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Article

Comparative Structural Dynamics of the Janj Mixed Old-Growth Mountain Forest in Bosnia and Herzegovina: Are Conifers in a Long-Term Decline?

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Abstract: Regression of conifers in European mixed old-growth mountain forests has been observed for a long period and studied from different aspects. Old-growth (OG) forests in Bosnia and Herzegovina (BiH) have not experienced heavy air pollution and chronic overbrowsing that have affected many other European OG forests, while climatic and anthropogenic disturbances have been well documented. We analysed stand structure in the Janj OG forest, compared it with inventories of Lom and Perucica OG forests (BiH) and with earlier inventories of the same reserves. At present, OG forest Janj is characterized by a high growing stock (1215 $m^3 \cdot ha^{-1}$). This is due to good site quality, prevalence of conifers (84%) and dominant endogenous processes in recent decades. In all three OG forests, indicators of structural change exhibited progression of European beech over time. Historical evidence revealed the occurrence of warm summers and droughts followed by bark beetle outbreaks in the 1920s, 1940s and early 1950s, which in turn influenced a marked conifer decline. It seems likely that repeated canopy opening released waves of European beech regeneration. These stand structural changes have delayed the rejuvenation of conifers and can help explain the early observations of conifer decline.

Keywords: mixed old-growth forest; structural attributes; *Fagus sylvatica* progression; climatic extremes

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1. Introduction

Mixed forests composed of *Fagus sylvatica* L. (hereafter beech), *Abies alba* Mill. (fir) and *Picea abies* (L.) Karst. (Norway spruce) represent one of the most ecologically and economically important forest categories of European mountainous regions [1]. They grow in the relatively humid and cold climates of the mountains [2]. These forest sites have never been intensively used for agriculture or settlements and are still well preserved. Many European old-growth forests are situated in this vegetation belt [3]. However, there are many reports of synchronous regression of conifers, especially of silver fir in old-growth forests (e.g., [4–7]) as well as in managed forests [8–11]. Many factors, natural and anthropogenic, influence the coexistence of beech, fir and spruce, making this topic challenging to study [12–15].

It is well established that, among the main species of this altitudinal belt, spruce is the most tolerant to the cold continental climate, followed by fir, while beech may better tolerate a warmer and dryer climate [16]. Both conifers are more successful on sites with less competition from ground vegetation (rocky outcrops, CWD) and on silicate bedrock [2]. Fir is the strongest competitor in low light levels under dense stands, while the competitive strength of beech increases within canopy gaps [17–19] and that of spruce after intermediate disturbances [6]. Silver fir is very vulnerable to browsing [20] and polluted air, especially SO_2 pollution [21]. Regarding species coexistence, not only are the direct effects of environmental changes important, such as higher temperatures or changes in the disturbance regime, but also indirect effects such as higher frequency of seed years in beech [22] or changes in ground vegetation structure due to nitrogen deposition and a prolonged growing season [23].

Neighbourhood effects [24] form an important group of coexistence factors. They include processes such as the changes in microsite conditions induced by the presence of certain canopy species. This variability may include light transmission [25], soil characteristics [4,26], nutrient availability [27,28] and biological factors and agents (e.g., allelopathy, species specific pathogens and predators) [29]. Such processes can lead toward reciprocal, random or self-replacement of different species in the canopy [12,30,31]. Thus, coexistence is driven by many factors, many of which are difficult to separate from the management regime in managed forests [3]. For this reason, the study of coexistence should involve research of old-growth forests. Since these are rare in Europe, comparative and integrative studies are important.

Most European old-growth forests are relatively small remnants surrounded by a buffer zone and located inside a matrix of managed forests. A common perception is that they have been well preserved from human impact. However, in past centuries rural areas were more densely inhabited than today and unregulated management that included felling of individual trees for fuel wood or construction on site, forest grazing and charcoal burning was common [7,9,15,32,33]. On the other hand, in the forest matrix surrounding old-growth forests, conifers were favoured for economic reasons. This enhanced their overall seed potential and likely positively influenced conifer regeneration in old-growth forests because of their limited size.

Moreover, in some regions deer became extinct, which additionally favoured regeneration of fir [14]. After WWII, deer densities in Europe sharply increased, and overbrowsing negatively influenced fir abundance [20]. Between the 1960s and 1980s, fir was heavily affected by air pollution [21]. Therefore, local direct historical influences and regional conditions (e.g., deer density, air pollution) are very important for understanding the recent structure of old-growth forests and their long-term dynamics [34].

Old-growth forests in Bosnia (Perucica, Lom and Janj) have not experienced chronic overbrowsing by deer as have other European old-growth forests [15,35], and environmental pollution has also been less acute [36]. These forests therefore represent an excellent resource for the study of interactions of climatic fluctuations and indirect anthropogenic disturbances, both of which are well documented in the literature [33,37–41]. The Janj old-growth forest has received less scientific attention [42,43] than the forests of Perucica (e.g., [5,19,44–46]) and Lom [32,47,48]. The aims of this study were (1) to describe the structural changes over a 60-year period in the Janj old-growth forest and (2) to compare and contrast the changes with those in the Lom and Perucica (Bosnia and Herzegovina) old-growth forests and other similar old-growth forests in Europe.

