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Dynamics and Structural Changes in the Janj Mixed Old-Growth Mountain Forest: Continuing Decline of Conifers

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Abstract: Old-growth forests are rare in Europe, yet they play a critical role in biodiversity and carbon storage. This study examines the structural dynamics of the Janj old-growth forest in the Dinaric Alps using repeated field measurements from 2011 and 2021 at 39 systematically arranged 12 m radius plots. All trees (DBH $\geq$ 7.5 cm), regeneration (10 cm height to 7.5 cm DBH), and coarse woody debris (CWD) were assessed. Results revealed that total basal area declined by 3.5 m^2 ha^{-1} over the decade, primarily driven by significant reductions in stem density for silver fir (p = 0.001) and Norway spruce (p = 0.001). In contrast, European beech maintained a stable basal area throughout the study period. Moreover, silver fir exhibited a significant increase in mean diameter (p = 0.032) and a pronounced rise in regeneration individuals (t = 3.257, p = 0.002). These findings underscore a gradual compositional shift towards European beech dominance, with conifers facing higher mortality in larger diameter classes. The substantial volume of CWD (463 m^3 ha^{-1}) highlights advanced decay dynamics consistent with mature forest conditions. This study emphasizes the value of repeated measurements to capture subtle yet important successional changes in primeval forests, which is essential for conservation planning and sustainable forest management.

Keywords: old-growth forest; structural dynamics; conifers decline; coarse woody debris; regeneration; monitoring of forest structure; beech; fir; spruce

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1. Introduction

Old-growth forests are exceedingly rare in Europe with less than 3%, likely only 0.9% [1,2], of Europe's total forested area, with only 46% currently under legal protection [3]. The lack of reference conditions for studying old-growth patterns and processes [4], combined with inconsistent inventory data assessment tools in Bosnia and Herzegovina [5,6] makes it difficult to ensure sustainability [7,8]. Numerous forests within the Southeastern Alps and Dinaric Mountains have reached an old-growth stage, yet a significant portion of these areas lacks a formal protection within forest reserves [9]. The Dinaric Mountains are recognized as a hotspot for the existence of late-successional mountain mixed old-growth forests. They are primarily composed of European beech (*Fagus sylvatica* L.), silver fir (*Abies alba* Mill.) and/or Norway spruce (*Picea abies* (L.) Karst). [1,10], with an unusually high amount of standing dead trees, without intensive anthropogenic disturbance over past millennia [11]. In contrast to the Western Carpathians, the Dinaric forests exhibit a notably higher proportion of conifers and the highest stand volumes [12].

Old-growth forests are critical reservoirs of biodiversity, carbon storage, and ecological processes essential for forest dynamics and resilience [13]. Studying and monitoring old-growth forests as a "school of nature" is essential for implementing a close-to-nature approach [14,15] and is crucial for understanding their dynamics in relation to ongoing environmental change disturbances [16–18]. Increased knowledge of forest disturbances also contributes to the development of close-to-nature forest management approaches for surrounding or similar forests [17–19]. In old-growth forests, natural processes have been the primary force driving forest dynamics for centuries [20], making it essential to mimic observed natural disturbance patterns in a given area through management practices [21], along with retaining sufficient deadwood and other structural elements, to maintain forest integrity and prevent significant biodiversity loss [22]. Monitoring and comprehending shifts in tree mortality across various scales is crucial [23], as increased tree mortality may alter forest population structures towards younger trees [24] subsequently diminishing the carbon-storage potential of old-growth forests [25,26]. Certainly, in the absence of datasets over a century or more, the integrative approach to consolidating multiple, smaller-scale, multidecade studies becomes an essential component of our science [27].

The current trends in mixed old-growth mountain forests of the Slovenian Alps [28,29] Carpathians [30–33] and Bosnian Dinarides [34–36] demonstrate a parallel decline of conifers alongside the progression of European beech, suggesting that the regeneration and future of fir as a species may be uncertain, particularly in light of large-scale disturbances [37]. In Bosnia and Herzegovina, game density does not limit the recruitment of fir [38], unlike in other European managed and unmanaged forests where such limitations have been observed [39–45]. In the absence of frequent gap-creating disturbances in old-growth forests, beech trees demonstrate significant dominance within their habitats [46,47] effectively inhibiting the growth of other broadleaved tree species and thereby maintaining their own composition [48].

Conversely, in many European old-growth forests, the proportion of fir trees is likely to decrease substantially or even disappear entirely in the near future [49]. The Janj old-growth forest (OGF) in Bosnia and Herzegovina, although less studied than Perućica and Lom, offers valuable insights into these dynamics. Previous research on Janj has primarily focused on the current structural composition [12,50–52] with less emphasis on temporal and spatial stand dynamics. However, comparative analyses of different studies suggest a consistent decline in coniferous trees, as also noted by Keren [35], between 1965 and 2011.

This research represents the first decadal-scale reassessment of the Janj old-growth forest in Bosnia and Herzegovina, providing an unprecedented temporal comparison of forest structural dynamics, regeneration, and mortality trends in this Dinaric primeval forest type. By integrating comprehensive field measurements with spatially explicit assessments of coarse woody debris (CWD), the study not only extends the limited knowledge base established by earlier studies but also establishes a critical reference for future monitoring efforts under changing environmental conditions. Moreover, this work applies a rigorous statistical framework to identify species- and diameter class-specific trends, thereby offering novel insights into the successional processes shaping the current and future composition of these unique forest ecosystems.

Therefore, the objectives of the research were (i) to investigate the structural changes, developmental dynamics, and mortality trends within the core area of *Piceo-Abieti-Fagetum* OGF in the Bosnian Dinaric Mountains, (ii) to assess the interrelationships between tree species composition, diameter size distribution and regeneration dynamics over a decade-long period, and (iii) to quantify CWD by categories and establish the ratio between total volume of CWD and living trees.

2. Materials and Methods

2.1. Study Site

The research was conducted in the core area of the Strict Nature Reserve (SNR) Prašuma Janj (IUCN category Ia). This reserve achieved a significant milestone in 2021 by being inscribed on the UNESCO list of Ancient and Primeval Beech Forests of the Carpathians and Other Regions of Europe. This recognition is particularly noteworthy, as the sole representative of its kind in Bosnia and Herzegovina [53]. The reserve covers 295 hectares and is located on the western slopes of Stolovaš (44°08′ N, 17°17′ E), a mountain in north-western Bosnia and Herzegovina (B&H) within the Dinaric massif (Figure 1). The core area of the reserve spans 57.2 hectares, with elevations ranging from 1260 to 1400 m above sea level, characterized by homogeneous stand conditions. The terrain has a gentle slope of three to four degrees, facing north-northwest. The parent rock consists of dolomite bedrock, resulting in rendzina and brown soils of varying depths. The vegetation cover contributes to the development of mesophilic conditions and the formation of raw humus, supporting diverse ground vegetation. This has further facilitated the formation of deeper soils, particularly on gentle slopes and flat areas. In addition to rendzina, brown rendzina and brown soils occur in a complex mosaic, while small units of illimerized soils are also present, reflecting the interplay of abiotic and biotic factors that enhance the site's overall productivity [54,55]. The mean annual rainfall is 1200 mm, with a mean annual temperature of approximately 5 °C.

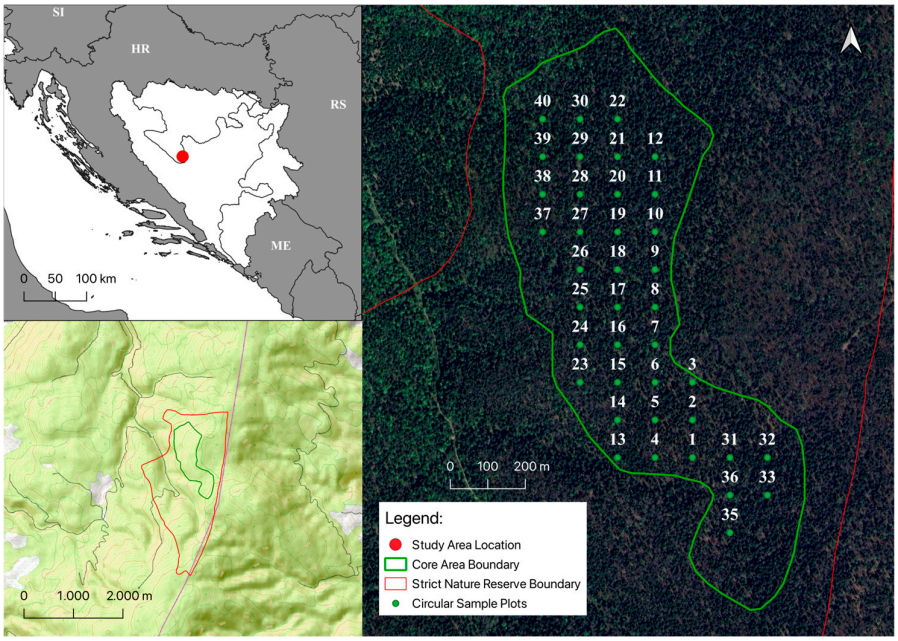


Figure 1. Location of the Janj Strict Nature Reserve in Bosnia and Herzegovina, showing the study area location (red dot), the core area boundary (green line), the strict nature reserve boundary (red line) and the distribution of circular sample plots (green circles).

