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Old-growth forests in the Dinaric Alps of Bosnia-Herzegovina and Montenegro: a continental hot-spot for research and biodiversity

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Introduction: According to various censuses, Europe has less than 1.5 million ha of old-growth forests (OGF). Most of them are in the boreal zone, while their presence in the temperate zone is residual and fragmented.In the framework of the EU biodiversity strategy, it has been adopted a broad definition of OGF which includes late-seral forests and forests with some management legacies. However, research purposes need to identify strictly defined OGFs characterized by structure, disturbance history, and processes typical and exclusive of the last stage of the forest dynamic.

Methods: The present paper wants to contribute to this debate by presenting a research network of four mixed (Fagus-Abies-Picea) montane OGFs in the Dinaric Alps (Lom, BiH; Janj, BiH; Perućica, BiH; Biogradska Gora, MNE), summarizing 20 years of multidisciplinary research by focusing on the structural characteristics and the disturbance history of the whole network and their coherency with strict OGF indicators. These sites were selected in relatively structurally uniform study areas, where 142 permanent plots have been established since 2002.

Results and discussion: The study sites have a high living (747–1,201 m3 ha–1) and coarse woody debris (CWD) biomass (304–410 m3 ha–1), resulting in the highest forest carbon sink at the continental level (398–484 Mg C ha–1). The presence of large and old trees is one of the critical characteristics of the old-growth stage: in Lom and Perućica, there are 19 trees and 14 ha–1 larger than 1m at breast height, respectively, and 14 trees and 15 trees ha–1 older than 400 years. In the last three centuries, continuous small-scale disturbances have driven forest dynamics, developing stands characterized by gap-phase dynamics and quasi-equilibrium structure. The Dinaric OGF network presents robust indicators of old-growthness, similar structural characteristics, and dynamic processes across all four sites. Identifying this sub-set of OGF using strict criteria is critical for recognizing conservation priorities and for quantifying, along an old-growthness chronosequence, the current structural differences of managed or recently abandoned forests. Besides, only OGF selected with rigorous criteria can act as a reliable reference for ecological restoration and sustainable forest management as a benchmark for carbon sink and for quantifying the impact of climate change on forests.

KEYWORDS

forest structure, forest dynamics, CWD (coarse woody debris), carbon stock, tree rings, natural disturbance regime, natural range of variability, European forest and environmental policies

1 Introduction

The first studies about old-growth forests (OGF) were developed in the Pacific Northwest in the last decades of the 20th century using structural and dynamic features (Franklin et al., 1981). Simultaneously, studies about the role of natural disturbances and natural disturbance regimes, the ecological role of coarse woody debris (CWD), and the old-growth stage have been started (Pickett and White, 1985; Harmon et al., 1986; Spies and Franklin, 1991). These studies have been developed in primary forests hosting a full range of stand development stages, from disturbance and cohort establishment to old-growth, describing structural features, age, and disturbance history (Franklin et al., 2002). The researchers have identified old-growth structural indicators, highlighted the importance of the OGF biodiversity, and delineated a major paradigm shift from one where equilibrium processes predominated in ecological systems (the Clementsian view) to one where forest systems are dynamic and are structured mainly by natural or anthropogenic disturbances (Clements, 1936; Oliver and Larson, 1996; Lindenmayer and Franklin, 2002). These studies were seminal in recognizing the critical role of OGF in biodiversity and conservation (Kormos et al., 2018; Watson et al., 2018).

Consequently, the term OGF became popular in other continents even where the primary forests are absent or rare (Jacobson et al., 2019) as OGF are not exclusively related to primary forests. However, secondary forests can also recover from human disturbances to develop secondary old-growth (O'Brien et al., 2021).

Due to the extreme variability in forest structures, disturbance regimes, land-use history, and ecological characteristics, a standard definition of the "old-growth" stage has always been challenging. A first attempt for a shared definition was made in 2001 during an FAO expert meeting where an OGF was defined as "*primary or a secondary forest which has achieved an age at which structures and species normally associated with old primary forests of that type have sufficiently accumulated to act as a forest ecosystem distinct from any younger age class*" (UNEP/CBD/SBSTTA, 2001).

In the late 20th century, the concept and interest in OGF also spread rapidly in Europe, where primary forests (undisturbed by man) were absent. Human interference during the past millennia led to intense and widespread forest and land use (Birks and Tinner, 2016) also in places that are currently identified as "natural" (Hejcman et al., 2013; Cagliero et al., 2023). The lack of primary forests is particularly evident in the temperate zone, one of the world's most heavily populated and long-term developed regions (Silander, 2001; Burrascano et al., 2013).

According to available different country censuses, mainly based on extensive and not homogeneous definitions of OGF, Europe currently has less than 1.5 million ha of OGF, about 0.9% of the total forest cover, mainly in the boreal zone (Sabatini et al., 2018; Barredo Cano et al., 2021). The distribution of European OGF in the temperate zone is residual, being less than 0.1% of the forest cover, and these forests are scarce or barely existent for many EU forest types (Meyer et al., 2021).

For this reason, the EU Commission has adopted a broad, even though less rigorous, definition of OGF: "*A forest stand or area consisting of native tree species that have developed, predominantly through natural processes, structures, and dynamics normally associated with late-seral developmental phases in primary or undisturbed forests of the same type. Signs of former human activities may be visible. Still, they are gradually disappearing or are too limited to significantly disturb natural processes*," including even "*forest stands that originate not only from natural regeneration but also from planted or sown native tree species*" (European Union Commission, 2023a). This broad definition includes not only primary and secondary OGF (which are very rare) but also late seral stands with some old-growth features that could potentially become OGF in the future. Thus the EU definition delineates a critical forest cover that could develop in "future old-growth" (Spies and Franklin, 1996), but it does not allow a realistic quantification of the current residual OGF such as those defined with more rigorous criteria that are crucial for protection and research purposes.

One of the European regions that still hosts OGF stands are the Dinaric Alps. This mountain range was a border region between European Kingdoms and the Ottoman Empire, and it experienced relatively low population densities for centuries. This translated into a history of less intensive and less widespread deforestation and land use than in other European mountain regions (Kaplan et al., 2009; Cagliero et al., 2023) with the conservation of large, well-preserved patches of forest that have been capturing the attention of European foresters, ecologists, and botanists since the beginning of the 20th century (Fröhlich, 1930; Tregubov, 1941; Jones, 1945; Susmel, 1956; Leibundgut, 1982).

A research network of four mixed (*Fagus-Abies-Picea*) montane OGF in the Dinaric Alps (Lom, BiH; Janj, BiH; Perućica, BiH; Biogradska Gora, MNE) was established in 2004. This forest type is typical of the mountain chains in central-southern Europe, covers more than 10 million hectares, is highly ecologically and socioeconomically significant, and provides various ecosystem goods and services (Hilmers et al., 2019). The selection of the study sites was based on strict structural criteria (Table 1) in order to

TABLE 1 Structural definition/indicators used in the Pacific Northwest (Franklin and Spies, 1991; Franklin et al., 2005), in the EU OGF Guidelines (European Union Commission, 2023a) and in the Dinaric OGF networks.