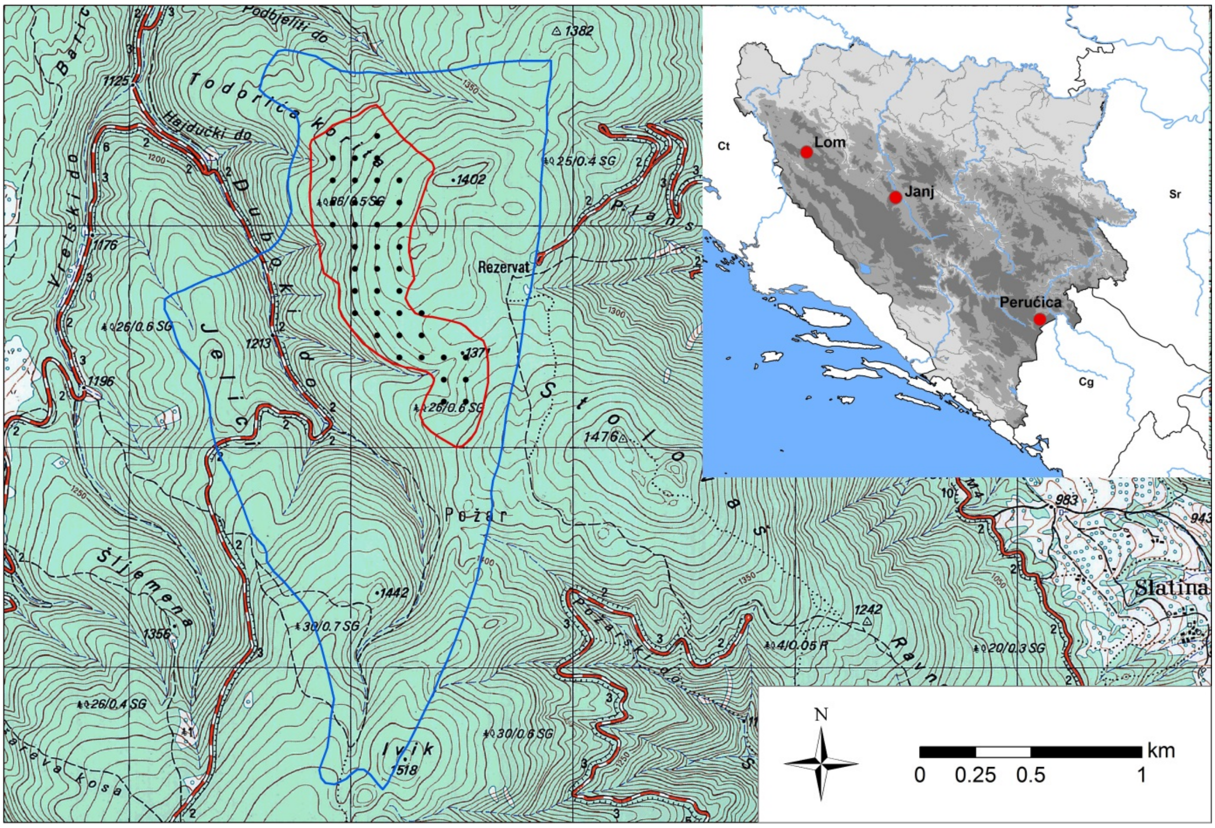
2. Materials and Methods

2.1. Study Site

The research was carried out in the Janj old-growth forest located on the mountainous massif of Stolovas near Sipovo, Bosnia and Herzegovina (BiH). The geographic position of the core area of Janj is 44°08'N, 17°17'E, and the altitude ranges from 1260–1400 m a.s.l. (Figure 1). The parent rock is made of dolomite bedrock on which deep rendzina and brown soil types of various depths are formed. Mean annual rainfall amounts to 1200 mm, and mean annual temperature is around 5 °C. The core area of old-growth forest at Janj has been classified as plant association *Piceo-Abieti-Fagetum* [49].

This virgin forest was protected by the decision of the State Institute for Protection of Cultural Monuments and Natural Rarities in Bosnia and Herzegovina (No. 245/54 from July 17, 1954). It is believed that even before the official protection of the Janj old-growth forest, this forest had not been exposed to organized logging activities. Unlike most European old-growth forests, Janj is a unique site for studying natural regeneration processes since previous studies have not reported the impact of ungulates as significant. The original purpose of the reserve was to serve primarily as an object for scientific research. Due to its inaccessibility, Janj has also remained undisturbed by human activities. However, for this reason combined with adverse historical circumstances (economic crisis, war, *etc.*), Janj has been little studied. In this old-growth forest there is a core area (57.2 ha; 1280–1400 m a.s.l.) surrounded by a buffer zone of 237.8 ha. Only low-intensity cuttings have been performed in the buffer zone, mostly in the form of salvage cuttings.

Figure 1. Geographic location, buffer zone and core area with research plot network in the Janj old-growth forest. The insertion at the upper right-hand side of the picture represents the location of the Lom, Janj and Perucica old-growth forests in Bosnia and Herzegovina.



Inventory data from Janj was compared with recent inventories of the Lom [47] and Perucica [50] old-growth forests. Perucica is located approx. 150 km southeast of Janj, while Lom is located about 80 km northwest (Figure 1). All three old-growth forests are situated approx. 90 km from the Adriatic coast. Lom (1250–1522 m a.s.l.), with a total protected area of 297.8 ha and a core area of 55.8 ha (1280–1350 m a.s.l.), is on prevalent limestone bedrock with numerous karst phenomena such as sinkholes and rock outcrops. The annual average precipitation is about 1600 mm, and the mean annual temperature is 7.8 °C (Drinic station, 730 m a.s.l.). Perucica (1000–1600 m a.s.l.), with total protected area of 1434.6 ha, is characterised by silicate parent material in the lower parts, while in the higher parts limestone is frequent [44,45]. The mean annual air temperature is between 5.9 and 8.6 °C and mean annual precipitation ranges from 1400–1900 mm (Suha and Cemerno station, 690–1329 m a.s.l., respectively).

