-growth forests (Bölöni et al., 2021). In Europe, we found data on large trees in dry-mesic old-growth oak stands from only two locations, Portugal (Carvalho, 2011) and Slovakia (Saniga et al., 2014). These two papers reported an average of 17 trees/ha DBH > 60 cm, based on a total sample area of 2.1 ha. In the Slovakian stand (Boky Forest Reserve) we found more than 21 large trees per hectare covering a larger total area, with a total sample area of 8 ha (unpublished information). There is much more data from the eastern half of the USA, where the number of large trees in the dry-mesic old-growth oak forests in a total sample area of 37.5 ha varies between 4 and 59 trees/ha, with an average of 21 trees/ha (Table 5.). Similar densities of 24 trees/ha with DBH > 60 cm have been detected at ForestGEO sites in the temperate belt, with a total sample area of more than 100 ha (Lutz et al., 2018).

The role of large trees is very important, they modulate stand-level leaf area, microclimate and water use (Martin et al., 2001; Rambo and North, 2009). Previous studies have showed that large-diameter trees comprise a large fraction of the biomass of many forests (Clark and Clark, 1996; Lutz et al., 2012, 2018; Bastin et al., 2015). If the minimum DBH is 1 cm, 1 % of the trees contain 50 % of the biomass (Lutz et al., 2018). Large size and longevity make trees with DBH > 60 cm particularly important for carbon storage, and small- and medium-diameter trees are not suitable even if they are present in large numbers (Lutz et al., 2018). They contribute the largest carbon stock in primary forests (Keith et al., 2024). There are a high number of different microhabitats on old trees, and their bark is becoming increasingly suitable for the colonisation of various epiphytic species (Paillet et al., 2019). They are associated with many organisms and are therefore of particular importance for the biodiversity of tree-associated organism groups (fungi, lichens, mosses, saproxylic beetles, birds, bats, Paillet et al., 2018; Asbeck et al., 2023). In addition, there are numerous threats to large trees, the most obvious being forest management, the decline in density of large-diameter trees due to timber harvesting is well known (Thomas et al., 2006). But their numbers are also declining for other reasons in areas with little or no forest management (Lutz et al., 2009; Lindenmayer et al., 2012). Once the large trees have disappeared from an area, it takes a long time, several centuries, for them to reappear (Lindenmayer and Laurance, 2016).

Table 5

Density of large trees (DBH > 60 cm) in old-growth dry-mesic oak forests.

Country, Wood, Site	Dominant tree taxa	Total area of sampling plots	Density of large trees, stem/ha	Reference
EU, Portugal, 4 sites	Quercus robur	0.6	39	Carvalho, (2011)
EU, Slovakia, Boky 1970s	Quercus petraea, Q. cerris	1.5	2	Saniga et al., (2014)
EU, Slovakia, Boky 2000s		1.5	10	
USA, Ohio 3 woods, 8 sites	Quercus alba, Q. prinus	0.4	6	Goebel and Hix, (1996)
USA, Missouri, Big Spring	Quercus alba, Q. velutina, Q. coccinea	3.0	4	Shifley et al., (1995)
USA, Virginia, Blue Ridge Mt.	Quercus prinus, Q. rubra	0.4	37	Abrams et al., (1997)
USA, Maryland, Coleman Hollow	Quercus prinus, Q. rubra, Betula lenta	0.2	33	Dodds and Smallidge, (1999)
USA, Maryland, Dans Mountain WMA	Quercus prinus, Q. rubra, Q. velutina	2.0	35	Heeter et al., (2019)
USA, Illinois, Dean Hills NP	Quercus alba, Q. rubra, Q. velutina	2.4	17	Feist et al., (2004)
USA, Indiana, Hemmer Woods, upland	Quercus alba, Q. velutina, Q. rubra	0.7	31	McCune et al., (1988)
USA, Illinois, Karcher's Post Oak Woods NP	Quercus stellata	4.5	8	Edgin et al., (2002)
USA, Kentucky, Lilley Cornett Woods, oak, 1979	Quercus prinus, Q. alba, Acer rubrum	1.3	18	Chapman and McEwan, (2016)
USA, Kentucky, Lilley Cornett Woods, oak, 2010		1.3	22	
USA, Indiana, Mauntel Woods, section A	Quercus alba, Q. velutina, Carya glabra	0.5	32	Potzger and Friesner, (1934)
USA, Pennsylvania, Mount Pleasure	Quercus pinus, Betula lenta, B. alleghaniensis	1.5	9	Mikan et al., (1994)
USA, West Virginia, Murphy Tract, MT2	Quercus alba	0.5	59	Rench, (2001)
USA, Missouri, Roaring River	Quercus alba, Q. velutina, Q. coccinea	3.0	6	Shifley et al., (1995)
USA, Tennessee, Savage Gulf Natural Area	Quercus alba, Acer rubrum, Oxydendrum arboreum	3.5	10	Hart et al., (2012)
USA, Illinois, Walnut Point State Park	Quercus alba, Q. velutina	12.5	7	Ebinger et al., (1977)