OGF indicator	PNW	EU Guidelines	Dinaric OGF networks
Native trees	Native trees species	Native tree species	Native tree species
Developmental processes		Developed, predominantly through natural processes	Disturbance history coherent with old-growth stage (long-term small scale disturbances)
Structures and tree size diversity	Tree size diversity; spatial heterogeneity, broken-topped crowns, and the presence of shade-tolerant tree species	Structures, and dynamics normally associated with late-seral developmental phases in primary or undisturbed forests of the same type	Vertical and horizontal diversification associate with small-scale disturbances (gap-phase and relative gap-fraction). The diameter distribution approaching the "rotated-sigmoid distribution" is a preferential criterion
Large trees and old trees	Large trees (number of trees ha^{-1} >100 cm DBH); dominant trees >200 years old (for Douglas fir)		Significative presence of large (>80 cm at DBH) and old trees (>3–400 years)
CWD	Volume of down woody debris (m^3 ha^{-1})		Volume of CWD associated with the long-term natural mortality dynamics (>300 m^3 ha^{-1})
Snags and logs	Large snags (number of standing dead trees ha^{-1} >50 cm dbh and >15 m tall)		Large snags and logs (>50 cm diameter) and presence of the whole decay phases
Human activities		Signs of former human activities may be visible. Still, they are gradually disappearing or are too limited to significantly disturb natural processes	No signs of former organized human activities (sporadic stumps could be present)
Artificial origin		Including forest stands that originate not only from natural regeneration but also from planted or sown native tree species	
Regeneration			Abundant regeneration of late seral species (related to gap-phase)

identify forests that have a structure and a disturbance history that are not affected by past and present human disturbances and that can reliably identify the old-growth stage *sensu* Oliver and Larson (1996). The used criteria are based on the seminal studies in the Pacific-North-West (Franklin and Spies, 1991; Franklin et al., 2005) and have been tailored to mixed, uneven-aged montane forests belonging to the *Abieti-Fagetum* forest type ecology and land-use history.

This paper presents the whole research Dinaric network coherently by summarizing 20 years of multidisciplinary research. It specifically aims to: (i) describe the structural characteristics and the disturbance history of the whole network and its coherency with the adopted OGF indicators; (ii) analyze structural commonalities and variabilities among these forests to delineate a common development process; (iii) compare structural and ecological differences at the studies sites with OGF criteria adopted by EU OGF Guidelines and discuss the scientific importance of rigorously characterizing OGF when used as a reference or benchmark for old-growthness, closer to nature forest management, ecological restoration, forest carbon policies, and climate change forest impacts; (iiii) supports the identification of a sub-set of OGF selected with more rigorous criteria, in the framework of the current OGF definition guidelines, for a better identification of conservation priorities and to be used as a reference or benchmark for research purposes.

2 Materials and methods

2.1 Study areas

Since 2004, we have selected four study sites in the Dinaric Alps by following strict criteria (Table 1): Lom (LOM), Janj (JAN), and Perućica (PER) in Bosnia-Herzegovina and Biogradska Gora (BGO) in Montenegro (Figure 1; Table 2). We have focused our selection on mixed, uneven-aged montane forests belonging to the *Abieti-Fagetum* forest type (Figure 2). During the last 20 years, more than 40 researchers from 7 countries have been studying forest dynamics and ecological processes at different scales and according to a multidisciplinary approach (Table 3).

LOM and JAN are Forest Reserves established by the State Institute for Protection of Cultural Monuments and Natural Rarities in Bosnia and Herzegovina (Maunaga et al., 2001). LOM reserve was set in 1956 (Pintarić, 1999; Motta et al., 2011). Initially, the Reserve was split between a core area of 55.8 ha under a strict protection and a buffer zone of 242 ha with low-intensity management. More recently (2021), strict protection was extended to the whole LOM reserve. JAN reserve was established in 1954 (Pintarić, 1999; Keren et al., 2017). As LOM, JAN was initially split between a strict protection core area (57.2 ha) surrounded by a buffer zone (237.8 ha) that were merged in 2021. In the same year, JAN was named a UNESCO World Heritage

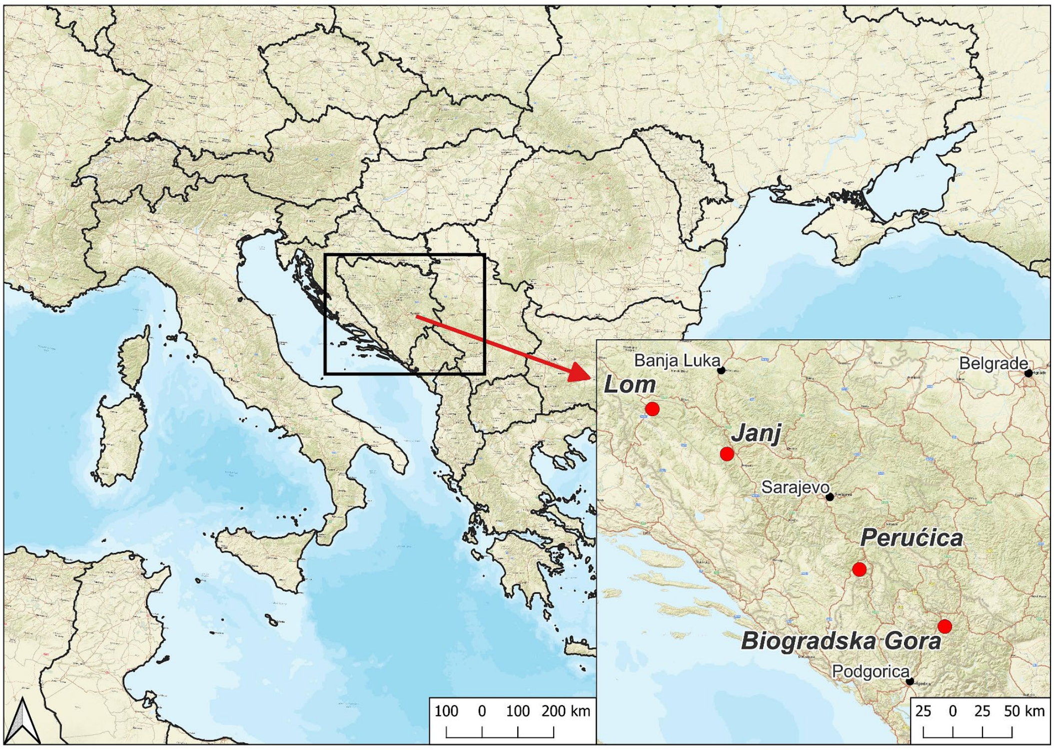

FIGURE 1
Location of the study sites.

TABLE 2 Study site description.

Site	Code	Study area (ha)	Coordinates	Plot (*n*)	Elevation (m a.s.l.)	Average slope (°)	Dominant aspect	Bedrock	Rainfall (mm year^{-1})
Lom	LOM	55.8	44.270°N–16.270°E	40	1,250–1,520	10°	South-east	Limestone	1,321
Janj	JAN	57.2	44.080°N–17.170°E	40	1,280–1,400	12°	South-west	Dolomite	1,120
Perućica	PER	35.2	43.360°N–18.620°E	32	1,340–1,510	15°	Northwest	Limestone and dolomite	1,220
Biogradska Gora	BGO	33.1	42.940°N–19.540°E	30	1,210–1,450	19°	North-east	Eruptive rocks	1,229

Site as an extension to the Ancient and Primeval Beech Forests of the Carpathians and Other Regions of Europe, and a new 295 ha buffer zone was delineated.