The research focuses on an old-growth forest (OGF) stand that is untouched by anthropogenic influence and develops exclusively under natural ecological conditions. The core area of the old-growth forest Janj has been classified as the plant association *Piceo-Abieti-Fagetum* [35,56,57]. Originally designated, the reserve's primary purpose was to serve as a focal point for scientific research. Data on the protection of this reserve traces back to the Austro-Hungarian era, but the first official protection began in 1954 when the State Institute for Protection of Cultural Monuments and Natural Rarities in Bosnia and Herzegovina made a conservation decision [12,57].

2.2. Field Measurements

Fieldwork and measurements in OGF Janj were conducted during the summer of both 2011 and 2021, encompassing comprehensive assessments of the study area at two distinct time points. A regular 100-m grid with 39 systematic sampling points in the core area was overlaid. Each grid intersection served as the center of a sampling plot, where inventories included recording species and diameter at breast height (DBH) to the nearest 0.01 m for all living trees above 7.5 cm within a 452 m^2 circular plot (radius = 12 m). Heights of living trees were measured (to the nearest 0.5 m) for a subset of 100 trees, including European beech, silver fir and Norway spruce with additional Sycamore maple in regeneration. Additionally, within a 78.5 m^2 circular plot (radius = 5 m), species of regeneration individuals ranging from 10 cm in height to 7.5 cm DBH were recorded [35,38,58]. Furthermore, measurements of coarse woody debris (CWD) were conducted on the same 39 permanent plots used for living tree measurements, ensuring identical sampling locations and thus enabling reliable temporal comparisons. CWD was classified into three groups: snags (standing dead trees with a DBH of $\geq$7.5 cm and a height of $\geq$1.3 m), logs (fallen stems or branches with a diameter of $\geq$7.5 cm measured at their midpoint and a length > 1 m), and stumps (short, vertical remnants from cutting or windthrow, with a top diameter $\geq$ 7.5 cm and a height < 1.30 m). The differentiation between snags and logs was determined based on a 45° leaning angle [35,59]. For each element of CWD, the decay class was determined (class 1—fresh, class 5—very old) [60,61].

2.3. Data Analysis

Data analysis was conducted using the software package Microsoft Excel Version 2019 and SPSS Statistics Version 26.0. Descriptive statistical analysis was utilized to compare the fundamental structural parameters and regeneration characteristics of the core area of OGF Janj at two time points (2011 and 2021). All mapping and spatial data analysis were conducted using QGIS 3.28.2., employing the Inverse Distance Weighting (IDW) interpolation method [62,63]). To assess site quality based on tree species, we compared height curves derived from this study with standardized site quality curves for European beech, silver fir and Norway spruce applicable in Bosnia and Herzegovina. The average height of the upper stand story was determined using the heights of the 20 largest diameter trees for each species. The volume of living trees and snags, comprising the whole stem with branches and twigs, was calculated following local volume tables [64]. To estimate the volume of logs, stumps, and broken snags, the method described by Motta was applied [60]. Basal area (m^2 ha^{-1}) was calculated as the sum of the cross sectional areas of all trees at breast height (1.3 m), using the Formula (1) for each individual tree:

$$BA = \frac{\pi \cdot DBH^2}{4 \cdot 10,000} \quad (1)$$

where, DBH is the diameter at breast height in centimeters [65].

Classical forest structure attributes for living trees (stem density, mean diameter, basal area and growing stock) and regeneration (density of understory trees from 10 cm in height to 7.5 cm DBH, divided by species) were utilized to assess difference between the measurements conducted in 2011 and 2021, as well as the structure dynamics between these two time points. Therefore, the following attributes were compared: stem density, distribution shapes of DBH, tree species composition, mean diameter, basal area (BA) and growing stock (GS). Analyzing the basic elements of the structure was conducted based on diameter classes with a width of 5 cm. A paired *t*-test for dependent samples was conducted at a significance level of 0.05 to compare the measurements taken in 2011 and 2021. This statistical method was chosen to evaluate whether there were statistically

significant differences within the structural attributes of OGF Janj over the course of one decade.

3. Results

3.1. Forest Structure Changes and Regeneration

Over the decade-long period from 2011 to 2021, the total estimated stem density, basal area (BA) and growing stock (GS) volume in OGF Janj decreased (Table 1). However, the decline varied among species within the mixture. The stem density of living trees per hectare, with DBH greater or equal to 7.5 cm, decreased by 3% per decade, an average of 15 trees ha^{-1}. The stem density of silver fir decreased by 12 trees ha^{-1} and Norway spruce by 9 trees ha^{-1}. In contrast, European beech density increased by 6 trees ha^{-1}, which is the opposite of the conifer trend.

Table 1. Structural characteristics of the Janj old-growth forest (core area) in 2011 and 2021.

Species	Year	Stem Density ($ha^{-1} \pm \sigma$)	Mean Diameter (cm $\pm \sigma$)	Basal Area ($m^2\ ha^{-1} \pm \sigma$)	Growing Stock ($m^3\ ha^{-1} \pm \sigma$)
Silver fir	2011	119 ± 53.6 *	60.1 ± 14.5 *	34.6 ± 3.4	623.4 ± 389.6
	2021	107 ± 48.5	62.2 ± 16.0	32.3 ± 3.1	579.1 ± 346.7
European beech	2011	327 ± 163.4	58.6 ± 18.7	12.1 ± 1.0	191.5 ± 141.5
	2021	333 ± 157.1	59.9 ± 20.1	12.1 ± 1.1	191.1 ± 150.1
Norway spruce	2011	73 ± 44.3 *	22.8 ± 9.0	21.1 ± 2.7	353.7 ± 282.9
	2021	65 ± 38.4	22.2 ± 8.7	19.9 ± 2.9	331.2 ± 296.2
Total	2011	520 ± 155.5	41.0 ± 7.1	67.8 ± 2.7	1168.7 ± 303.1
	2021	504 ± 147.0	41.6 ± 6.9	64.3 ± 2.7	1101.4 ± 286.4

*—significant difference between 2011 and 2021 ($p < 0.05$); σ—standard deviation.

The analysis of stem density change by DBH class reveals distinct trends among the dominant tree species (Figure 2). Conifers, particularly silver fir, exhibited notable reductions in the 50–85 cm DBH range, suggesting elevated mortality and limited recruitment in these size classes. Norway spruce showed a widespread decline across most classes, aligning with its known sensitivity to drought and biotic stress. In contrast, European beech displayed a consistent increase in stem density in smaller DBH classes (≤30 cm), indicating successful regeneration and potential structural expansion. These patterns further support the hypothesis of a compositional shift favoring shade-tolerant broadleaves under conditions of prolonged canopy openings and reduced conifer competitiveness.

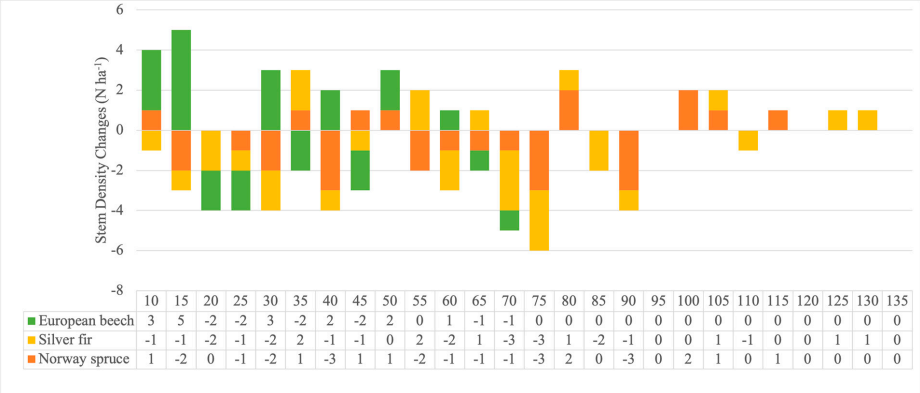


Figure 2. Change in stem density by DBH class (cm) between 2011 and 2021. Values represent changes in the number of trees per hectare within each DBH class. Positive values indicate an increase in stem count, while negative values indicate a decrease.