4.2. Structure of canopy layer

Based on our results, the structure of the managed stands is very homogeneous. This is not only indicated by the very low density of large trees with DBH > 60 cm discussed above, but this also by the often low density of DBH 40–60 cm trees, the narrow DBH range and the low maximum DBH values. The plot level Gini coefficient indicate similar homogeneity, which were very low compared to abandoned stands. The

structure of abandoned stands (age class 5) over 120 years of age already shows the decadal absence of forest management and the higher age of these stands. Their more diverse structure is indicated by a larger DBH range and a higher maximum DBH. The values of the Gini coefficient calculated on plots were higher in this age class than in the managed age classes. This suggests that as age increased and abandonment occurred, a higher proportion of small diameter and younger trees began to appear. It is connected to the more open canopy conditions and the presence of canopy gaps. The unimodal DBH distribution changed in this age group to a bimodal pattern with two peaks. However, the DBH distribution of the abandoned stands with two peaks differed significantly from the typical reverse-J (negative exponential) or rotated sigmoidal distribution in old-growth oak stands (Bőlöni et al., 2021).

Theoretically, the small patches, homogeneous on a scale of 500–1000 m², could form a more diverse age class overall. However, this was not the case for the managed age classes based on our data, which remained homogeneous on a larger scale, while in abandoned stands over 120 years old, the diversity of patches with a more diverse structure also increases with increasing area. But even so, the structural diversity of abandoned stands is still below that of old-growth oak stands, the shape of DBH distribution is also different, showing that these are “only” abandoned former managed forests, which have started to convert towards a more natural structure, but are still at the beginning of this process.

The age classes correspond to some extent to the developmental stages of natural oak forests (Johnson et al., 2019) and that of natural temperate deciduous or mixed deciduous-coniferous forests (Leibundgut, 1959; Oldemann, 1990; Standovár and Kenderes, 2003; Kral et al., 2010). However, the structure of the developmental stages is heterogenous formed by small scaled gap dynamics or intermediate severity disturbances (Aszalós et al., 2022). Not only the DBH distribution of living trees shows higher heterogeneity than that of managed stands, but the higher volume of deadwood also increase the structural complexity. On the other hand, some phases were completely or almost completely missing from the managed age classes (e.g. late biostatic or ageing and degradation stages, Korpel, 1995; Emborg et al., 2000). In addition, these missing stages in natural forests cover a large area and last for a long time, and are therefore very important elements of natural forest dynamics (Miscicki 1994; 2012; Bobiec et al., 2000, Emborg et al., 2000, Christensen et al., 2007, Král et al., 2010, 2014, Lorimer and Harpin, 2014).