PER and BGO are among Europe's most significant and best-preserved OGF (Sabatini et al., 2018). At both sites, the OGF covers more than 1,000 ha, including different forest types along an altitudinal gradient. The *Abieti-Fagetum* is the most represented one, covering more than 500–600 ha at both sites. The first official "protection" measures for these forests date back to 1893 for PER (Fukarek and Stefanović, 1958; Pintarić, 1978) and 1878 for BGO (Motta et al., 2015a; Stupar and Milanović, 2017), respectively. In both cases, the primary protection goal was hunting and game protection. BGO was declared a National Park (Biogradska Gora National Park) in 1952, while PER acquired the same status in 1962 (Sutjeska National Park).

All the sites are characterized by high fertility (Drinic, 1957), are among the highest carbon reserves in Europe (Keith et al., n.d.), and host some of the tallest European native trees, reaching more than 60 m height in PER and BGO and more than 55 m in LOM and JAN (Leibundgut, 1976; Diaci, 1999).

2.2 Dendrometric characteristics

2.2.1 Network of plots (forest inventory)

We identified a structurally uniform and representative study area at each site ranging from 33.1 to 57.2 ha. These areas were selected in the original reserve core area in LOM and JAN and after an intensive survey in the core area of *Abieti-fagetum* OGF in PER and BGO (Motta et al., 2011, 2015a; Keren et al., 2014). In each area, a regular grid (100 m for LOM, JAN, and PER and 120 m for BGO) was superimposed on the 1:10.000 raster map (see Supplementary material for further details).

FIGURE 2
The four study sites of the Dinaric Alps in Bosnia-Herzegovina and Montenegro: **(A)** Biogradska Gora (MNE), **(B)** Perućica (BiH), **(C)** Janj (BiH) and **(D)** Lom (BiH). The forests are mixed with beech, fir, Norway spruce and sporadic broadleaves. The study sites are characterized by high living and CWD biomass, large and old trees, vertical multilayered structure and horizontal structure shaped by a small scale gap disturbance regime.

In each plot, four types of measurement approaches were applied (Castagneri et al., 2010): (a1) in circular plots of 12 m of radius (14 m in LOM), we recorded species diameter at breast height (DBH) and height (to the closest 0.5 m) for all living trees with DBH >7.5 cm; (a2) in a 113.1 m^2 round plot (radius = 6 m), species and height of each regeneration individual ($h > 10$ cm and DBH <7.5 cm) were recorded; (a3) on two 50 m intersecting lines oriented northward and eastward from the center of the sampling point, we measured the logs crossing the line (Van Wagner, 1968); and (a4) in a 50 × 8 m rectangular plot centered on the previous line we measured stumps (diameter at the ground and the top) and snags (DBH). For each element of coarse woody debris (CWD), size, species (when possible), and decay class were recorded (Maser et al., 1979). Volume for living trees and snags was calculated according to local volume tables. Volume for snags, logs, and stumps was calculated according to methods described in Motta et al. (2015b). Total deadwood carbon (C) stock was calculated using basic wood densities and C content for different decay stages derived from field sampling (Bono et al., n.d.). Litter and soil (down to 30 cm) were estimated through the Global Soil Organic Carbon Maps (FAO and ITPS, 2018), but also directly sampled (down to 90 cm) in PER and BGO (Bono et al., n.d.). The other C stocks were estimated using IPCC allometric algorithms (IPCC, 2006).

2.2.2 Intensive permanent plots

At three of the four study sites (LOM, PER, BGO), we have established a 1 ha intensive permanent plot (IPP) where all the trees with DBH >7.5 cm and CWD have been measured (DBH, height, and four canopy projections on the ground for the trees, diameters, height, and decay stage for the CWD) and mapped (Motta et al., 2011). The cores, due to the restrictions posed by the Biogradska Gora National Park Administration, were collected only in two sites (LOM and PER) that were analyzed for tree age and growth patterns.

2.3 Growth pattern and age

We collected one core from the living trees with DBH >10 cm from all the trees in the IPP of LOM and from 75% of the trees, randomly selected, in the IPP of PER. The cores were collected at 50 cm height from the ground to better estimate tree age and reconstruct the stand age structure. They were also used to analyze growth patterns and reconstruct disturbance history at the stand level. In addition, in each research sites, 12–30 dominant trees randomly selected in the study areas were cored (two cores for each tree) at DBH to analyze climate growth relationships (Castagneri et al., 2014; Bosela et al., 2017; Martinez del Castillo et al., 2022) and to estimate the maximum age reached by dominant trees of each species. In BGO, due to the restrictions posed by the National Park Administration, only standing or lying dead trees were cored, resulting in an under-representation of dominant Norway spruces.

All cores were fixed to wooden supports in the laboratory and prepared with a razor until an optimal surface resolution was achieved.

TABLE 3 Research infrastructures and main fields of research developed in the last 20 years at the four old-growth forests in the Dinaric Alps in Bosnia-Herzegovina and Montenegro.

	LOM	JAN	PER	BGO	Main references
Study area (SA) structure	X	X	X	X	Motta et al. (2011, 2015a) and Keren et al. (2014), this paper
Intensive permanent plot (IPP) structure (1 ha)	X		X	X	Motta et al. (2011), this paper
Age structure (IPP)	X		X		Motta et al. (2011)
Disturbance history (IPP)	X	X	X	X	Motta et al. (2011, 2023), this paper
Tree rings from dominant trees and climate growth relationships SA (3 species)	X	X	X	X	Castagneri et al. (2014), Bosela et al. (2017) and Martinez del Castillo et al. (2022)
Gap fraction SA	X			X	Bottero et al. (2011), Garbarino et al. (2012) and Cagliero et al. (2022a)
Carbon stock and fluxes SA			X	X	Palandrani et al. (2021), Bono et al. (n.d.) and Keith et al. (n.d.)
Paleoecology			X	X	Finsinger et al. (2022) and Cagliero et al. (2022b, 2023)
Biodiversity (saproxylic species, microsites, vegetation)	X	X	X	X	Maunaga et al. (2001), Čurović et al. (2011), Curovic et al. (2020) and Parisi (2022, 2023, 2024)
Reference for old-growthness and for closer-to-nature management	X	X	X	X	Castagneri et al. (2010), Motta et al. (2015b, 2023), Keren et al. (2017) and Keren and Diaci (2018)

Tree ring widths were measured to the nearest 0.01 mm using the LINTAB device and TSAP-Win software package (Rinntech, Heidelberg, Germany). The tree-ring series were visually and statistically cross-dated by CooRecorder software (Larsson and Larsson, 2018).