Statistical differences were assessed using a *t*-test ($p < 0.05$). The t-test results indicated significant changes in the stem density between 2011 and 2021 for silver fir (t = −3.747, df = 38, $p = 0.001$) and Norway spruce (t = −3.794, df = 38, $p = 0.001$), suggesting a notable decline. However, the change for European beech was not significant (t = 0.666, df = 38, $p = 0.509$). The total number of trees also did not exhibit a significant change (t = −1.592, df = 38, $p = 0.12$), suggesting overall stability in tree counts over the specified period (Figure 3a).

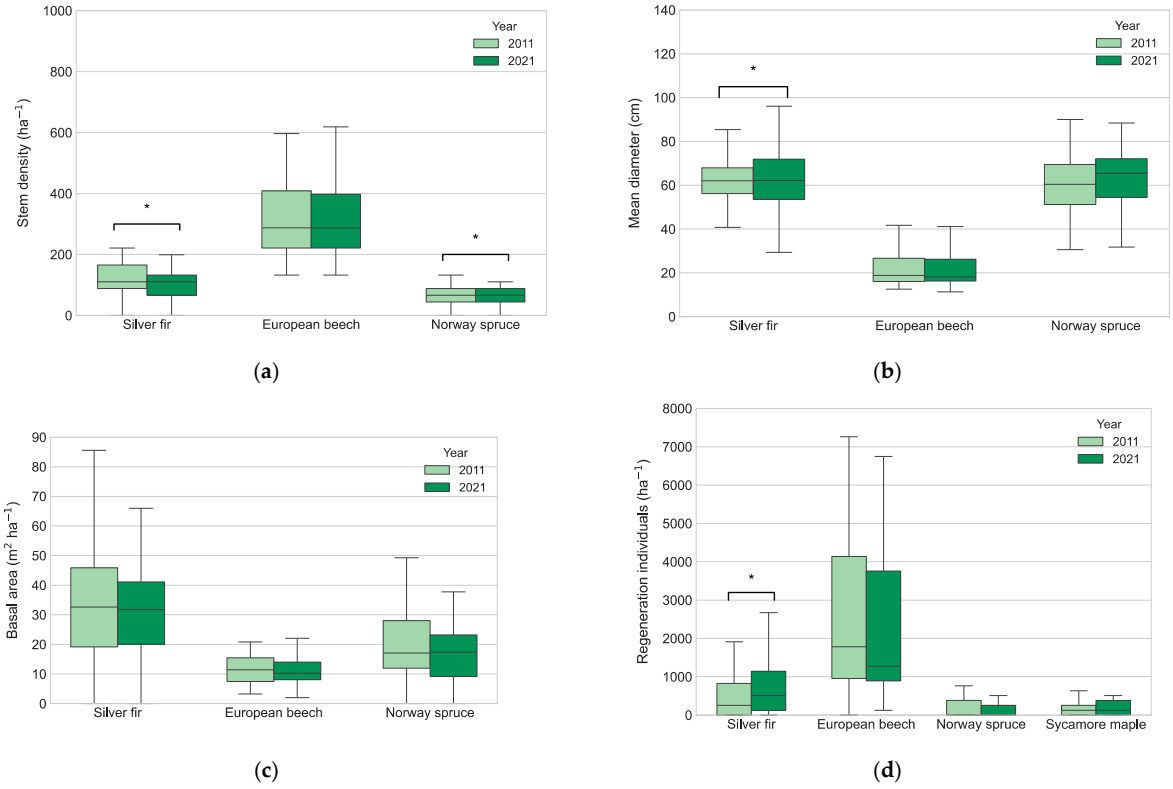


Figure 3. Boxplot comparison of structural attributes of the Janj old-growth forest between 2011 and 2021: (**a**) Stem density (ha^{-1}); (**b**) Mean diameter (cm); (**c**) Basal area (m^2 ha^{-1}); (**d**) Regeneration individuals (ha^{-1}); An asterisk (*) indicates a statistically significant difference between 2011 and 2021 ($p < 0.05$).

Over the observed decade-long period, the mean diameter of silver fir and Norway spruce has increased (2.04 and 1.25 cm, respectively), while the mean diameter of European beech has decreased (0.66 cm). Overall, the total mean diameter of trees did not exhibit a significant change (t = 0.923, $p = 0.362$), indicating relative stability in tree diameters over the specified period (Figure 3b).

The total basal area (BA) decreased from 67.8 in 2011 to 64.3 m^2 ha^{-1} in 2021, with an average of 5% (Figure 3c). BA of silver fir decreased by 2.3 m^2 ha^{-1} and Norway spruce by 1.3 m^2 ha^{-1}, whereas European beech showed no change. The t-test results indicate a significant increase in the mean diameter of silver fir (t = 2.223, $p = 0.032$). However, for European beech and Norway spruce, the changes in mean diameter were not significant (t = −1.015, df = 38, $p = 0.316$ and t = 0.652, $p = 0.519$, respectively).

Most of the core area showed minor changes (−10 to +10 m^2/ha), while significant reductions (up to −20 m^2/ha) were concentrated in plots 11, 15, and 28, indicating mortality in dominant trees. Positive dynamics (>10 m^2/ha) were recorded in peripheral plots, particularly in plot 32, suggesting vigorous growth or ingrowth (Figure 4a).

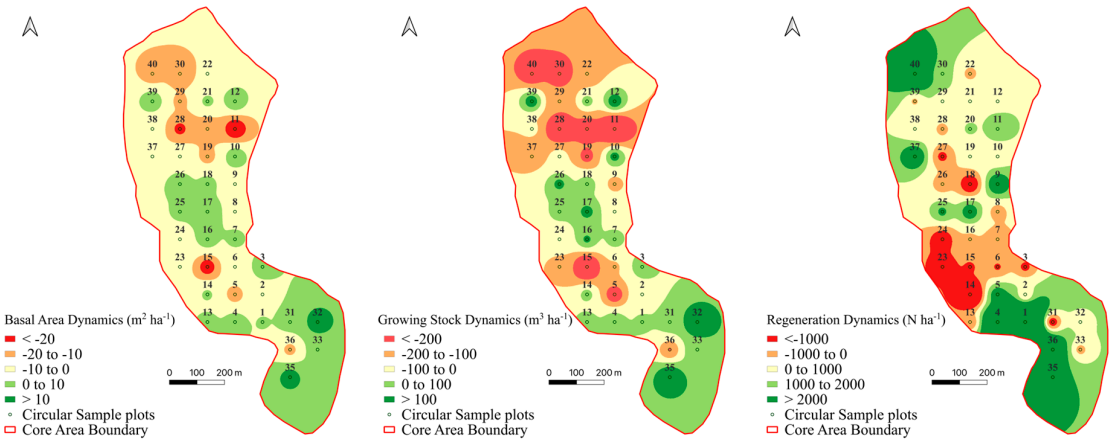


Figure 4. Changes in forest structural attributes in the core area of the Janj old-growth forest over a ten-year period (2011–2021): (**a**) Changes in basal area (m^2 ha^{-1}) by species; (**b**) Changes in growing stock volume (m^3 ha^{-1}) by species; (**c**) Changes in regeneration density (individuals ha^{-1}).

The total growing stock (GS) volume decreased by 68 m^3 ha^{-1}, from 1169 to 1101 m^3 ha^{-1} per decade. Conifers had the most impact on the decline in total GS volume. Notably, there was a continuous decline of 7% for silver fir and 6% for Norway spruce, whereas European beech showed no change.

The paired samples t-test results for both GS and BA, as well as overall and for all tree species, indicated no statistically significant differences at the 95% confidence interval. However, within the diameter class of 52.5 to 82.5 cm, both GS and BA exhibited statistically significant differences for silver fir ($t = -2.077$, $p = 0.045$ for BA; $t = -2.078$, $p = 0.044$ for GS) and overall ($t = -2.545$, $p = 0.015$ for BA; $t = -2.552$, $p = 0.015$ for GS). However, no significant differences were observed for European beech and Norway spruce.

There is a clear decline in the northern and central parts of the core area (e.g., plots 11, 15, 28, and 40), with losses exceeding 200 m^3/ha, while strong positive dynamics (>100 m^3/ha) occurred in southeastern plots (e.g., 32, 35), implying localized structural buildup, possibly due to lower disturbance (Figure 4b).

The estimated total number of regeneration individuals (understory), from 10 cm height to 7.5 cm DBH, increased from 4733 to 5828 individuals ha^{-1} during the period 2011–2021, representing a 23% increase. All species in the mixture contributed to the increase in the number of regeneration individuals, except for Norway spruce with a decrease of 14%. Silver fir increased the number of regeneration individuals by 84%, sycamore maple by 53% and European beech by 8.4% (Figure 3d).