There are very few studies comparing the structure and tree species composition of managed and unmanaged (abandoned) stands in dry-mesic oak dominated forests. It was found (Merino et al., 2007; Motta et al., 2015; Pach and Podlaski, 2015; Dieler et al., 2017; Matovic et al., 2018) that deadwood volume, microhabitat abundance and tree size diversity is decreased by forest management. A study comparing managed and protected (i.e. approximately unmanaged) *Q. robur* stands in Poland also suggested that the protected stands were still more diverse than the managed ones (Szmyt, 2017). His study showed smaller differences than our, but in his case the managed stands were relatively old (140 years), which are richer in old-growth structural characteristics (e.g. large trees, diverse DBH distribution). In a study of North American mixed hardwood forests several DBH distribution shape has been found in managed stands (Janowiak et al., 2008), but they tended to indicate more homogeneous stands. From the same sites, unmanaged stands (old-growth remnants) were predominantly rotated sigmoid in shape, a distribution that suggests a more diverse stand structure. This has been studied primarily through European examples, where forests have an extremely long management history and the impacts of management on biodiversity may depend on this history (Biber et al., 2015). The extent of the impact depends not only on the time from abandonment, but also on the intensity of management in the managed stands. It was concluded that biodiversity (species composition, structure, ecological functions) changed only moderately by low intensity forest management (continuous cover forestry, selection system, coppice with standards). Under

intensive management (shelterwood and clear-cutting systems), the effect can be very strong, as in our study focused on dry-mesic oak forests.

Dead wood is an important part of the stand structure and has been previously analysed in a separate study (Bőlöni et al., 2017). For completeness, we only mention here that below 100 years of age the volume of deadwood was low (15 m³/ha), while above 100 years it was relatively high, approaching the mean volume of deadwood found in old-growth stands (45 m³/ha, Bőlöni et al., 2017). Large deadwood (D>30 cm) occurs almost only in abandoned stands.

4.3. Overstorey composition

The admixed tree species play an important role in the semi-dry oak old-growth forests (Bőlöni et al., 2021). The average number of species and especially the relative dominance of other tree species in the studied forests was very low. Although the vast majority of the data are from the eastern USA with different climatic conditions and tree species pool, the dominance of oaks was much lower in natural old-growth semi-dry oak forests than in managed forests of Hungary. In old-growth dry-mesic oak forests relative basal area of oaks averages 74 %, ranges from 60 % to 90 % (Bőlöni et al., 2021). In Europe, only two old-growth dry-mesic oak forests were studied. In a mixed stand in Portugal, the relative basal area of oaks was 48–64 % (Carvalho, 2011), while in Boky forest Reserve in Slovakia, previous surveys have shown 95–98 % (Saniga et al., 2014). The European phytosociological literature also suggested the presence of a higher abundance and cover of admixed trees (e.g. Chytrý, 1997; Roleček, 2005). However, the total number of species we found in the canopy (31) did not seem to be low, admixed tree species are present in the stands, but their density is extremely low in the overstorey.

The lower relative basal area of oaks in the old-growth forests compared to the managed stands indicates that the relatively high density of other tree species in oak stands is very important in addition to oaks. As shown in this study, dry-mesic forest types are strongly dominated by oaks in Hungary, which is a result of forest management focused on oak production. Although the number of tree species in Central Europe is significantly lower than in the USA, this alone could only partly explain the high relative basal area of oaks. The high oak dominance is more due to the management practices of the last 100–150 years. In the Hungarian forestry literature and in forest management practice, there was a clear tendency to reduce the density of admixed trees. Even in stands that have been abandoned for decades, the average relative basal area of other tree species was only 5 %. This low relative basal area and the fact that the species are concentrated in the smaller size classes are a combination of former deficits and the onset of regeneration. No such regeneration remained in the managed stands. Any admixed trees that do appear in the stand, are removed during the selection or increment thinning processes. This was indicated by their decreasing relative density with age and by the virtual absence of admixed trees larger than 20 cm DBH in the managed stands. Out of the 378 managed plots examined, only 29 (8 %) contained any admixed trees larger than 20 cm DBH, their total relative density was shown to be less than 1 % of the total density of trees.