To describe past disturbance events, we analyzed the growth pattern in cores from permanent plots to identify releases from suppression. The detection of growth releases was obtained with Jolt software (version 6.01P by R. L. Holmes, University of Arizona, Tucson, Arizona), using the running mean radial-averaging method (Rubino and McCarthy, 2004; Fraver and White, 2005) and taking into account abrupt growth increment over 166% of the previous years in a window of 10 years. Only the growth increments that last at least 4 years were classified as releases from suppression (Schweingruber et al., 1990). A chronology of the releases found in the analyzed trees, all the species together, was constructed for each site. As the time to respond to stand opening is highly variable among species and individuals, the results were grouped at 10-year intervals (Altman, 2020; Izworska et al., 2022). The percentage of trees showing a growth release in a given decade was then plotted against time (Motta et al., 1999) starting from 1700 when at least 15 trees were available in both sites.

For age estimation, tree age from cross-dated cores was taken as the number of rings between the pith and the cambium (age at the coring height) when cores included the pith. In the other cases, if possible, the pith location was geometrically estimated (Motta and Nola, 2001). The missing radius was measured as the distance from the estimated pith location and the innermost ring. Then, missing rings to the pith were estimated by counting the number of rings in a segment equivalent to the length of the missing radius in the innermost part of the core. This number was added to the number of rings counted on the core to obtain the estimated tree age at the coring height. When it was impossible to estimate the age, e.g., for the decay or because the missing part could not be estimated reliably, we used the number of rings counted, indicating the presence of a missing part not counted (e.g., >480 years).

2.4 Patterns of forest structure

Between-plot and between-forest variability was explored using a multivariate approach based on PCA free ordination analysis employing a single matrix (142 plots and 20 structural variables). Forest structure variables for living trees (basal area, density, volume, quadratic mean diameter, standard deviation of diameter, Shannon diameter diversity), coarse woody debris (overall CWD volume, volume of stumps, logs, snags having a diameter >47.5 cm), and regeneration (overall density of saplings and divided by species) were used to assess the between-forest and the between-plots variability. Species composition was measured as a proportion of single species (beech, silver fir, Norway spruce, and others) on the plot basal area. A particular focus on large (DBH >80 cm) and medium-size (DBH >50 cm) trees was adopted by measuring the densities of these two diameter classes. PCA was performed to explore the correlation structure among living trees, regeneration, and CWD attributes. The average structures of old-growth forests were indicated by centroids, and convex hulls indicated their range of variability. PCA was performed using the PC-ORD 7.10 (McCune and Mefford 1999) statistical package. The axes' statistical significance was tested using the Monte Carlo permutation method based on 10,000 runs with randomized data.

TABLE 4 Structural characteristics of the four studied old-growth forests.

		Units	LOM	JAN	PER	BGO
DEN	Tree density	n ha^{-1}	469 ± 17	516 ± 25	432 ± 21	412 ± 22
BA	Basal area	m^2 ha^{-1}	45.3 ± 1.8	66.7 ± 2.8	59.1 ± 4.2	60.1 ± 3.9
VOL	Volume of living trees	m^3 ha^{-1}	747.3 ± 31.0	1.201.4 ± 53.6	993.8 ± 74.4	1.021.9 ± 79.7
D80	Trees with dbh >80 cm	n ha^{-1}	13 ± 2	38 ± 5	37 ± 4	35 ± 5
D50	Trees with dbh >50 cm	n ha^{-1}	73 ± 4	114 ± 7	79 ± 8	95 ± 6
PERCFASY	Percent basal area by beech	%	32.2 ± 2.0	19.6 ± 2.0	36.9 ± 4.6	38.3 ± 4.4
PERCABAL	Percent basal area by silver fir	%	46.7 ± 2.9	50.4 ± 4.0	59.8 ± 4.5	51.5 ± 4.5
PERCOT	Percent basal area by other species	%	21.2 ± 2.8	30.1 ± 3.4	3.3 ± 1.5	10.2 ± 2.6
QMD	Quadratic mean diameter	cm	35.4 ± 0.8	41.3 ± 1.1	41.7 ± 1.5	43.2 ± 1.6
HD	Shannon diversity diameter classes	cm	2.0 ± 0.03	1.9 ± 0.04	1.7 ± 0.04	1.7 ± 0.04
SDD	Standard deviation of the diameter	cm	21.8 ± 0.5	25.4 ± 0.8	25.9 ± 1.1	27.2 ± 1.2
LGT	Diameter average of the largest 10 trees ha^{-1}	cm	95.0 ± 1.6	103.0 ± 1.2	116.6 ± 1.1	124.0 ± 2.3
STATU	Stature (average height of the 5 highest trees ha^{-1})	m	46.8 ± 0.6	48.5 ± 0.7	47.0 ± 0.3	55.5 ± 0.8
CWD	Volume of coarse woody debris	m^3 ha^{-1}	305.0 ± 18.8	371.2 ± 24.4	410.7 ± 25.6	374.5 ± 28.6
SNAG50	Snags with dbh >50 cm	n ha^{-1}	18 ± 2	18 ± 2	27 ± 3	20 ± 3
VSNAG50	Volume of snags with dbh >50 cm	m^3 ha^{-1}	57.2 ± 10.1	77.1 ± 13.4	103.6 ± 16.9	97.8 ± 18.1
LOG50	Log with dbh >50 cm	n ha^{-1}	33 ± 3	40 ± 3	46 ± 5	41 ± 5
VLOG50	Volume of logs with diameter >50 cm	m^3 ha^{-1}	126.8 ± 13.8	167.9 ± 14.5	182.1 ± 19.3	179.8 ± 20.4
STUMP	Stumps	n ha^{-1}	77 ± 7	48 ± 3	28 ± 4	20 ± 3
VSTUMP	Volume of stumps	m^3 ha^{-1}	9.6 ± 1.2	8.2 ± 0.8	5.7 ± 0.9	5.7 ± 1.1
REGEN	Regeneration density	n ha^{-1}	4.772 ± 633	4.685 ± 740	2.313 ± 357	3.107 ± 566
REGFABAL	Percent regeneration by silver fir	%	40.1 ± 4.2	15.1 ± 2.9	81.7 ± 6.1	44.6 ± 5.4
REGFASY	Percent regeneration by beech	%	36.5 ± 4.5	65.3 ± 4.6	13.6 ± 3.1	13.7 ± 3.1
REGOT	Percent regeneration by other species	%	23.4 ± 2.8	19.6 ± 3.9	4.8 ± 3.1	41.7 ± 3.1
C_stock	Above and below-ground carbon stock	Mg ha^{-1}	398 ± 8.6	484 ± 15.2	461 ± 22.3	466 ± 23.4