2.2. Field Measurements

Measurements and recordings in Janj were carried out during summer 2011. To allow direct comparison with Lom, we followed the methodology described in Motta *et al.* [47]. A regular 100 m grid with 40 sampling points in the core area was superimposed (Figure 1). Each grid intersection defined the centre of a sampling plot where the following inventories were carried out: in a 452 m^2 circular plot (radius = 12 m) species dbh (to the nearest 0.01 m) for all living trees above 7.5 cm was measured; heights of living trees were measured (to the nearest 0.5 m) for a sample of 100 trees for each species (spruce, fir and beech); in a 78.5 m^2 circular plot (radius = 5 m) species and height of regeneration individuals from 10 cm height to 7.5 cm diameter at breast height (dbh) were tallied.

With respect to course woody debris (CWD), the following measurements were carried out: on two 50 m line intersects oriented northward (the first) and eastward (the second) from the centre of the sampling point, logs crossing the line were measured (see [51]); in two 50 × 4 m rectangular plots centred on the previous line, stumps (diameter at the ground and at the top) and snags (dbh) were measured. For each element of CWD, decay classes were recorded (class 1 fresh, class 5 very old) (see [52]); CWD was grouped into snags (standing dead trees, dbh $\geq$ 7.5 cm and height $\geq$ 1.3 m), downed logs (fallen stems or branches $\geq$ 7.5 cm diameter and length > 1 m) and stumps (short, vertical remains from cutting or windthrow, top diameter $\geq$ 7.5 cm and height < 1.30 m). The separation of snags from logs was established at a 45° leaning angle.

Data for the recent inventory of old-growth Lom originates from Motta *et al.* [47], while data for Perucica was measured in 2011 on 12 square sampling plots (0.50 ha) installed on a regular 1000 × 1000 m grid covering the whole core area of the reserve. Within plots, all trees with dbh $\geq$ 10 cm were tallied according to species and dbh was measured by Lucic [47]. The data for comparison of structural changes in the three old-growth forests originates from the study of Drinic [44]. In 1952/53, he installed 14 approximately one-hectare plots within the old-growth forests of Perucica (six plots), Janj (four plots) and Lom (four plots). On these plots, dbh and height of all trees with dbh $\geq$ 10 cm and some additional structural parameters were measured. Inventories in 1952/1953 were not carried out on the same plots as in the recent inventories; therefore, some bias may be expected. However, the ecological and terrain characteristics of the Lom and Janj old-growth forests are similar across the core area and Drinic's sample size in each old-growth forest was large (ca. 4 ha). Therefore, we believe this first inventory provides good insight into the overall structural characteristics at that time. Perucica is larger and more variable. For all these reasons, special care was taken in the analyses to account for possible bias. Data was summarised and we focused only on the most persistent and clear trends.

For the Janj old-growth forest, data on dbh structure from the state forest inventory in 1965 published by Matic *et al.* [53] and the inventory in 2003 published by Maunaga *et al.* [43] were also available. Both studies followed official procedures for forest inventory in BiH, meaning that concentric circles were superimposed in a regular 100 × 100 m grid and the inventory threshold was set with dbh $\geq$ 10 cm.

2.3. Analyses

To determine site quality by tree species, we compared height curves from this study with standardized site quality curve lines for spruce, fir and beech valid in BiH [54]. For determining the average height of the upper stand story, we used the heights of the 20 largest diameter trees for each species. Volume of living trees and snags was calculated according to local volume tables. For estimating volume of logs, stumps and broken snags, the same method as described in Motta *et al.* [55] was applied.

The shape of diameter distributions was analysed using the methodology presented in Leak [56] and Janowiak *et al.* [57]. For cumulative dbh frequency distribution and for each tree species, a series of multiple regressions between the base 10 logarithm of trees per hectare (dependent variable) and all possible combinations of the dbh class midpoint, the midpoint squared and the midpoint cubed (independent variables) were calculated. The highest adjusted R^2 and lowest root mean square error values were used as a basis for selection of the best-fitting model from all significant models ($p < 0.05$). Based on the sign of the coefficient, dbh distribution shapes could be classified into rotated sigmoid (RS), unimodal (UNI), negative exponential (NE), increasing-q (IQ) and concave (CO). If shapes were inconsistent or variable, the second best-fitting model was selected.

We studied neighbourhood effects based on transition probabilities between distinct stories of old-growth forest. We compared relative tree species abundance in each sampling plot in three layers: (1) regeneration from 10 cm in height to 7.5 cm dbh (understory); (2) poles with dbh from 7.5–27.5 cm (middle-story) and (3) canopy trees with dbh over 27.5 cm (upper-story). We created three transition matrices to avoid possible oversimplification of the data as observed by White *et al.* [58]. Transition matrices were based on the proportions of understory to upper-story trees, middle-story to upper-story trees and understory to middle-story trees. Further, we calculated relative abundances of tree species after 20 generations, after species composition was stabilized, using present abundances and transition probabilities as described by Stevens [59]. In these calculations, Sycamore maple (*Acer pseudoplatanus* L.) was not considered since it was not present in the middle or upper-story. Because of the many assumptions of these models, which are difficult to verify, and because we did not sample regeneration below each tree on sampling plots, we focused only on the most obvious relationships.

Changes in relative tree species composition of the three old-growth forests according to tree density and basal area in plots for the last six decades was tested with a *t*-test. Species proportions per plot were obtained from species counts, thus the arcsine transformation was applied to meet the assumptions of normality.

3. Results

3.1. Structure and Site Quality of the Janj Old-Growth Forest

In the Janj old-growth forest, the mean tree density was 516 ha^{-1} (Table 1). Density varied from 243–995 trees ha^{-1}. Species composition in regard to the number of trees was strongly in favour of beech with 63%, followed by fir and spruce with 23% and 14%, respectively. The total number of trees with dbh over 50 cm amounted to 115 (fir 64 trees ha^{-1}, spruce 37 trees ha^{-1}, beech 14 trees ha^{-1}). Only fir (27 trees ha^{-1}) and spruce (15 trees ha^{-1}) were present above 80 cm dbh.