The t-test results suggest a significant increase in the regeneration individuals for silver fir ($t = 3.257$, $p = 0.002$). However, for European beech, Norway spruce and sycamore maple, the changes were not statistically significant ($t = 0.467$, $p = 0.643$; $t = -0.731$, $p = 0.469$; $t = 2.008$, $p = 0.052$, respectively). Overall, the total change in regeneration individuals did not show statistical significance ($t = 1.693$, $p = 0.099$).

Regeneration increased significantly in the southern part of the core (plots 31–36), where gains exceeded 2000 individuals/ha, whereas severe declines were observed in central plots like 15, 18, and 23. This uneven pattern suggests a strong spatial differentiation in microsite conditions, where factors such as light availability and species composition interact to create varying competitive environments. In particular, competitive release may have favored regeneration in certain areas where canopy gaps or local mortality events reduced overstory competition, allowing greater light penetration and resource availability to understory seedlings (Figure 4c).

3.2. Recruitment, Transition and Mortality

In the core area, for the period 2011–2021, the average number of recruits was 31 ha^{-1} and the average mortality was 46 trees ha^{-1}. The mortality rate over a period of 10 years was 8%. The highest mortality is found among silver fir trees, with 20 trees ha^{-1}, followed by Norway spruce with 17 trees ha^{-1} and European beech with 9 trees ha^{-1}.

In contrast, European beech exhibited the highest tree recruitment with 15 trees per hectare, while both silver fir and Norway spruce showed an identical recruitment of 8 trees per hectare. The highest mortality rates are observed among European beech trees in thin DBH classes, while coniferous species experience the highest mortality in thick classes exceeding 80 cm.

Unlike stem density, conifers have a basal area mortality of 17%, while European beech has only 8%. Similarly, regarding ingrowth intensity, Norway spruce exhibits the highest rate at 28%, followed by silver fir at 25%, whereas European beech shows the lowest at 15%. Moreover, in recruitment to the next diameter class, Norway spruce also demonstrates the most intense recruitment at 16%, followed by silver fir at 14%, while European beech exhibits the lowest at 7% (Table 2).

Table 2. Basal area dynamics by species: mortality, recruitment and transition (2011–2021).

Species	BA 2011 (m^2 ha^{-1})	Mortality (m^2 ha^{-1})	%	Recruitment	%	Transition	%	BA 2021 (m^2 ha^{-1})	Difference (m^2 ha^{-1})
Silver fir	34.6	−5.9	−16.9	8.5	24.5	−4.9	−14.1	32.3	−2.3
European beech	12.1	−0.9	−7.7	1.5	14.9	−0.8	−6.9	12.1	0.0
Norway spruce	21.1	−3.8	−17.8	5.9	28.1	−3.4	−16.2	19.9	−1.3
Total	67.8	−10.6	−15.6	13.7	20.1	−6.6	−9.7	64.3	−3.5

The dynamics of basal area (m^2 ha^{-1}) across diameter classes revealed pronounced structural changes in the forest stand (Figure 5). The most substantial declines in basal area were observed within the 70 cm, 75 cm, and 90 cm diameter classes, where losses exceeded 1.2 m^2 ha^{-1}. These declines likely reflect mortality processes affecting mature trees, including natural senescence or disturbance-induced events that predominantly impact larger diameter classes. Conversely, increases in basal area were detected in the largest diameter classes (125 cm and 130 cm), suggesting the transition of dominant trees into these upper diameter categories. Such transitions often occur through individual tree growth and competitive release, contributing to the maintenance of large structural elements within the stand. Smaller diameter classes (20–60 cm) exhibited moderate but consistent gains in basal area, indicating continuous recruitment and ingrowth processes that sustain the stand's basal area dynamics. Interestingly, the diameter classes between 85 cm and 100 cm displayed relatively stable basal area levels, suggesting a demographic balance between recruitment and mortality processes in these classes.

The mortality of basal area varied across DBH classes and tree species, highlighting distinct patterns in stand dynamics (Figure 6). Silver fir exhibited the highest contribution to mortality, accounting for a cumulative 5.85 m^2/ha. Its mortality was particularly pronounced in the largest diameter classes (70–100 cm), indicating that dominant trees in these cohorts are increasingly vulnerable, possibly due to competition-induced stress or senescence. European beech contributed moderately to overall mortality (cumulative 0.87 m^2/ha), with scattered occurrences in mid-diameter classes (10–65 cm), reflecting occasional mortality of mid-sized individuals but generally stable survival in larger classes. Norway spruce had a cumulative mortality of approximately 3.53 m^2/ha, with consistent

values across both small and medium diameter classes and a notable presence in larger classes (75–95 cm). Overall, the data emphasize the structural complexity and the ongoing turnover in the stand, driven largely by silver fir mortality, which may be a sign of successional processes or ongoing disturbances. The relatively low mortality of European beech suggests resilience and an increasing ecological role of this species in the stand composition.

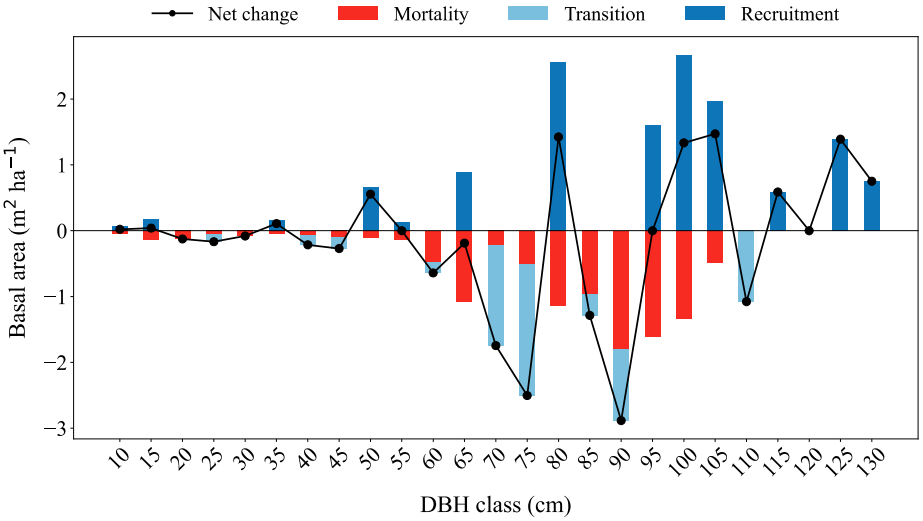


Figure 5. Comparative dynamics of total basal area (m^2 ha^{-1}) by DBH class for 2011 and 2021, including net change over the decade.

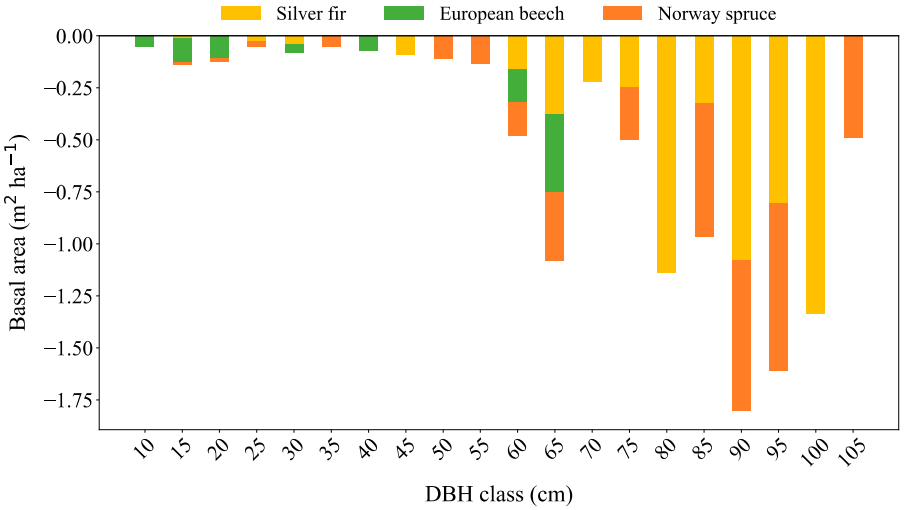


Figure 6. Species-specific basal area mortality (m^2 ha^{-1}) by DBH class for silver fir, European beech, and Norway spruce.

3.3. Coarse Woody Debris

The presence of coarse woody debris (CWD) was observed across various forms and decay classes. The estimated total volume of CWD amounts to 463 m^3 ha^{-1} (Table 3). The highest proportion consists of fallen logs at 64%, followed by standing dead trees (snags) at 33%, while stumps represent the smallest percentage at 2%. The ratio of CWD in the total GS volume amounted to $p = 0.42$. Out of the total volume of CWD, the largest portion belongs to the fifth decay class at 26% and the second decay class at 25%, while the smallest portion is attributed to the first decay class at 7%.