3 Results

3.1 Dendrometric characteristics at the forest inventory plots and intensive permanent plots

The density of living trees with a diameter greater than or equal to 7.5 cm was between 412 and 516 trees per hectare in BGO and JAN, respectively (Table 4). The basal area and volume ranged from 45.3 to 66.7 m^2 ha^{-1} and from 747.3 to 1201.9 m^3 ha^{-1} in LOM and JAN, respectively, with JAN having the highest values and LOM having the lowest. It is worth noting that the average volume data from LOM is influenced by the karstic morphology with sinkholes that limit the occupancy of the forest cover. In fact, the 1 hectare permanent plot in LOM, situated on a relatively uniform slope, has a volume of 1,116 m^3, which is the same order as the other three sites (Motta et al., 2011). The beech accounts for 19.6 to 38.3% of the basal area in JAN and BGO, respectively. Silver fir is the dominant species at all sites, ranging from 46.6% in LOM to 59.8% in PER. The incidence of Norway spruce is higher in the northern sites (LOM and JAN) than in the southern ones (PER and BGO). Additionally, all sites have an impressive amount of CWD, ranging from 305.0 m^3 ha^{-1} in LOM to 410.7 m^3 ha^{-1} in BGO. Despite having high densities and volumes, all sites are relatively rich in regeneration, with LOM having the highest density with 4,772 individuals per hectare and PER having the lowest with 2,312 individuals per hectare. The carbon stocks range from 398.0 MgC ha^{-1} in LOM to 484.0 MgC ha^{-1} in JAN. The diameter distribution (Figure 3) has the structure of the uneven-aged forests and has a rotated sigmoid shape (Motta et al., 2015b) which is the typical distribution of the old-growth stage (Goff and West, 1975; Lorimer et al., 2001). The stature (i.e., the average of the five highest trees) a fertility index for uneven-aged and multilayered forests (Susmel, 1980) ranges between 55.8 m in BGO and 46.8 m in LOM (see Supplementary material for further details).

The in-depth study of the two IPP in LOM and PER has shown a density of large trees (DBH >1 m) of 19 trees per hectare in LOM (11 silver firs and 8 Norway spruce) and 14 trees in PER (11 silver firs and 3 Norway spruce). The largest beech has a DBH of 82 cm and 90 cm in LOM and PER, respectively (see Supplementary material for further details).

3.2 Growth patterns and age

We detected 564 releases in the IPP of LOM (493 trees analyzed) and 469 releases in PER (296 trees analyzed). The mean percentage of release per tree and the percentage of trees with release are slightly lower in LOM (about one release/tree and 64% of trees with release) than in PER (about 1.5 release/tree and 80% of trees with release).

Eighty-seven percentage of the decades in LOM and 77% of the decades in PER have less than 10% of the trees showing a release

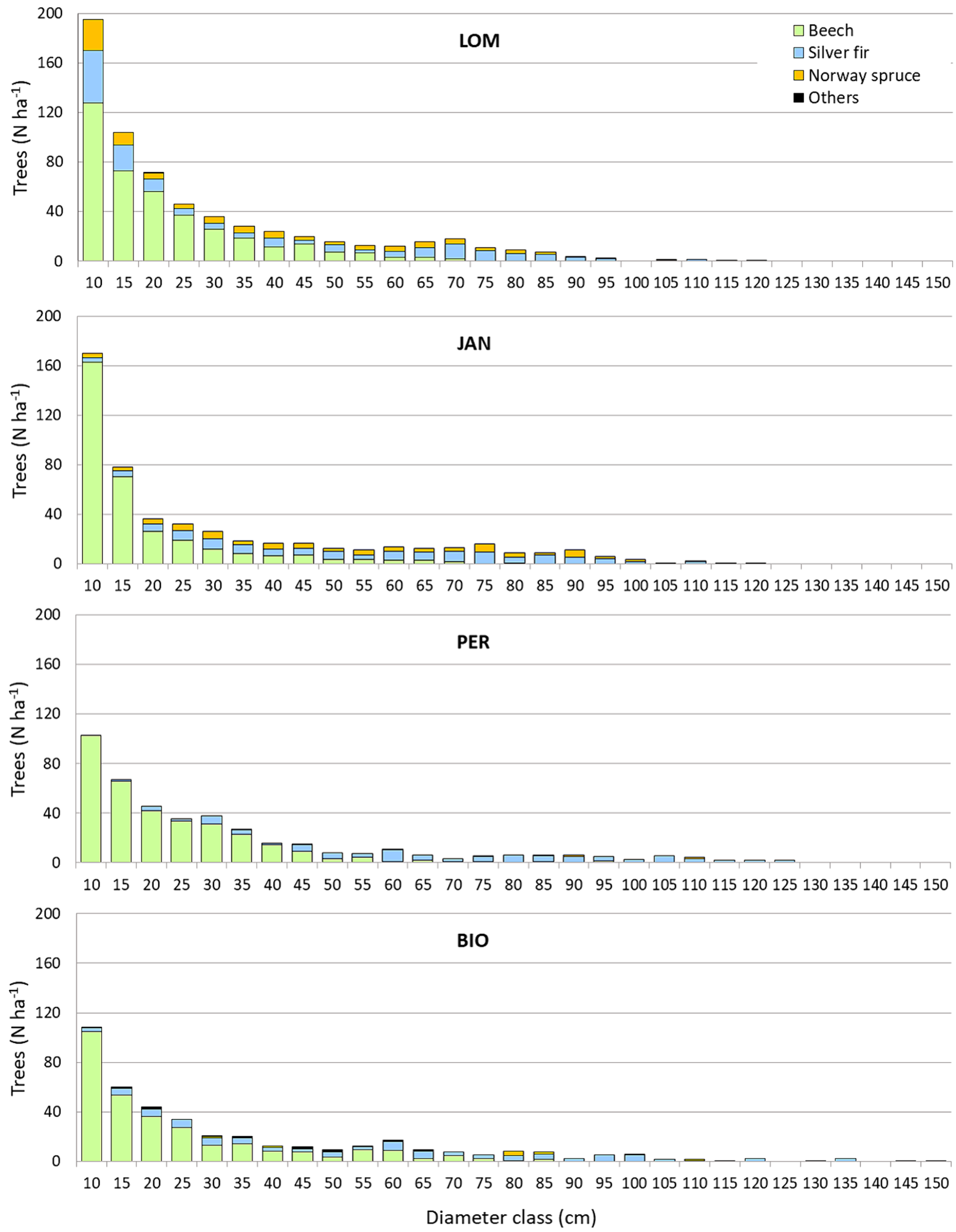

FIGURE 3
Diameter distribution in the four study sites.

(Figure 4). At both sites, 13% of the decades have between 11 and 20% of trees with releases. In LOM, there is a low and regular distribution of the percentage of released trees, with a maximum percentage of about 13%. In PER, the pattern is characterized by slightly higher inter-decadal variability. However, the percentage of trees with release is over 20% (maximum 26%) only in two decades: 1880 and 1960. These conditions of low and quite regular % of releases for each decade have been relatively stable in both forests for the last three centuries.

The age of dominant trees by species and site is summarized in Table 5. The three species showed similar maximum ages (except for Norway spruce in BGO affected by sampling limitations), and the age of oldest trees are near to the maximum biological age of the species (Castagneri et al., 2013; Piovesan and Biondi, 2020). Maximum age is achieved by silver fir in PER (487 years) and by beech in BIO (486 years). For Norway spruce, we cannot estimate the age of the oldest trees, neither in LOM nor in PER, due to the decay, but the maximum age is of the same order (>454 years in PER). As the estimated age is related to the coring height (130 cm above the ground), we can suppose that, taking into account the years employed by the tree to reach the sampling height, the oldest dominant trees should have an age >500 years. The two 1 ha sampling plots (see Supplementary material for further details) have a density of 15 trees ha^{-1} having >400 years at the sampling height (50 cm) in LOM (2 beeches, 7 silver firs, and 7 Norway spruces) and 11 trees ha^{-1} in PER (4 beeches, 5 silver firs, and 2 Norway spruces).