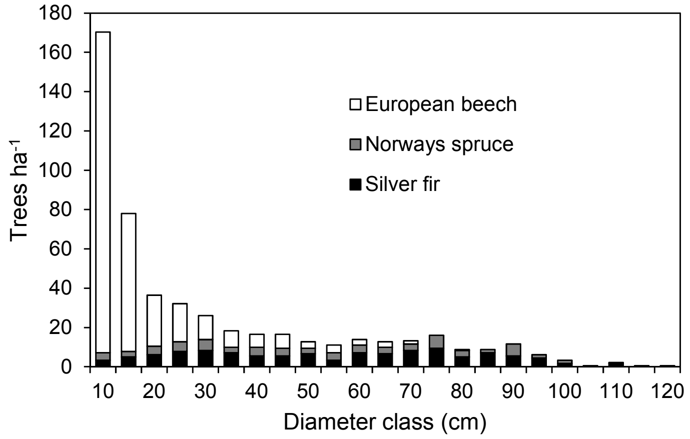
Table 1. Structural characteristics of the Janj old-growth forest (core area).

	Mean diameter (cm)	**Density (trees ha^{-1})**	**%**	**Basal area ($\text{m}^2\cdot\text{ha}^{-1}$)**	**%**	**Volume ($\text{m}^3\cdot\text{ha}^{-1}$)**
European beech	22.5	327	63	11.7	18	192
Silver fir	60.6	117	23	34.7	52	648
Norway spruce	58.2	72	14	20.2	30	376
Sycamore maple	–	<1	<1	–	<1	–
Total	46.7	516		66.7		1215
Range	9.0–100.1	243–995		26.1–102.5		419–1946
St. deviation	23.0	155		17.7		347

Basal area on sample plots varied from 26.1–102.5 m^2. Average basal area was 34.7 m^2, 20.2 m^2 and 11.7 m^2 for fir, spruce and beech, respectively. The share of sycamore maple in basal area was negligible although the site conditions suit this species well. With respect to basal area, fir dominated with 52%, followed by spruce and beech with 30% and 18%, respectively. Thus, species composition was significantly different when estimated according to the tree density and basal area.

The frequency distribution of diameters was dominated by beech within the small diameter classes, but its share sharply declined towards the medium and large diameter classes (Figure 2). Large diameter classes were dominated by fir and spruce. For 20 cm dbh class widths, the best-fitting multiple regression model of dbh frequency distribution indicated an UNI shape for fir, IQ shape for spruce, CO shape for beech, while for the cumulative distribution an RS shape was indicated (Table 5).

Figure 2. Diameter distribution of living trees in the core area of Janj.



The relation between dbh and height of trees suggested that site quality for all three species (beech, fir, spruce) could be assigned to the first class, indicating that these species grow in the most favourable conditions for their development. In younger stages, beech was taller than its competitors of the same diameter, while within large dbh classes (≥70 cm) spruce and fir were taller. The largest diameter and tallest individuals measured were firs with a dbh of 124 cm and a height of 50.5 m, respectively. Spruce reached 110 cm in dbh and 47.5 m in height, while beech grew to 92 cm in dbh and 44.7 m in height, respectively. There were no occurrences in any of the species of the largest diameter tree concurrently being the tallest. The mean values of height and corresponding dbh for the 20 largest diameter trees of each species are presented in Table A1.

3.2. Coarse Woody Debris

The total volume of CWD in Janj was 386.5 m^3·ha^{-1}, which was 32% of the growing stock (Table 2). Most of the CWD volume was in logs, followed by snags and stumps with 79%, 19% and 2%, respectively. Logs were also more frequent than snags and stumps combined.

All five CWD decay classes were present only in logs, where the fifth decay class was prevalent. Most snags were in the first decay class, while the fifth was not present. Stumps were mostly in the fourth decay class. The first and fifth decay classes of stumps were completely absent in the core area (Table 3). On the other hand, large standing snags (≥50 cm dbh) were present with 19 trees ha^{-1}, contributing to biodiversity and the survival of other species, especially nesting birds that depend on them. Interestingly, the number of smaller diameter snags (7.5–50 cm dbh) was lower, amounting to 17 trees ha^{-1}. We also tested for relations between CWD volume and growing stock, but the results were not significant.

Table 2. Volume of coarse woody debris types in the core area.

	Snags ($m^3 \cdot ha^{-1}$)	**Logs ($m^3 \cdot ha^{-1}$)**	**Stumps ($m^3 \cdot ha^{-1}$)**	**Total ($m^3 \cdot ha^{-1}$)**
Volume	70.9	306.7	8.8	386.5
Range	0–510.2	103.8–582.5	0–26.1	162.1–892.6
SD	107.8	125.2	5.5	169.7

Table 3. Different decay classes of coarse woody debris in the core area.

Decay classes	**Snags ($m^3 \cdot ha^{-1}$)**	**Logs ($m^3 \cdot ha^{-1}$)**	**Stumps ($m^3 \cdot ha^{-1}$)**
1	20.1	2.2	0
2	16.2	30.3	0.5
3	18.8	64.2	3.0
4	15.8	88.8	5.3
5	0	121.2	0

3.3. Replacement Patterns and Neighbourhood Effects

There were several indices that suggested a prevalent endogenous disturbance regime in the Janj old-growth forest in recent decades. This offered favourable conditions for investigation of neighbourhood effects of tree species. In the understory and middle-story, beech was by far the most frequent species, at 69% and 83%, respectively (Table 4). Fir was the second most abundant species in the understory and middle-story at 15% and 10% and prevailed in the upper-story at 48%. Between the understory and upper-story, beech was the most abundant species under its conspecific, while between the understory and middle-story, as well as between the middle-story and upper-story, it was more frequent under conifers. Fir indicated some signs of reciprocal replacement since in all three matrices it was more frequent under beech or spruce. Also, spruce was not the most frequent species under its conspecific in any of the comparisons. Models of future relative abundance indicated a strong increase of beech in the upper story and a moderate decrease in the middle story and *vice versa* for both conifers.