Table 3. Volume (m^3 ha^{-1}) of coarse woody debris (CWD) by type and decay class.

Decay Class	%	Snags	Logs	Stumps	Total CWD
1	7.9	29.2	7.4	0.0	36.7
2	25.1	71.4	44.2	0.2	115.9
3	17.9	36.4	45.5	1.0	82.8
4	22.7	17.3	82.7	5.1	105.1
5	26.4	1.5	117.4	3.3	122.2
Total	100.00	155.8	297.2	9.6	462.7

Snags accounted for a total volume of 155.8 m^3 ha^{-1} across all decay classes, with the highest volume observed in decay class 2 (71.4 m^3 ha^{-1}). The density of snags was 93 individuals per hectare, with the majority represented in the first DBH class and in trees larger than 52.5 cm in diameter, collectively comprising 60% of the total snag population. The ratio of the number of snags to living trees was p = 0.17. Logs were present in all decay classes, with the highest proportion found in the fifth decay class. Most snags were in the second decay class with 71.4 m^3 ha^{-1}. Stumps were not present in the first decay class, with the highest representation occurring in the fourth decay class with 5.1 m^3 ha^{-1}. The spatial analysis of the CWD to GS ratio reveals pronounced heterogeneity within the core zone of the Janj old-growth forest. The ratio ranges from below 0.2 to above 0.8, indicating varying degrees of natural disturbance and structural development across the plots (Figure 7). The lowest ratios ($\leq$0.2) are found along the outer edges of the core area, where stand structure remains relatively stable with minimal deadwood accumulation. In contrast, plots with ratios exceeding 0.8 (dark green) reflect areas with substantial deadwood presence, suggesting intense mortality processes—likely of conifer species—or an advanced successional phase with reduced canopy turnover. These findings underscore the potential of the CWD/GS ratio as a reliable indicator of stand development stage and vitality, particularly in unmanaged old-growth conditions where endogenous mortality and disturbance govern structural dynamics. High CWD/GS values also highlight the ecological importance of deadwood as a critical component of forest biodiversity, nutrient cycling, and microhabitat provision.

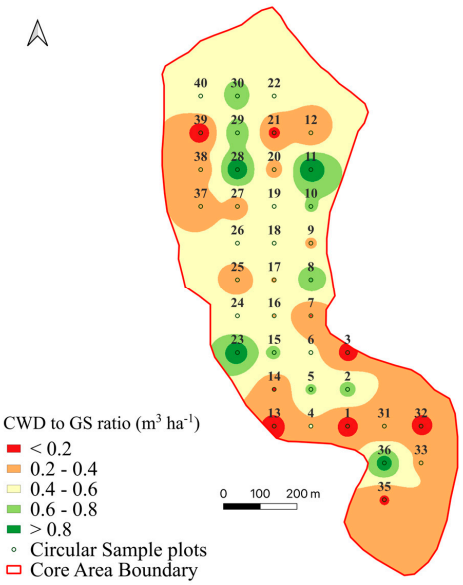


Figure 7. Spatial distribution of the ratio between coarse woody debris (CWD) volume and living tree volume (growing stock, GS) across circular sample plots within the core area of the Janj Strict Nature Reserve.

4. Discussion

4.1. Structural Changes

The present study offers valuable insight into the structural dynamics of the Janj old-growth forest over a ten-year period (2011–2021), complementing and extending earlier findings by Keren et al. [35]. While the previous work documented a long-term decline of conifers and a rise of beech dominance over a six-decade trajectory, our decadal reassessment confirms that this trend has not only continued but intensified moderately. Between 2011 and 2021, the total basal area decreased by 3.5 m^2 ha^{-1}, primarily due to losses in silver fir (–2.3 m^2 ha^{-1}) and Norway spruce (–1.3 m^2 ha^{-1}). Interestingly, while earlier findings by Keren et al. [35] noted an increase in fir basal area from 1952 to 2011, our results now suggest a turning point, with fir entering a phase of structural regression.

4.2. Developmental Dynamics

Our structural transition analysis reveals a noteworthy degree of ingrowth and recruitment in silver fir and Norway spruce, yet not at levels sufficient to offset their elevated mortality. This aligns with findings from similar forest systems, where conifers regeneration beneath dense beech layers fails to develop competitive potential, reinforcing a slow but persistent shift in species dominance. The volume of coarse woody debris (CWD), measured at 463 m^3 ha^{-1}, exceeds the European average for beech-dominated old-growth stands [66]. The high presence of logs in advanced decay classes suggests limited recent disturbance and a stable decay dynamic—consistent with earlier observations for Janj and other forests in the region (Figure 8). Although changes in overall structural parameters (stem density, basal area, growing stock) were not statistically significant at the stand level, species- and diameter class-specific differences were pronounced.



Figure 8. Natural canopy gap and deadwood accumulation in the core area of the Janj old-growth forest.

4.3. Mortality Patterns

Mortality trends reinforce this interpretation: over the ten-year period, silver fir exhibited the highest mortality rate (20 trees ha^{-1}), followed by spruce (17 trees ha^{-1}), while beech mortality was lowest (9 trees ha^{-1}). These declines align with broader regional trends, particularly in the case of spruce, whose vulnerability to drought stress and bark

beetle outbreaks has been widely documented [35,67–69]. Numerous previous studies on old-growth forests have demonstrated that an increasing dominance of European beech often coincides with a reduction in overall stand productivity [56,70–73]. Similar structural trends—characterized by a decline of silver fir and an expansion of European beech—have also been reported in the old-growth forests of the Slovenian Alps [29] and the Western Carpathians [32] where disturbances such as windthrow and air pollution were identified as primary drivers of fir regression in favor of beech. Over the past decades, such disturbances—particularly wind-related canopy openings—have become increasingly frequent across Europe [74] further destabilizing the balance between species. Norway spruce, in particular, exhibits the highest mortality and ingrowth intensity, whereas European beech shows low mortality and a more stable ingrowth pattern. This indicates a growing long-term competitive advantage of beech under unmanaged forest conditions. Although no known fire disturbances have been recorded in the Janj old-growth forest over the past few decades, it is important to acknowledge that fire events can represent a significant threat to the stability and composition of similar old-growth forest ecosystems [75].

4.4. Tree Species Composition and Diameter Distribution

Perhaps the most striking observation is the structural resilience and regenerative success of European beech. Its basal area remained stable over the decade, while regeneration increased by 8.4%, underscoring its continued recruitment advantage in the understory. Paired sample t-tests revealed significant declines in stem density for silver fir and Norway spruce ($p = 0.001$), and a marked increase in silver fir regeneration ($p = 0.002$). Additionally, statistically significant reductions in basal area and growing stock for silver fir were observed in the 52.5–82.5 cm diameter class ($p < 0.05$), suggesting that structural changes are most acute in these larger cohorts.

4.5. Implications for Regeneration Dynamics

These observations underscore the complexity of interpreting forest dynamics based solely on stand-level averages. Even in the absence of widespread statistical significance, the consistent decline in conifers and expansion of beech—supported by both empirical data and ecological reasoning—signal a clear successional trajectory. The patterns observed in Janj mirror those in other primeval forests across the Dinaric and Carpathian ranges [29,32,34], strengthening the hypothesis that conifer decline and beech ascendancy reflect broader long-term ecological processes.

4.6. Broader Ecological and Management Implications

The persistence of large-diameter silver fir and European beech in the Janj old-growth forest demonstrates that natural forest dynamics in mountain ecosystems can significantly contribute to carbon storage, supporting the importance of maintaining diverse species composition and protecting these forests from anthropogenic disturbance to enhance carbon accumulation and ecosystem resilience [76]. This supports the long-standing hypothesis of beech expansion in mixed Dinaric old-growth stands—particularly under conditions of prolonged canopy openness and diminishing conifer competition. These findings are consistent with the idea that beech trees benefit from warming climates and internal disturbance cycles, whereas conifers—particularly at their lower elevation limits—are disproportionately affected by climatic stressors. From a conservation standpoint, these results highlight the importance of continued long-term monitoring, especially in the context of climate change, which is likely to amplify existing successional patterns. The ongoing shift from conifer-dominated to beech-dominated forest structures may have far-reaching implications for biodiversity, carbon dynamics, and ecosystem resilience. In sum, Janj remains a structurally rich and ecologically valuable primeval forest, yet is

clearly entering a phase of compositional transition. If current trends persist, the long-term character of this unique forest may be redefined through subtle, persistent processes that reflect both natural succession and climate-driven pressures.