4.4. Density and composition of understorey

The density values of saplings and seedlings were similar between the age classes and did not differ significantly from the old-growth stands. Only in the age class 4 (100–119 years old) was it slightly lower, indicating an advanced felling of the lower layers in these stands. At the sapling layer, the relative density of oaks is very low (10 %), except for the youngest age class 1 (28 %). This proportion is much lower than the relative density of oaks in the canopy, and lower than the relative density of oaks in the smaller DBH classes (10–20 cm DBH). At the seedling layer, we found a similar pattern. It seems that the density and relative density of oaks in the understorey, especially below 10 cm

DBH is often relatively low in oak forests. For these layers, the impact of forest management seems to be smaller or undetectable, interestingly, understorey has not been significantly affected by the long-standing schematic clearcutting and shelterwood system.

Based on the regeneration data of the oldest stands, it appears that the density of oaks may decrease over time. However, the investigation of old-growth oak stands suggests that this phenomenon may be a natural occurrence (Bölöni et al., 2021). In dry-mesic oak old-growth forests, where repeated surveys have been conducted, a shift in species dominance in the canopy layer has been observed. While the density of oaks is generally reduced, the basal area and relative basal area of oaks have increased in some cases (e.g. Chapman and McEwan, 2016; Rhoades, 1992; Saniga et al., 2014). However, the relative density of oaks in the regeneration layers of many dry-mesic old-growth forests was found to be less than 50 % (e.g. Abrams et al., 1997; Carvalho, 2011; Chapman and McEwan, 2016; Dodds and Smallidge, 1999; Edgin et al., 2002; Feist et al., 2004). The sift in tree species composition of the canopy does not necessarily imply that oaks will be unable to maintain at least part of their dominance in the future. Numerous studies on the composition and structure of oak-dominated forests suggest that the regeneration of oaks is sufficient to maintain their dominance (Abrams et al., 1997; Saniga et al., 2014; Sano, 1997).

4.5. Management recommendations

If we want to bring forests closer to their natural state, some changes in the management are necessary. For the compensation of missing structural elements (large trees, deadwood, more diverse DBH distribution) and restore forest biodiversity, several changes in management are proposed, which are not fully independent of each other. First, since the current cutting age of these stands is 80–100 (–120) years, which is far below the upper limit of the natural age of oaks (which is over 300 years), one of the most important things would be to increase the cutting age of the stands managed by rotation forestry system by 20–50 years.

If clear-cutting and gradual regeneration cutting are still practised in such forests, it would be important to leave intact areas and habitat trees, which are excluded from forestry activities (retention areas or individuals). These retention patches would ideally cover 5–25 % of the total area. These includes larger areas (reserves, subcompartments of 5–50 ha) as well as small areas (stepping stones) within managed stands of 0.2 – 1 ha (Mergner, 2021, Kraus and Krum, 2013). The continuous protection of large trees should be integrated into forest management, and this can be facilitated by the designation of habitat trees, which are removed from management, i.e. never felled. Taking economic considerations into account, these should reach a density of between 3 and 5 per hectare.

Another solution to bring back missing forest structural elements would be to switch to continuous cover forestry. In this case, in addition to the commonly used maximum of 500 m² of gaps, the presence of larger gaps of 1–2 thousand m² is also an important consideration, as these dry-mesic oak forests originally contained light-rich, open patches. In addition to productive areas managed by continuous cover forestry, there should be large areas (min. 10 ha) taken out of management in the landscape.