3.4. Structural Changes of the Janj, Lom and Perucica Old-Growth Forests over Six Decades

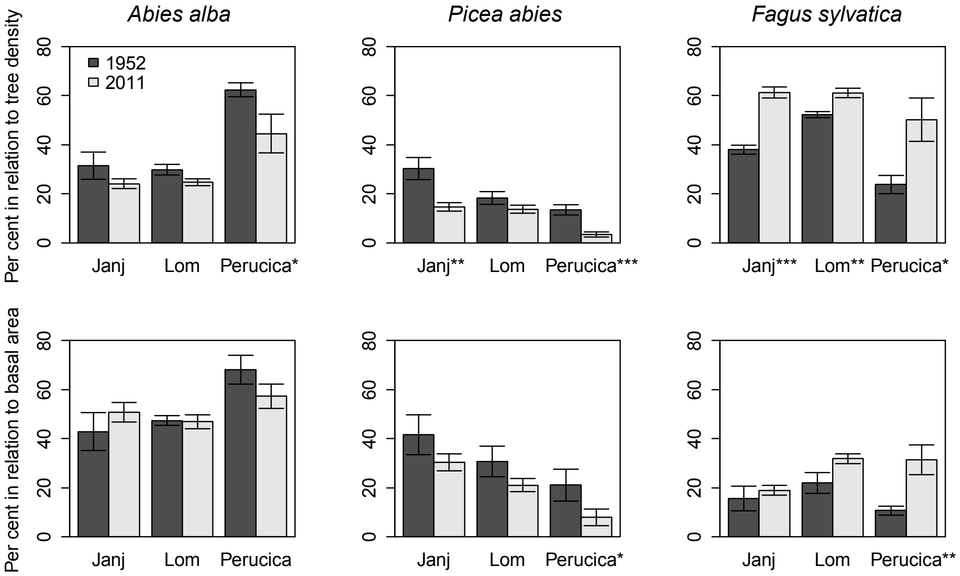
In Janj, the share of beech in tree density was similar in the first two inventories of 1952 and 1965, at 38% and 37%, respectively. It substantially increased to 54% and 63% in the last two inventories of 2003 and 2011, respectively. From 1952–2011, spruce decreased from 30%–14%, while the share of fir decreased less intensively from 32%–23%, respectively. A similar pattern of beech progression and conifer decline was indicated in Lom and Perucica (Figure 3). This trend was also comparable regarding the shares of tree species in relation to basal area. Here, the only exception was an increase in the share of fir in Janj, from 43%–52% from 1952–2011, respectively. The increase in the share of beech in density was statistically significant for all three old-growth forests, while its increase in basal area was only significant for Perucica.

Table 4. Transition probabilities of species between three canopy stories, based on 40 sample plots. Present species mixture in individual stories is given in parentheses next to the species. Relative abundances of the species after 20 generations are listed in the far right column.

Understory	Upper story beech (0.24)	fir (0.48)	spruce (0.28)	Relative abundances
beech (0.69)	0.73	0.69	0.68	0.74
fir (0.15)	0.14	0.11	0.20	0.16
spruce (0.05)	0.07	0.09	0.05	0.10
maple (0.11)	0.06	0.11	0.06	/*
Understory	**Middle story beech (0.83)**	**fir (0.10)**	**spruce (0.07)**	
beech	0.63	0.75	0.68	0.69
fir	0.16	0.13	0.16	0.19
spruce	0.10	0.04	0.09	0.12
maple	0.11	0.08	0.07	/*
Middle story	**Upper story beech**	**fir**	**spruce**	
beech	0.75	0.83	0.83	0.77
fir	0.15	0.10	0.09	0.14
spruce	0.10	0.07	0.08	0.09