4.7. Study Limitations

Despite the valuable insights provided, this study is not without limitations. First, the temporal scope of a single decade (2011–2021) might not fully capture the long-term successional dynamics typical of old-growth forests, where processes often unfold over centuries. Consequently, caution is warranted when extrapolating short-term trends to predict long-term trajectories. Additionally, while the study employed 39 permanent plots, some diameter classes, especially those at the higher end (e.g., >105 cm), had low sample sizes, potentially affecting the precision of mortality and recruitment estimates for these classes. Another limitation arises from the lack of direct monitoring of disturbance events—such as windthrow or pest outbreaks—which, although documented regionally, were not always individually verified at each plot during the study period. Finally, while changes in overall stand-level metrics were analyzed, interactions between species, competition dynamics, and micro-environmental factors could not be fully disentangled, potentially influencing observed mortality and recruitment patterns. Future studies could address these limitations by integrating longer-term datasets, including more frequent and spatially detailed monitoring of disturbance events, and applying models that explicitly account for interspecies competition and climate influences.

5. Conclusions

This study provided valuable insights into the dynamics of the Janj old-growth forest over a ten-year period, offering a deeper understanding of structural changes, developmental processes, and mortality patterns. The findings revealed a subtle yet consistent compositional shift, with conifers—especially silver fir and Norway spruce—experiencing some declines in basal area, while European beech maintained its structural stability and demonstrated remarkable regenerative success.

Statistically significant differences were observed for silver fir regarding the reduction in stem density ($p = 0.001$), the increase in mean diameter ($p = 0.002$), and the increase in regeneration ($p = 0.002$). The paired samples t-test results for both growing stock (GS) and basal area (BA), considered overall and by tree species, showed no statistically significant differences at the 95% confidence interval.

Although overall stand-level metrics such as total basal area and growing stock did not show statistically significant changes, species-specific analyses highlighted clear patterns of compositional adjustment that are consistent with broader regional trends. However, within the diameter class of 52.5 to 82.5 cm, both GS and BA exhibited statistically significant differences for silver fir and overall. No significant differences were found for European beech and Norway spruce. Mortality was most pronounced in silver fir, followed by Norway spruce, with European beech exhibiting the lowest mortality rate. These patterns align with known species-specific vulnerabilities, where conifers are more susceptible to climate stress and biotic disturbances, while beech appears more resilient under current conditions. The recruitment and ingrowth of silver fir and Norway spruce, although present, were insufficient to fully compensate for their elevated mortality, indicating a gradual shift towards beech dominance—a pattern commonly reported in other primeval forests across the Dinaric and Carpathian ranges. The high volume of coarse woody debris and the dominance of advanced decay classes reflect a relatively stable decomposition process, suggesting a mature forest with limited recent disturbance. Overall, the findings emphasize the importance of long-term monitoring and species-specific analysis to fully understand

forest dynamics, especially in the context of climate change and shifting disturbance regimes. Conservation strategies should prioritize maintaining species diversity and protecting forest structure to sustain ecosystem resilience and carbon storage potential.

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Abbreviations

The following abbreviations are used in this manuscript:

BA	Basal Area
CWD	Coarse Woody Debris
DBH	Diameter at breast height measured in centimeters
GS	Growing Stock
SNR	Strict Nature Reserve

References

1. Sabatini, F.M.; Burrascano, S.; Keeton, W.S.; Levers, C.; Lindner, M.; Pötzschner, F.; Verkerk, P.J.; Bauhus, J.; Buchwald, E.; Chaskovsky, O.; et al. Where Are Europe's Last Primary Forests? *Divers. Distrib.* **2018**, *24*, 1426–1439. [CrossRef]
2. Stubenrauch, J.; Garske, B. Forest Protection in the EU's Renewable Energy Directive and Nature Conservation Legislation in Light of the Climate and Biodiversity Crisis—Identifying Legal Shortcomings and Solutions. *For. Policy Econ.* **2023**, *153*, 102996. [CrossRef]
3. Barredo, J.I.; Brailescu, C.; Teller, A.; Sabatini, F.M.; Mauri, A.; Janouskova, K. *Mapping and Assessment of Primary and Old-Growth Forests in Europe*; Publications Office of the European Union: Luxembourg, 2021; ISBN 978-92-76-34230-4. [CrossRef]
4. Nagel, T.A.; Svoboda, M.; Kobal, M. Disturbance, Life History Traits, and Dynamics in an Old-Growth Forest Landscape of Southeastern Europe. *Ecol. Appl.* **2014**, *24*, 663–679. [CrossRef] [PubMed]
5. Forest Europe. *State of Europe's Forests 2020*; Köhl, M., Linser, S., Prins, K., Eds.; Forest Europe: Jönköping, Sweden, 2020.
6. Čilaš, M.; Leiter, M.; Višnjić, Ć.; Hasenauer, H. Adapting the Tree Growth Model MOSES to Manage Uneven-Aged Mixed Species Forests in Bosnia & Herzegovina. *Trees For. People* **2023**, *14*, 100433. [CrossRef]
7. O'hara, K.L.; Hasenauer, H.; Kindermann, G. Sustainability in Multi-Aged Stands: An Analysis of Long-Term Plenter Systems. *Forestry* **2007**, *80*, 163–181. [CrossRef]
8. Leiter, M.; Hasenauer, H. Continuous Cover Forestry: Which Sampling Method Should Be Used to Ensure Sustainable Management? *Trees For. People* **2023**, *13*, 100419. [CrossRef]
9. Nagel, T.A.; Cerioni, M. Structure and Dynamics of Old-Growth Pinus Nigra Stands in Southeast Europe. *Eur. J. For. Res.* **2023**, *142*, 537–545. [CrossRef]
10. Cagliero, E.; Morresi, D.; Paradis, L.; Čurović, M.; Spalevic, V.; Marchi, N.; Meloni, F.; Bentaleb, I.; Motta, R.; Garbarino, M.; et al. Legacies of Past Human Activities on One of the Largest Old-Growth Forests in the South-East European Mountains. *Veg. Hist. Archaeobotany* **2022**, *31*, 415–430. [CrossRef]
11. Nagel, T.A.; Mikac, S.; Dolinar, M.; Klopcic, M.; Keren, S.; Svoboda, M.; Diaci, J.; Bončina, A.; Paulic, V. The Natural Disturbance Regime in Forests of the Dinaric Mountains: A Synthesis of Evidence. *For. Ecol. Manag.* **2017**, *388*, 29–42. [CrossRef]