3.3 Patterns of forest structure

The forest structure of the four old-growth forests of the Dinaric Alps suggests some similarities and differences among sites. The difference is expressed by the distance among their centroids in the ordination environment and the similarities are expressed by the overlap among convex hulls polylines indicating the maximum surface area occupied by plots belonging to the same site: blue JAN, yellow LOM, grey BGO, and green PER (Figure 5). Considering the whole surface area occupied by the convex hulls, we observed that overlapping sites occupied 61.1% of this surface area and 15.3% was the proportion occupied by all the 4 sites. Instead, only 38.9% of this surface area was occupied by non-overlapping convex hulls. PER and BGO emerged as being quite similar regarding forest structure expressed by many structural data but particularly by a higher quantity of CWD and a lower proportion of Norway spruce. LOM and JAN were characterized by denser (De) and diverse (HD) stands with a higher density of regeneration (R-tot) and a higher volume of stumps (most of the stumps are of natural origin but in JAN and LOM there are also a few signs of human activity at the borders between the former core area and the buffer zone). JAN resulted separated from LOM along a gradient of overall basal area (BA), volume (Vol) and a lower proportion of beech. Therefore, the structural variability is PER > BGO > JAN > LOM. The overlapping is very high between PER and BGO and decreases following a latitudinal gradient towards JAN and LOM. The surface area proportion occupied by the convex hulls of the

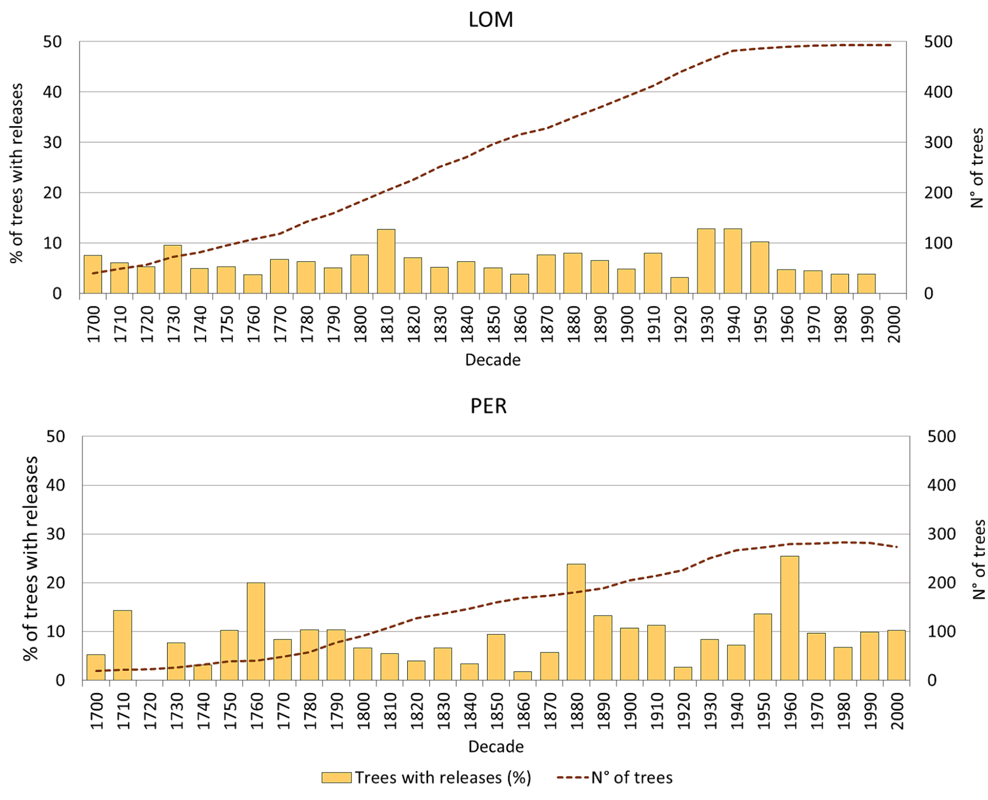

FIGURE 4
Release from suppression chronologies for the two 1 ha permanent plots analyzed (percent of trees showing abrupt growth release in a decade), including sample depth.

TABLE 5 Maximum ages of the dominant trees in the four study sites.

	Abies alba		*Picea abies*		*Fagus sylvatica*	
	No. trees	Max age	No. trees	Max age	No. trees	Max age
LOM	28	441	30	>430	30	>409
JAN	17	>403	23	403	21	472
PER	13	487	19	>454	20	>479
BIO	17	>359	12	299	18	486

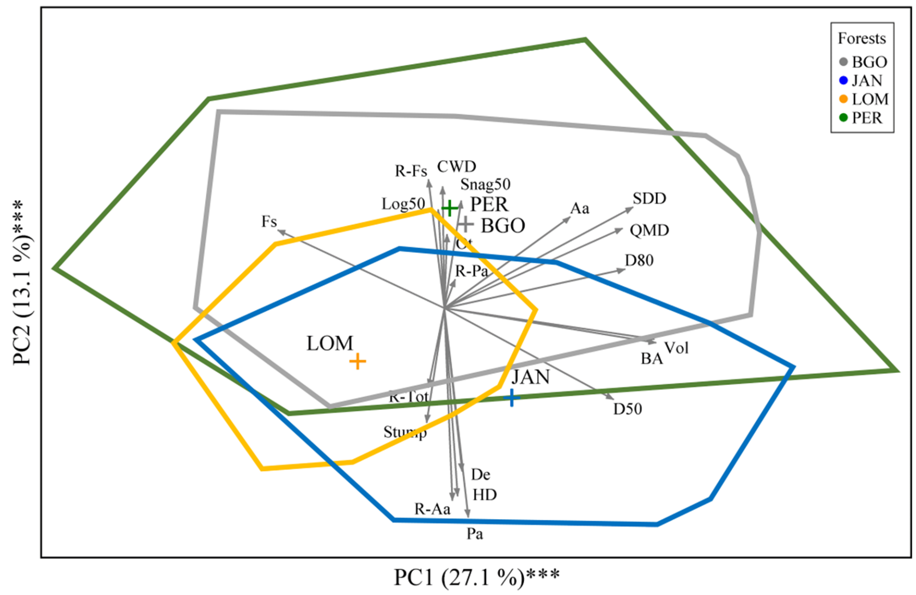

FIGURE 5
Principal component analysis of 142 plots of 4 old-growth forests of the Dinaric Alps indicated by colored lines with (blue for JAN, yellow for LOM, grey for BGO, and green for PER). Gray arrows indicate forest structure variables (*n* = 20) and colored polygons indicate convex hulls.

4 study sites was 12.3% (LOM), 22.1% (JAN), 26.3% (PER), and 39.4% (BGO).