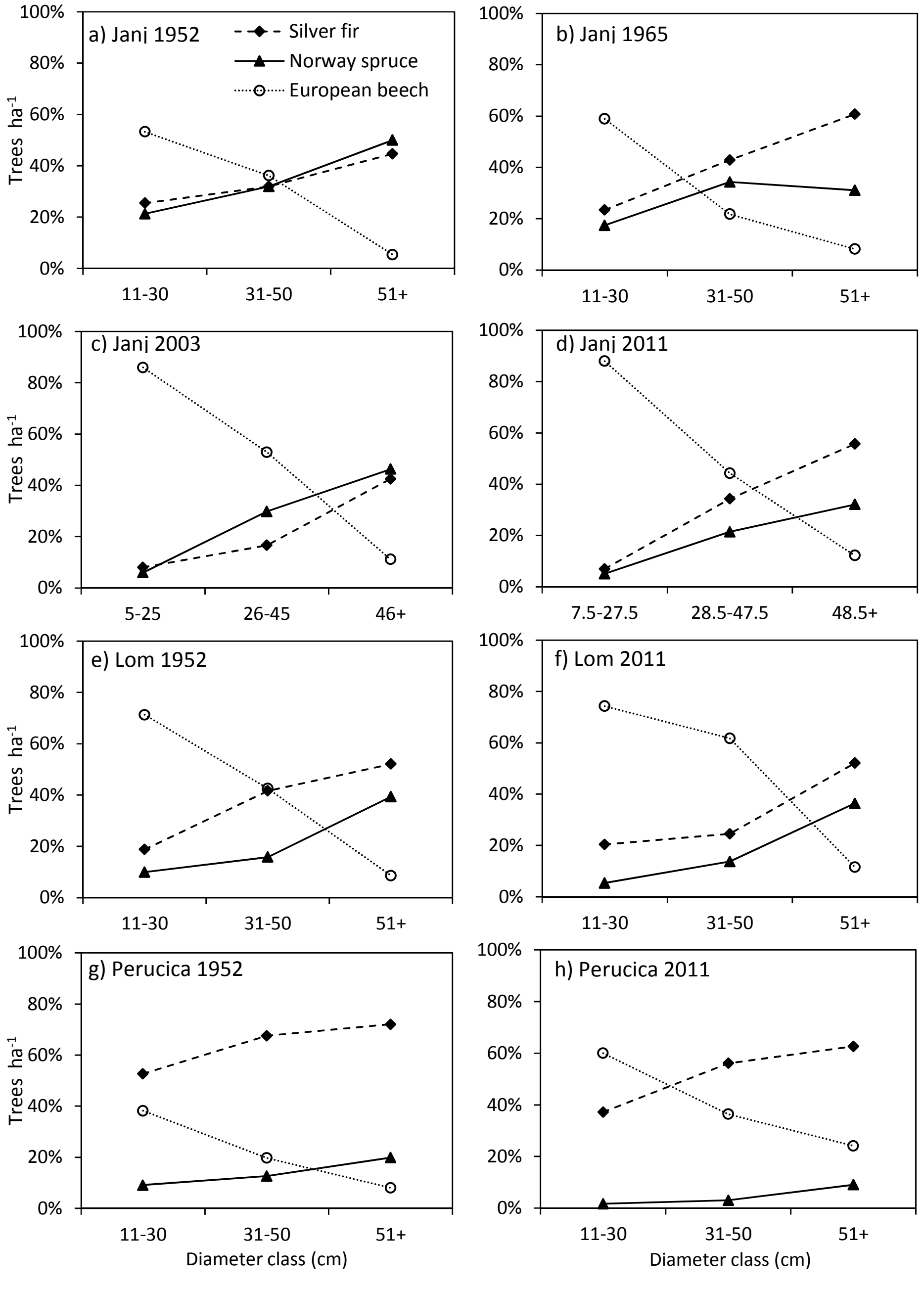
* Maple was not present in the middle or upper layer.

Figure 3. Change in tree species composition according to tree density (**above**) and basal area (**below**) in the last six decades. Three, two and one stars denote a significance code of $p < 0.05$, $p < 0.01$ and $p < 0.001$, respectively.



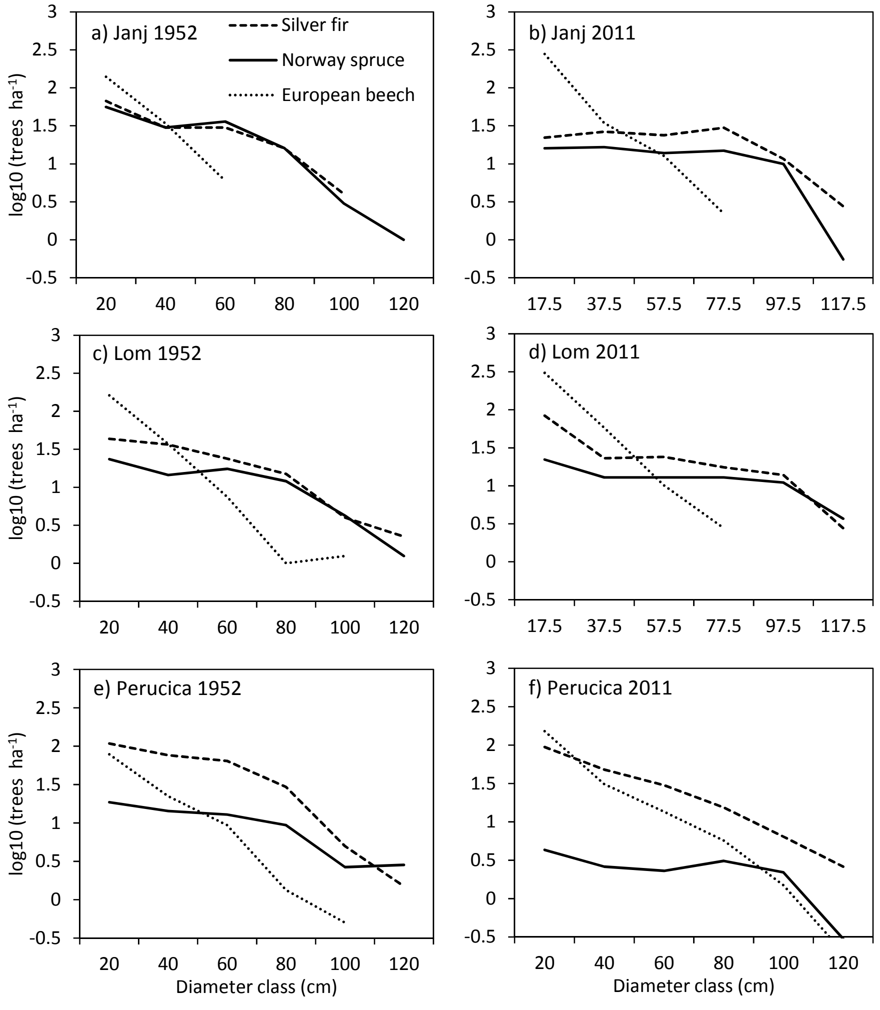
In all inventories, tree species composition according to number of individuals in extended dbh size classes in Janj and Lom showed a similar overall pattern (Figure 4). Beech significantly prevailed in the first extended dbh class, while spruce and fir dominated in the third class. The exception was Perucica in 1952 where silver fir was dominant across all dbh classes, while spruce and beech showed a similar pattern according to increasing dbh classes as in the other sites, but with a smaller share.