12. Paluch, J.; Keren, S.; Govedar, Z. The Dinaric Mountains versus the Western Carpathians: Is Structural Heterogeneity Similar in Close-to-Primeval *Abies–Picea–Fagus* Forests? *Eur. J. For. Res.* **2021**, *140*, 209–225. [CrossRef]
13. Chen, B.; Wang, Y.-C. Carbon Storage in Old-Growth Homestead Windbreaks of Small Islands in Okinawa: Toward the Sustainable Management and Conservation. *Forests* **2020**, *11*, 448. [CrossRef]
14. Remeš, J. Development and Present State of Close-to-Nature Silviculture. *J. Landsc. Ecol.* **2018**, *11*, 17–32. [CrossRef]
15. Schütz, J.-P.; Saniga, M.; Diaci, J.; Vrška, T. Comparing Close-to-Nature Silviculture with Processes in Pristine Forests: Lessons from Central Europe. *Ann. For. Sci.* **2016**, *73*, 911–921. [CrossRef]
16. Bugmann, H.; Brang, P. Ausgewählte Ergebnisse Aus Fünfzig Jahren Forschung in Schweizer Naturwaldreservaten. *Forum Für Wissen WSL* **2009**, *2009*, 93–102.
17. Chiti, T.; Benilli, N.; Mastrolonardo, G.; Certini, G. The Potential for an Old-Growth Forest to Store Carbon in the Topsoil: A Case Study at Sasso Fratino, Italy. *J. For. Res.* **2023**, *35*, 10. [CrossRef]
18. Zhang, Y.; Wang, A.; Liu, Y.; Shen, L.; Cai, R.; Wu, J. Disturbance of Wind Damage and Insect Outbreaks in the Old-Growth Forest of Changbai Mountain, Northeast China. *Forests* **2023**, *14*, 368. [CrossRef]
19. Bauhus, J.; Puettmann, K.; Messier, C. Silviculture for Old-Growth Attributes. *For. Ecol. Manag.* **2009**, *258*, 525–537. [CrossRef]
20. Nagel, T.A.; Firm, D.; Rozman, A. Intermediate Disturbances Are a Key Driver of Long-Term Tree Demography Across Old-growth Temperate Forests. *Ecol. Evol.* **2021**, *11*, 16862–16873. [CrossRef]
21. Boncina, A. Comparison of Structure and Biodiversity in the Rajhenav Virgin Forest Remnant and Managed Forest in the Dinaric Region of Slovenia: Structure and Biodiversity of Forests in Slovenia. *Glob. Ecol. Biogeogr.* **2000**, *9*, 201–211. [CrossRef]
22. Frankovič, M.; Janda, P.; Mikoláš, M.; Čada, V.; Kozák, D.; Pettit, J.L.; Nagel, T.A.; Buechling, A.; Matula, R.; Trotsiuk, V.; et al. Natural Dynamics of Temperate Mountain Beech-Dominated Primary Forests in Central Europe. *For. Ecol. Manag.* **2021**, *479*, 118522. [CrossRef]
23. Senf, C.; Sebald, J.; Seidl, R. Increasing Canopy Mortality Affects the Future Demographic Structure of Europe's Forests. *One Earth* **2021**, *4*, 749–755. [CrossRef]
24. Anderson-Teixeira, K.J.; Miller, A.D.; Mohan, J.E.; Hudiburg, T.W.; Duval, B.D.; DeLucia, E.H. Altered Dynamics of Forest Recovery under a Changing Climate. *Glob. Change Biol.* **2013**, *19*, 2001–2021. [CrossRef] [PubMed]
25. Luyssaert, S.; Schulze, E.-D.; Börner, A.; Knohl, A.; Hessenmöller, D.; Law, B.E.; Ciais, P.; Grace, J. Old-Growth Forests as Global Carbon Sinks. *Nature* **2008**, *455*, 213–215. [CrossRef] [PubMed]
26. Zhou, G.; Liu, S.; Li, Z.; Zhang, D.; Tang, X.; Zhou, C.; Yan, J.; Mo, J. Old-Growth Forests Can Accumulate Carbon in Soils. *Science* **2006**, *314*, 1417. [CrossRef]
27. Woods, K.D.; Nagel, T.A.; Brzeziecki, B.; Cowell, C.M.; Firm, D.; Jaloviar, P.; Kucbel, S.; Lin, Y.; Maciejewski, Z.; Szwagrzyk, J.; et al. Multi-Decade Tree Mortality in Temperate Old-Growth Forests of Europe and North America: Non-Equilibrial Dynamics and Species-Individualistic Response to Disturbance. *Glob. Ecol. Biogeogr.* **2021**, *30*, 1311–1333. [CrossRef]
28. Diaci, J.; Roženbergar, D.; Anić, I.; Mikac, S.; Saniga, M.; Kucbel, S.; Višnjić, C.; Ballian, D. Structural Dynamics and Synchronous Silver Fir Decline in Mixed Old-Growth Mountain Forests in Eastern and Southeastern Europe. *Forestry* **2011**, *84*, 479–491. [CrossRef]
29. Firm, D.; Nagel, T.A.; Diaci, J. Disturbance History and Dynamics of an Old-Growth Mixed Species Mountain Forest in the Slovenian Alps. *For. Ecol. Manag.* **2009**, *257*, 1893–1901. [CrossRef]
30. Jaloviar, P.; Saniga, M.; Kucbel, S.; Pittner, J.; Vencurik, J.; Dovciak, M. Seven Decades of Change in a European Old-Growth Forest Following a Stand-Replacing Wind Disturbance: A Long-Term Case Study. *For. Ecol. Manag.* **2017**, *399*, 197–205. [CrossRef]
31. Parobeková, Z.; Pittner, J.; Kucbel, S.; Saniga, M.; Filípek, M.; Sedmáková, D.; Vencurik, J.; Jaloviar, P. Structural Diversity in a Mixed Spruce-Fir-Beech Old-Growth Forest Remnant of the Western Carpathians. *Forests* **2018**, *9*, 379. [CrossRef]
32. Šamonil, P.; Doleželová, P.; Vašíčková, I.; Adam, D.; Valtera, M.; Král, K.; Janík, D.; Šebková, B. Individual-Based Approach to the Detection of Disturbance History through Spatial Scales in a Natural Beech-Dominated Forest. *J. Veg. Sci.* **2013**, *24*, 1167–1184. [CrossRef]
33. Vrška, T.; Adam, D.; Hort, L.; Kolář, T.; Janík, D. European Beech (*Fagus sylvatica* L.) and Silver Fir (*Abies alba* Mill.) Rotation in the Carpathians—A Developmental Cycle or a Linear Trend Induced by Man? *For. Ecol. Manag.* **2009**, *258*, 347–356. [CrossRef]
34. Diaci, J.; Roženbergar, D.; Mikac, S.; Anić, I.; Hartman, T.; Bončina, A. Long-Term Changes in Tree Species Composition in Old-Growth Dinaric Beech-Fir Forest. *Glas. Za Šumske Pokuse* **2007**, *42*, 13–28.
35. Keren, S.; Motta, R.; Govedar, Z.; Lučić, R.; Medarević, M.; Diaci, J. Comparative Structural Dynamics of the Janj Mixed Old-Growth Mountain Forest in Bosnia and Herzegovina: Are Conifers in a Long-Term Decline? *Forests* **2014**, *5*, 1243–1266. [CrossRef]
36. Nagel, T.A.; Svoboda, M.; Rugani, T.; Diaci, J. Gap Regeneration and Replacement Patterns in an Old-Growth *Fagus–Abies* Forest of Bosnia–Herzegovina. *Plant Ecol.* **2010**, *208*, 307–318. [CrossRef]
37. Čater, M. Response and Mortality of Beech, Fir, Spruce and Sycamore to Rapid Light Exposure after Large-Scale Disturbance. *For. Ecol. Manag.* **2021**, *498*, 119554. [CrossRef]