For both types of management, the aim should be to leave dead wood, with a minimum of 25–30 m³/ha (Bölöni et al., 2017). Efforts should also be made to make the DBH distribution as less homogeneous as possible, so that understorey thinning should be reduced or eliminated. It is necessary to ensure the sparing of admixed trees, as several studies have shown that the stability and the production is also higher in mixed stands compared to monocultures (Forrester and Bauhus, 2016, Dieler et al., 2017).

Even in the case of shelterwood system, the permanent maintenance of retention tree patches of min. 0.1 ha is necessary, which should reach about 10 % of the productive area. In the managed stands, the DBH class of 10–20 cm is absent or rare in all but the youngest age class 1 (40–69

years old), and trees in this size range should be maintained in the future. The low density of trees in the 10–20 cm size class may be related to the current forest management practice of subcanopy layer thinning and frequent sapling layer control. We suggest that thinning of the understorey should be replaced by overstorey thinning, combined with the opening of smaller gaps to stimulate the growth of dominant trees and strengthen the seedlings and saplings layer.

The abandoned stands with the most natural structure (age class 5) still did not reach the old-growth level. There are hardly any stands of this type in Hungary, so it is important to maintain the exclusion of management in these stands. Moreover, based on the literature review (Bölöni et al., 2021), published data on old-growth dry-mesic oak forests are only available from the two stands in Europe (Carvalho, 2011, Saniga et al., 2014), which shows that very few old-growth reference stands remained of this forest type in the continent.

5. Conclusions

Centuries of forest management have significantly altered the dry-mesic oak forests. Density of admixed species in the canopy has been reduced to a minimum, oaks have become dominant, with an average relative basal area of 98 % in the managed stands. In the abandoned stands, relative basal area of oaks is slightly lower, but still 95 % on average, due to the natural forest dynamics that are slowly reasserting themselves. Forest management has also significantly transformed the structure of the stands, which in most cases have become homogeneous. Most striking is the low DBH range and the almost complete absence of large (DBH > 60 cm) trees. Thus, the average density of large trees in the managed stands barely exceeds 0.2 trees/ha. In the older abandoned stands, the density of large trees reaches 5 stem/ha, which is a little closer to the 10–30 stem/ha expected on average in old-growth dry-mesic oak stands.

If the composition and structure of the dry-mesic oak forests of the Hungarian Carpathians are to approach that of the old-growth oak forests, fundamental changes in forest management will be required. The key is to remove from management, at least in part of the area, groups of trees that are already large or have the potential to become so in the relatively short term. Obviously, the larger the better, but it would be desirable to have a proportion of 5–20 % of the total area of the stands. In the framework of clear-cutting and shelterwood cutting system, management should change for sustainability. These changes are the raising the cutting age, elongation of regeneration period, retaining unaffected patches, maintaining admixed tree species, and even favouring them within certain limits. It would be even better to replace traditional shelterwood system with a more close-to-nature technology, such as continuous cover forestry, in as many places as possible. Even with any of the proposed changes, it would still be many decades before any meaningful changes in the structure and composition of the dry-mesic oak forests. Large trees are also old trees, so it takes several decades for them to develop. The changes in structure and composition after abandonment is slow, as has been shown in this study. All these desirable changes could be facilitated and accelerated by interventions specifically designed for this purpose (conservation-oriented management).

CRedit authorship contribution statement

Bölöni János: Writing – original draft, Methodology, Investigation, Funding acquisition, Formal analysis, Conceptualization. **Aszalós Réka:** Writing – review & editing, Funding acquisition, Conceptualization. **Ódor Péter:** Writing – original draft, Methodology, Funding acquisition, Formal analysis, Conceptualization.

Declaration of Competing Interest

The authors declare that they have no known competing financial

interests or personal relationships that could have appeared to influence the work reported in this paper.

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Appendix A. Supporting information

Supplementary data associated with this article can be found in the online version at [doi:10.1016/j.foreco.2025.122706](https://doi.org/10.1016/j.foreco.2025.122706).

Data Availability

Data will be made available on request.

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