Figure 4. Changes in tree species composition with respect to density within extended dbh size classes in the Janj old-growth forest at different inventory years (**a**–**h**) and comparison with the Lom and Perucica old-growth forests. (**a**) Share of silver fir, Norway spruce and European beech in Janj old-growth forest in 1952 according to extended dbh classes; (**b**–**d**) Same data for Janj old-growth forest in 1965, 2003 and 2011, respectively; (**e**,**f**) Same data for Lom old-growth forest in 1952 and 2011, respectively; (**g**,**h**) same data for Perucica old-growth forests in 1952 and 2011, respectively.



During the last half of the century, the proportion of beech in the first extended dbh class in Janj continually increased, from 53% in 1952 to 88% in 2011. On the other hand, the share of both spruce and fir in the same size class was in constant decline. In recent decades, beech has become prevalent in the second extended dbh class. Its share also increased in the third extended dbh class, from a modest 5% in 1952 to 12% in 2011. The relative abundance of fir in the second and third extended diameter class was relatively unchanged, while that of spruce moderately decreased (Figure 5a–d). Also, in Lom the share of beech from 1952–2011 increased from 71%–74%, 43%–62% and 9%–12% within the first, second and third extended diameter classes, respectively. During the same period, the share of spruce moderately decreased over all classes, while the share of silver fir decreased only in the mean dbh class (Figure 5e,f). In Perucica, the increase in beech and decrease in conifers were similar to Janj and Lom, but were more pronounced (Figure 5g,h).

Figure 5. Comparison of diameter distributions for the Janj old-growth forest in 1952 (**a**) and 2011 (**b**); Lom in 1952 (**c**) and 2011 (**d**); and Perucica in 1952 (**e**) and 2011 (**f**).



For cumulative tree dbh distributions (20 cm dbh classes), the best-fitting multiple regression models changed from IQ to RS in Janj, from NE to RS in Lom and from VAR to NE in Perucica (Table 5, Figure 5). In all three old-growth forests, the total number of trees in the first diameter class (7.5–17.5 cm) increased, while it decreased through medium diameters. In 1952, the best-fitting model for both conifers in all three old-growth forests was IQ. This indicates increasing reduction rate in the number of trees from one diameter class to the next with increasing tree size and could be indicative of past disturbance within the group of large diameter trees. In the following 60 years, the fir model changed to UNI in Janj, to RS in Lom and to CO in Perucica. The UNI model may indicate problems with recruitment. The spruce model changed to RS in Lom and remained of the same IQ shape in Janj and Perucica. Changes from IQ to RS and CO may indicate improved conditions for large diameter trees. During the observed period, the shape of beech frequency distributions changed from NE, VAR and CO to CO. This indicates a shift to larger diameter trees.

Table 5. Parameters of the best-fitting model for multiple regressions between the base 10 logarithm of trees per hectare and all possible combinations of dbh.

	Janj 1952				**Janj 2011**			
	Fir	**Spruce**	**Beech**	**Cumulative**	**Fir**	**Spruce**	**Beech**	**Cumulative**
RMSE	0.12	0.11	0.09	0.12	0.12	0.23	0.13	0.06
Adj. R^2	0.92	0.93	0.99	0.95	0.95	0.78	0.99	0.99
N (dbh class)	5	5	4	5	6	6	6	6
Shape	IQ	IQ	NE	IQ	UNI	IQ	CO	RS
	Lom 1952				**Lom 2011**			
RMSE	0.09	0.09	0.15	0.10	0.08	0.02	0.09	0.04
Adj. R^2	0.97	0.96	0.91	0.98	0.97	0.99	0.99	0.99
N (dbh class)	6	6	5	6	6	6	6	6
Shape	IQ	IQ	VAR	NE	RS	RS	CO	RS
	Perucica 1952				**Perucica 2011**			
RMSE	0.18	0.09	0.08	0.14	0.03	0.10	0.08	0.09
Adj. R^2	0.94	0.95	0.99	0.97	0.99	0.86	0.99	0.99
N (dbh class)	7	7	7	7	7	7	7	7
Shape	IQ	IQ	CO	IQ	CO	IQ	CO	NE

RMSE—root mean square error; UNI—convex or unimodal shape; RS—rotated sigmoid shape; IQ—increasing-q; CO—concave; VAR—variable (sensu Janowiak, *et al.* [57]).

Graphical comparison of empirical dbh distributions revealed several similarities among old-growth forests and inventories (Figure 5). In addition to empirical dbh distributions, curves of the best regression models were also inspected (Figure A1). This enabled a direct comparison despite different dbh class thresholds between years of measurements. In all cases, beech dbh distribution follows an approximate straight line if densities are plotted in a logarithmic scale, indicating the closest match with NE. In the recent inventory, beech was more frequent across all dbh classes and also shifted to larger dbh classes. However, the shape remained relatively similar between years and old-growth forests. Beech distribution had the steepest slope of all tree species, which may be attributed to a higher mortality rate.

Distributions of conifers were more irregular in shape and indicated for both species a non-constant q ratio across dbh classes. In all inventories and old-growth forests, the spruce curve was consistently the most "flattened" within smaller dbh classes among all species. Between inventories, spruce density decreased over all classes in Janj and Perucica, but this was more pronounced within small dbh classes.

In Lom, spruce density decreased across medium dbh classes and slightly increased in smaller and larger classes (Figure 5c,d). The same was true for fir, while in Perucica fir decreased over all classes.

4. Discussion

4.1. Recent Stand Structure in Janj and Comparison with Similar Old-Growth Forests

Tree species composition according to growing stock in Janj comprised one of the highest shares of conifers (84%) when compared to other old-growth forests in the region [15,44,47,60]. A similar low percentage of beech (18%) was found in the Igman old-growth forest in BiH, which is located about 92 km in the southeast direction. In Janj, spruce was present with an especially high percentage (30%), which can be compared with more continental Carpathian or Alpine old-growth forests, for example Lucka Bela, which also has a 30% share [61]. It is very likely that continentality and high altitude positively influenced the share of spruce in Janj [62]. However, past natural or anthropogenic disturbance events cannot be ruled out. Near the Janj core area is the geographical name “Pozar” in the Serbian language, which translates to fire in English (Figure 1).