4 Discussion

4.1 Old-growthness

All the selected study sites fit in the strict old-growth structural criteria reported in Table 1. The four sites have the highest volume of living trees for the mixed montane forests of the central-southern part of Europe (Table 6). The high quantity of living biomass is typical of the old-growth stage. However, this characteristic is not an indicator of naturalness itself since high levels of biomass can also be found in managed forests or in forests that are in development stages (e.g., mature or transition) earlier than the old-growth one (Castagneri et al., 2008; Molina-Valero et al., 2021). The four sites have a stratified vertical structure, an uneven-aged age structure with low relationships between age and diameter (Motta et al., 2011), a rotated sigmoid diameter distribution (Motta et al., 2015b), and a clumped horizontal structure (Lingua et al., 2011). All these structural characteristics are peculiar of the old-growth developmental stage. The tree species approach their maximum age expectancy not with sporadic individuals but with many dominant trees ($15\,ha^{-1}$ older than 400 years in LOM and $11\,ha^{-1}$ PER) and are richer in large and old trees (Table 5) compared to other OGF of the Carpathians (Pavlin et al., 2021).

All the study sites have impressive amounts of CWD ranging between 305.0 and 410.7 $m^3\,ha^{-1}$ (Table 4). The high quantity of CWD is peculiar to the old-growth stage and is the legacy of the long-term small-scale disturbance history that has characterized the dynamics in the last centuries (Lombardi et al., 2012; Mikolas et al., 2021; Motta et al., 2023). Besides, all sites have a high density of large (>50 cm DBH) snags (ranging between 18 and 27 ha^{-1}) and logs (between 33 and 46 ha^{-1} with largest diameter >50 cm) (Table 4).

The high regeneration density is related to the fact that all the dominant species are shade-tolerant and can regenerate and establish below the forest cover and to the small-scale disturbances that create gaps that allow the regeneration to establish and grow continuously in the stand. The canopy gap fraction in the studied sites is 19.3% in LOM, 17.2% in PER, and, in extended gaps fraction, 41.4% in LOM, and 39.7% in PER (Nagel and Svoboda, 2008; Bottero et al., 2011).

Tree rings provided detailed insight into temporal patterns of forest disturbance history in LOM and PER. In both forests, most decades in the last three centuries experienced less than 10% of

TABLE 6 Stand characteristics of some of the most important mixed *Abies-Fagus-Picea* old-growth forests in central and south-east Europe.

Site	Altitude (m a.s.l.)	Density (N ha^{-1})	Basal (m^2 ha^{-1})	Volume living trees (m^3 ha^{-1})	CWD volume (m^3 ha^{-1})	Reference
Zofínský prales (CZE)	735–825	206	40.9	695	202	Kral et al. (2010)
Dobroč (SVK)	720–1,000	388	43.8	687	256	Saniga et al. (2011)
Badínsky prales (SVK)	700–850	394	42.3	794	200	Kucbel et al. (2010)
Hrončokovský Grúň (SVK)	730–1,050	243	41.8	724	306	Holeksa et al. (2009)
Dobročský prales (SVK)	885–965	413	44.9	731	313	Parobeková et al. (2018)
Sinca (ROM)	790–1,400	556	57.6	918	135	Petritan et al. (2015)
Slătioara (ROM)	800–1,510	860	49.6	659	158	Duduman et al. (2020)
Čorkova uvala (CRO)	860–1,030	510	46.1	753	291	Saniga et al. (2011)
Lom (BiH)	1,250–1,520	468	45.3	747	305	This paper
Janj (BiH)	1,280–1,400	516	66.7	1,201	371	This paper
Perućica (BiH)	1,340–1,510	432	59.1	994	411	This paper
Biogradska Gora (MNE)	1,210–1,450	412	60.1	1,022	374	This paper

canopy opening signs (release from suppression). We have observed in one decade a maximum of 16% of trees showing a release in LOM and 26% in PER, with only two decades with >20% of trees showing a release in PER. Thus, the dynamics of these stands have been strongly controlled by small-scale disturbances that have maintained a typical small-gap structure for a relatively long time. According to this small level of disturbances, these stands can be classified at the limit of the range of dynamics, from disturbance-structured to near steady-state (Antos and Parish, 2002; Halpin and Lorimer, 2016).

The methodological approach used here has the potential to reconstruct the disturbance history carefully, but conversely, this can be done at a relatively small scale, in this case one hectare (Nagel et al., 2014). Thus, these results have to be taken with caution as, if we had expanded the structural analysis at the landscape scale, we could have detected some legacies of past infrequent intermediate severity-disturbances from fire (PER), wind (PER, BGO, LOM) and from small landslides and snow avalanches (BGO), large enough to favor the regeneration of more light-demanding tree species like maple and other broadleaves (Nagel et al., 2014; Motta et al., 2015a). Besides, more intensive past land use by the local population has been observed locally and at the regional scale during the middle ages (Finsinger et al., 2022; Cagliero et al., 2022b). The extensive overlap between convex hulls (Figure 5) confirms the commonality of structures and processes already observed in the structural data and the disturbance regime.

4.2 Old-growth forests as reference or benchmark

The current forest cover of OGF in Europe is residual (or even absent for many forest types, particularly in temperate and Mediterranean forests), since most European forests have been intensively managed and, even if withdrawn from regular management, show structural legacies of the past land use. After the cessation of the management, some structural elements can recover faster, and, in contrast, others recover only in the long term. For example, large dead trees, old trees, rotated sigmoid diameter distribution, gap fraction, development of microhabitats (von Oheimb et al., 2005; Paillet et al., 2010; Meyer and Schmidt, 2011; Albrich et al., 2021; Kõrkjas et al., 2021) and the time framework of the restoration (Frelich et al., 2005; Nagel et al., 2013) is often measured not by decades but by centuries (Motta et al., 2015b; Albrich et al., 2021; Meyer et al., 2021; Martin-Benito et al., 2022; Larrieu et al., 2023).

The criteria adopted by the recent EU Guidelines (European Union Commission, 2023a) "Defining, Mapping, Monitoring and Strictly Protecting EU Primary and Old-Growth Forests" are relatively broad and not well-defined. Consequently, most of the selected and mapped OGF according to the EU guidelines could have a low rate of old-growthness and could not adequately represent the final stage of the forest dynamics. The EU approach considers as OGF those stands "*relatively old and relatively undisturbed by humans*." As such, it identifies a critical amount of forests mostly represented by "*future potential old-growth*" (Spies, 2004), but, even if it is an appropriate approach to protect the residual biodiversity related to late seral developmental stages, has limits both for strict protection of current OGF and for those scientific goals that need an absolute reference of the final stage of the forest dynamic processes. The priority of biodiversity conservation would be to accurately select the "current" old-growth stands, analyze their distribution, and protect them at the continental scale. These forests represent a residual fraction of the continental forest cover and deserve a different recognition and designation among the massive selection made by the EU Guidelines. A fundamental issue is related to the scientific purposes connected to the old-growth designation. Indeed, for scientific research, only OGF selected with strict criteria can be reliably used as a reference or benchmark (Table 7). Another issue to be taken into account when research and benchmarking are involved is the need to

TABLE 7 Reference and benchmark roles played by old-growth forests for which a strict definition is necessary.