38. Keren, S.; Diaci, J.; Motta, R.; Govedar, Z. Stand Structural Complexity of Mixed Old-Growth and Adjacent Selection Forests in the Dinaric Mountains of Bosnia and Herzegovina. *For. Ecol. Manag.* **2017**, *400*, 531–541. [CrossRef]
39. Ammer, C. Impact of Ungulates on Structure and Dynamics of Natural Regeneration of Mixed Mountain Forests in the Bavarian Alps. *For. Ecol. Manag.* **1996**, *88*, 43–53. [CrossRef]
40. Roženbergar, D.; Mikac, S.; Anić, I.; Diaci, J. Gap Regeneration Patterns in Relationship to Light Heterogeneity in Two Old-Growth Beech–Fir Forest Reserves in South East Europe. *For. Int. J. For. Res.* **2007**, *80*, 431–443. [CrossRef]
41. Ficko, A.; Roessiger, J.; Bončina, A. Can the Use of Continuous Cover Forestry Alone Maintain Silver Fir (*Abies alba* Mill.) in Central European Mountain Forests? *For. Int. J. For. Res.* **2016**, *89*, 412–421. [CrossRef]
42. Vacek, Z. Structure and Dynamics of Spruce-Beech-Fir Forests in Nature Reserves of the Orlické Hory Mts. in Relation to Ungulate Game. *Cent. Eur. For. J.* **2017**, *63*, 23–34. [CrossRef]
43. Bernard, M.; Boulanger, V.; Dupouey, J.-L.; Laurent, L.; Montpied, P.; Morin, X.; Picard, J.-F.; Saïd, S. Deer Browsing Promotes Norway Spruce at the Expense of Silver Fir in the Forest Regeneration Phase. *For. Ecol. Manag.* **2017**, *400*, 269–277. [CrossRef]
44. Diaci, J.; Adamic, T.; Fidej, G.; Rozenbergar, D. Toward a Beech-Dominated Alternative Stable State in Dinaric Mixed Montane Forests: A Long-Term Study of the Pecka Old-Growth Forest. *Front. For. Glob. Change* **2022**, *5*, 937404. [CrossRef]
45. Unkule, M.; Piedallu, C.; Balandier, P.; Courbaud, B. Climate and Ungulate Browsing Impair Regeneration Dynamics in Spruce-Fir-Beech Forests in the French Alps. *Ann. For. Sci.* **2022**, *79*, 11. [CrossRef]
46. Govedar, Z.; Krstić, M.; Keren, S.; Babić, V.; Zlokapa, B.; Kanjevac, B. Actual and Balanced Stand Structure: Examples from Beech-Fir-Spruce Old-Growth Forests in the Area of the Dinarides in Bosnia and Herzegovina. *Sustainability* **2018**, *10*, 540. [CrossRef]
47. Petrovska, R.; Bugmann, H.; Hobi, M.L.; Brang, P. Replace Me If You Can: Abundance of Advance Regeneration under Canopy Trees in a Primeval Beech Forest. *For. Ecol. Manag.* **2023**, *537*, 120939. [CrossRef]
48. Kanjevac, B.; Babić, V.; Stajić, S.; Martać, N.; Pavlović, B.; Furtula, D.; Čokeša, V. Key Drivers Affecting the Spatial Heterogeneity of the Regeneration Process in Old-Growth Beech Forests in Southeastern Europe. *Front. For. Glob. Change* **2023**, *6*, 1304037. [CrossRef]
49. Braga, C.I.; Crisan, V.E.; Petritan, I.C.; Scarlatescu, V.; Vasile, D.; Lazar, G.; Petritan, A.M. Short-Term Effects of Anthropogenic Disturbances on Stand Structure, Soil Properties, and Vegetation Diversity in a Former Virgin Mixed Forest. *Forests* **2023**, *14*, 742. [CrossRef]
50. Govedar, Z.; Prokhorova, N.; Babić, V.; Dukić, V.; Kanjevac, B.; Bilić, S. Natural Regeneration on Deadwood in the Primeval Forest Janj. *Lesn. Zhurnal For. J.* **2023**, *5*, 90–102. [CrossRef]
51. Govedar, Z. Elementi Strukture i Prirodno Podmlađivanje Mješovite Sastojine Bukve, Jele i Smrče u Prašumi Janj. *Šumarstvo* **2002**, *4*, 9–24.
52. Keren, S.; Diaci, J. Comparing the Quantity and Structure of Deadwood in Selection Managed and Old-Growth Forests in South-East Europe. *Forests* **2018**, *9*, 76. [CrossRef]
53. UNESCO Ancient and Primeval Beech Forests of the Carpathians and Other Regions of Europe—UNESCO World Heritage Centre. Available online: https://whc.unesco.org/en/list/1133 (accessed on 21 March 2023).
54. Maunaga, Z.; Burlica, Č.; Pavlović, B.; Bozalo, G.; Koprivica, M.; Lazarev, V.; Mataruga, M.; Repajić, Ž.; Govedar, Z.; Stanivuković, Z.; et al. *Plan Gazdovanja Za Šume Sa Posebnom Namjenom u Strogim Rezervatima Prirode "Janj" i "Lom*; Šumarski Fakultet Univerziteta u Banjoj Luci: Banja Luka, Bosnia and Herzegovina, 2005.
55. Manuševa, L.; Fukarek, P.; Panov, A. *Proučavanje Sastojina Prašumskog Tipa*; Šumarski fakultet u Sarajevu: Sarajevo, Bosnia and Herzegovina, 1967.
56. Govedar, Z. Načini Prirodnog Obnavljanja Mešovitih Šuma jele i smrče (*Abieti—Piceetum Illyricum*) na Području Zapadnog Dijela Republike Srpske. Ph.D. Thesis, University of Beograd, Beograd, Serbia, 2005.
57. Keren, S. Complexity of Stand Structures in Two Mixed Mountain Old-Growth Forests and Adjacent Managed Forests in Bosnia and Herzegovina. Ph.D. Thesis, Biotechnical Faculty, University of Ljubljana, Ljubljana, Slovenia, 2015.
58. Motta, R.; Berretti, R.; Castagneri, D.; Dukić, V.; Garbarino, M.; Govedar, Z.; Lingua, E.; Maunaga, Z.; Meloni, F. Toward a Definition of the Range of Variability of Central European Mixed *Fagus–Abies–Picea* Forests: The Nearly Steady-State Forest of Lom (Bosnia and Herzegovina). *Can. J. For. Res.* **2011**, *41*, 1871–1884. [CrossRef]
59. Lojo, A.; Balić, B.; Mekić, F.; Beus, V.; Koprivica, M.; Treštić, T.; Musić, J.; Čabaravdić, A.; Hočevar, M. Državna Inventura Šuma—Bosna i Hercegovina—Faza 2: Manual—Uputstvo Za Snimanja Na Terenu. *Rad. Šumar. Fak. Univ. U Sarajevu* **2008**, *20*, 1–82. [CrossRef]
60. Motta, R.; Berretti, R.; Lingua, E.; Piussi, P. Coarse Woody Debris, Forest Structure and Regeneration in the Valbona Forest Reserve, Paneveggio, Italian Alps. *For. Ecol. Manag.* **2006**, *235*, 155–163. [CrossRef]
61. Nagel, T.A.; Svoboda, M. Gap Disturbance Regime in an Old-Growth *Fagus–Abies* Forest in the Dinaric Mountains, Bosnia-Herzegovina. *Can. J. For. Res.* **2008**, *38*, 2728–2737. [CrossRef]

62. Le Roux, R.; Henrico, S.; Bezuidenhout, J.; Henrico, I. Inverse Distance Weighting as an Alternative Interpolation Method to Create Radiometric Maps of Natural Radionuclide Concentrations Using QGIS. *Proc. Int. Cartogr. Assoc.* **2023**, *5*, 1–7. [CrossRef]
63. QGIS.org. QGIS 3.28. Geographic Information System. 2023. Available online: https://qgis.org/en/site/ (accessed on 31 March 2023).
64. Drinić, P.; Matić, V.; Pavlič, J.; Prolić, N.; Stojanović, O.; Vukmirović, V.; Koprivica, M. *Tablice Taksacionih Elemenata Visokih i Izdanačkih šuma u SR Bosni i Hercegovini*; Šumarski Fakultet Univerziteta u Sarajevu: Sarajevo, Bosnia and Herzegovina, 1990; Volume Posebno Izdanje.
65. Avery, T.E.; Burkhart, H.E. *Forest Measurements*; McGraw-Hill: New York, NY, USA, 2002; ISBN 978-0-07-113005-9.
66. Motta, R.; Alberti, G.; Ascoli, D.; Berretti, R.; Bilić, S.; Bono, A.; Milić, Ć.; Vojislav, D.; Finsinger, W.; Garbarino, M.; et al. Old-Growth Forests in the Dinaric Alps of Bosnia-Herzegovina and Montenegro: A Continental Hot-Spot for Research and Biodiversity. *Front. For. Glob. Change* **2024**, *7*, 1371144. [CrossRef]
67. Krause, G.H.M.; Arndt, U.; Brandt, C.J.; Bucher, J.; Kenk, G.; Matzner, E. Forest Decline in Europe; Development and Possible Causes. *Water. Air. Soil Pollut.* **1986**, *31*, 647–668. [CrossRef]
68. Mina, M.; Bugmann, H.; Klopcic, M.; Cailleret, M. Accurate Modeling of Harvesting Is Key for Projecting Future Forest Dynamics: A Case Study in the Slovenian Mountains. *Reg. Environ. Change* **2017**, *17*, 49–64. [CrossRef]
69. Piedallu, C.; Dallery, D.; Bresson, C.; Legay, M.; Gégout, J.-C.; Pierrat, R. Spatial Vulnerability Assessment of Silver Fir and Norway Spruce Dieback Driven by Climate Warming. *Landsc. Ecol.* **2023**, *38*, 341–361. [CrossRef]
70. Drinić, P. Taksacioni Elementi Sastojina Jele, Smrče i Bukve Prašumskog Tipa u Bosni. *Rad. Poljopr. Šumar. Fak. Univ. U Sarajev.* **1956**, *4*, 107–160. [CrossRef]
71. Anić, I.; Mikac, S. Struktura, tekstura i pomlađivanje dinarske bukovo-jelove prašume Čorkova uvala. *Šumar. List* **2008**, *132*, 505–515.
72. Korpel, Š. Razvoj i Struktura Bukovo-Jelovih Prašuma i Njihova Primjena Kod Gospodarenja Prebornom Šumom. *Šumar. List* **1996**, *120*, 203–208.
73. Pantić, D.; Medarević, M.; Banković, S.; Obradović, S.; Šjukić, B.; Pešić, B. Structural, Production and Dynamic Characteristics of the Strict Forest Reserve "Račanska Šljivovica" on Mt. Tara. *Glas. Šumar. Fak.* **2011**, *103*, 93–114. [CrossRef]
74. Seidl, R.; Schelhaas, M.-J.; Lexer, M.J. Unraveling the Drivers of Intensifying Forest Disturbance Regimes in Europe: Drivers of Forest Disturbance Intensification. *Glob. Change Biol.* **2011**, *17*, 2842–2852. [CrossRef]
75. Paillet, Y.; Parvainen, J.; Gosselin, M.; Gosselin, F.; Lier, M. Monitoring Forest Biodiversity in Europe: State of the Art, Challenges, and Opportunities. In *Integrative Approaches as an Opportunity for the Conservation of Forest Biodiversity*; European Forest Institute: Joensuu, Finland, 2013; p. 242. Available online: https://hal.inrae.fr/hal-02599083 (accessed on 9 June 2025).
76. Solomon, L.W.; Arunrat, N.; Phutthai, T.; Wisawapipat, W.; Sereenonchai, S.; Hatano, R. Carbon Stock Estimation and Human Disturbance in Selected Urban Un-Conserved Forests in Entoto Mountain Forest, Addis Ababa, Ethiopia. *Diversity* **2025**, *17*, 225. [CrossRef]

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