OGF scientific role	Main references
Reference to measure the rate of the current old-growthness of managed forests and forests withdrawn from regular management	Bauhus et al. (2009), Paillet et al. (2015), Motta et al. (2015b, 2023), Albrich et al. (2021), Meyer et al. (2021) and O'Brien et al. (2021)
Reference to model the closer-to-nature silviculture and resource sustainable management	Kuuluvainen et al. (2021), Larsen et al. (2022), Mason et al. (2022) and European Union Commission (2023b)
Reference for climate change impact in forests not affected by human activities	Castagneri et al. (2014), Bosela et al. (2017), D'Amato and Palik (2020), Colangelo et al. (2021), Mercer et al. (2022) and Máliš et al. (2023)
Reference for restoration of high-value forest habitats and for the rewilding strategies	Götmark (2013), Jamie et al. (2020), Sabatini et al. (2020), Ding et al. (2021), Palli et al. (2022) and Kuuluvainen and Nummi (2023)
Hot spot of genetic conservation	Spies and Franklin (1996), Frelich and Reich (2003), Mosseler et al. (2003) and Hamrick et al. (2006)
Carbon storage benchmark for sustainable forest management and for climate-change mitigation policies	Hoover et al. (2012), Liu et al. (2014), Matuszkiewicz et al. (2021), González et al. (2022), Birdsey et al. (2023), Fraser et al. (2023), Hoover and Smith (2023), Bono et al. (n.d.) and Keith et al. (n.d.)

assure long-term potential conservation of the whole range of variability (Hansen et al., 1991) inherent to the complete forest dynamics, including stand-replacing disturbances and early seral stages. For this purpose, it would be necessary to define a minimal critical size of old-growth sites (Landres et al., 1999; Veblen, 2003; Peck et al., 2015). The *Abieti-fagetum* is not characterized by high severity and large disturbance events (Senf and Seidl, 2021), and in the studied Dinaric forests, we have not observed stand-replacing disturbances larger than 1 ha, even at the landscape scale (Garbarino et al., 2012; Motta et al., 2015a). However, considering a comprehensive variability covering the European range of the montane forest types, we have to take into account the occurrence in this forest type of high-severity stand-replacing events larger than 15 ha (Maroschek et al., 2023). In a temperate primary forest, depending on the longevity of the trees and on the persistence of each developmental stage, the percentage of the forest covered with old-growth stage can vary approximately from 25 to 60% (Swanson et al., 1994; Oliver and Larson, 1996). As a consequence, we can hypothesize, in a prudential way and according to the information currently available, a size of at least 25–30 ha to host the current and future entire range of variability of the different developmental stages of the forest dynamics (Landres et al., 1999; Keane et al., 2009) and to guarantee long-term conservation of the whole biodiversity associated to the forest type. A more detailed study will be necessary to explore the range of variability in the European forest types as natural disturbance regimes and interactions among disturbances at different spatial and temporal scales are poorly understood (Landres et al., 1999). Besides, future climate change impacts can significantly impact the current framework (Seidl et al., 2017; Thom et al., 2017).

5 Conclusion

Old-growthness is a dynamic process and the development of the old-growth stage takes a long time (Oliver and Larson, 1996). This time depends on forest type and on-site characteristics, but the old-growth stage's structural characteristics are similar among forests belonging to the same forest type (Franklin et al., 1981).

The four studied Dinaric forests have all the basic and seminal structural indicators of an OGF: large trees (>10 trees per ha with DBH above 100 cm), old trees (more than 10 trees per ha older than 400 years old), a huge amount of CWD (>300 m^3 ha^{-1}) and a diversified vertical and horizontal structure (Franklin et al., 1981, 2005). The structure shows the same structural patterns and developmental processes across all the studied sites. All three main species are approaching their maximum age expectancy. The four studied forests share a set of most refined structural and functional indicators (e.g., rotated sigmoid diameter distribution, gap fraction, disturbance history) that are critical to defining the threshold between late seral and over-mature forests and strict old-growth (Whitman and Hagan, 2007; Motta et al., 2015b; Meyer et al., 2021; Price et al., 2023).

In Europe, there are very few forests that fit strict OGF parameters. Most of the research and the governance guidelines currently focus on protecting the residual OGF biodiversity using broad definitions of old-growth and including late-seral stands and forests that have been withdrawn from management for a few decades. This policy is commendable for identifying a critical amount of forest cover at the continental scale. Besides this, we need to define a sub-set of forests using a "robust" and "reliable" definition of strict OGF to be considered a priority for biodiversity conservation against late seral, transition, and future OGF (Woodall et al., 2023). We must recognize the irreplaceable conservation and scientific value of the current OGF (selected with strict criteria), and if we did not take apart the strict OGF from the other forests, any use of them as a reference or benchmark would be impossible or misleading (Table 7).

As it is not possible to define a threshold that covers different forest types, fertility classes, and regional-local peculiarities, basic structural parameters associated with a "combined provisions" made by experts and supported by field, remote sensing data, adjusted to criteria at local scales, and incorporating social and traditional knowledge could be used to define the old-growthness of each forest. We can expect that it will not be possible to identify stands with these characteristics in all the European forest types, but this information is currently missing and will be relevant for future European policies regarding forest conservation. Finally, the definition and mapping of strict OGF, given the importance of these references also for EU forests, should be expanded on sites currently outside the EU's borders, like most of the OGF in the Dinaric mountains.

Data availability statement

The raw data supporting the conclusions of this article will be made available by the authors, without undue reservation.

Author contributions

RM: Conceptualization, Data curation, Formal analysis, Funding acquisition, Investigation, Methodology, Supervision, Writing – original draft, Writing – review & editing. GA: Data curation, Investigation, Methodology, Writing – original draft, Writing – review & editing. DA: Data curation, Investigation, Writing – original draft, Writing – review & editing. RB: Data curation, Formal analysis, Investigation, Writing – original draft, Writing – review & editing. SB: Data curation, Investigation, Writing – original draft, Writing – review & editing. AB: Data curation, Formal analysis, Investigation, Writing – original draft, Writing – review & editing. CM: Investigation, Writing – original draft, Writing – review & editing. DV: Investigation, Writing – original draft, Writing – review & editing. WF: Data curation, Formal analysis, Investigation, Methodology, Writing – original draft, Writing – review & editing. MG: Data curation, Formal analysis, Investigation, Methodology, Writing – original draft, Writing – review & editing. ZG: Data curation, Investigation, Writing – original draft, Writing – review & editing. SK: Data curation, Formal analysis, Investigation, Writing – original draft, Writing – review & editing. FM: Investigation, Writing – original draft, Writing – review & editing. FR: Data curation, Formal analysis, Investigation, Writing – original draft, Writing – review & editing. PN: Data curation, Investigation, Methodology, Writing – original draft, Writing – review & editing.

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Conflict of interest

The authors declare that the research was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

The author(s) declared that they were an editorial board member of Frontiers, at the time of submission. This had no impact on the peer review process and the final decision.

Publisher's note

Supplementary material

The Supplementary material for this article can be found online at: https://www.frontiersin.org/articles/10.3389/ffgc.2024.1371144/full#supplementary-material

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