In Lom and Perucica conifers were also dominant in BA, with 68% and 65%, respectively [47,50]. With respect to the tree density in all three old-growth forests, beech was the dominant species with 63%, 60% and 50% in Janj, Lom and Perucica, respectively. The average growing stock of 1215 $m^3 \cdot ha^{-1}$ and basal area of 67 $m^2 \cdot ha^{-1}$ in Janj were also among the highest when measured over larger areas and not on a particular selected permanent plot in this type of forest [5,6]. Average growing stock in Lom was lower with 763 $m^3 \cdot ha^{-1}$, and Perucica was between these two values with 937 $m^3 \cdot ha^{-1}$.

The high growing stock in Janj is likely a result of the high percentage of conifers, good site quality and a relatively long period (up to 60 years) without significant natural disturbances. The latter was also indicated by the forest structure, which is absent of large gaps or cohorts of small trees. In Janj, the average CWD volume of 387 $m^3 \cdot ha^{-1}$ was above the average value in Lom (327 $m^3 \cdot ha^{-1}$). Motta [63] observed comparable values of 406 and 420 $m^3 \cdot ha^{-1}$ in mixed Dinaric old-growth forests in Perucica and Biogradska gora, respectively. CWD values from Bosnian mixed old-growth forests were well above the European average of 220 $m^3 \cdot ha^{-1}$ [64] for beech old-growth forests. This may be attributed to the slower decomposition rate of conifers compared to beech [65], their higher overall growing stock and productive sites. The CWD volume to GS ratio in Janj (32%) was lower than in Lom (43%) and also below the European average ratio of 37%, which again may indicate lesser intensity of recent disturbances.

In Janj, the understory and the middle-story were dominated by beech in regard to tree density, while the upper-story was dominated by fir and spruce. Despite beech dominance in lower stories and frequent replacement patterns by beech, there was some indication of reciprocal replacement between species. Moderate reciprocal replacement was often reported for mixed forests with silver fir (e.g., [12,32,66]). Transition matrices indicate the future decrease of beech in the middle-story and increase in the upper-story if the assumptions of the model are to be met [58,59]. The probability that canopy fir and spruce will be replaced by middle story beech does not depend solely on its frequency since both conifers attain a higher position within the canopy. Thus, the assessment of the future species mixture with transition probabilities is above all an indication of potential beech progression.

4.2. Six Decades of Structural Changes in the Janj, Lom and Perucica Old-Growth Forests

Comparison of recent inventories (Motta *et al.* [47], Lucic [50] and this study) with studies from Drinic [44], Matic *et al.* [53] and Maunaga *et al.* [43] may be biased since data were not collected on the same plots. Therefore, emphasis was on changes that were strongly expressed, preferably synchronous across old-growth forests and consistent with the data from recent, more intensive inventories. During the past six decades, the average tree density in Janj and Lom increased by 25% and 10%, respectively, while in Perucica a decrease was indicated. The density increase in Janj and Lom may be attributed to the recent history of endogenous disturbance, but partially also to the 2.5 cm lower dbh limit at the recent inventory. Total basal area increased in Janj by 13%, while it decreased in Lom and Perucica by 6% and 26%, respectively.

The share of spruce and fir in tree density decreased in all reserves, while the share of beech increased. Also, the share of beech in BA increased, while the share of spruce decreased. The share of fir in BA increased in Janj, remained stable in Lom and decreased in Perucica. It seems that fir better compensated for the decrease in density by diameter growth when compared to spruce. Another reason for the more stable fir structure might lie in the lower intensity of indirect anthropogenic disturbance in Bosnia compared to Slovenia, Croatia and Slovakia. Namely, lower SO_2 emissions [36] and lower deer densities [35] may be responsible for the less pronounced silver fir decline in Bosnia. Diaci *et al.* [15] indicated a synchronous silver fir decline in most studied southeast European mixed old-growth mountain forests, while the share of fir in BA increased in the Igman and Trstionica mixed old-growth mountain forests in Bosnia. The data from this study indicated a more pronounced spruce decline in comparison to fir, which may be attributed to its greater susceptibility to drought and high temperatures at the limit of its geographic range towards the Adriatic Sea [62], or its successional stage due to past (anthropogenic) disturbance. This is also in line with the current spruce decline in the northern Velebit National Park in Croatia, but see Battipaglia *et al.* [67] for different results.

For all inventories and old-growth forests, comparison of tree species composition showed beech dominance in the first extended dbh class, its decrease along extended dbh classes and an increase in conifers. This may be due to the inferior competitive ability of beech in larger dbh classes (see Motta *et al.* [47]), but since the species mixture changed with time in favour of beech, it may also indicate the onset of beech progression before the 1950s. The lower density of conifers compared with beech may, to some extent, not be in conflict with the demographic equilibrium due to lower mortality of conifers. This was also indicated by the less steeply sloped curves of their dbh distributions (comp. Shimano [68]). However, stable dbh frequency shapes would be expected in time if the different natural mortality rates were the main reason for the dbh distribution shape patterns.

The best fitting curves for dbh frequency of conifers indicated an IQ shape in 1952, while in the recent inventory their shapes were more variable. For conifers, IQ distributions may indicate, due to increasing Q, a higher mortality rate in large-diameter trees and potentially past disturbance, while a unimodal shape (Janj) may indicate heavier past disturbance, a succession or insufficient recruitment [56,57]. NE and RS shapes are often reported as common in old-growth forests [15,56]. In old-growth northern hardwoods, Ducey *et al.* [69] found deviations from the classic "balanced" exponential distribution on plots heavily stocked with beech; however, in our study beech was sub-dominant to conifers and exhibited a tendency towards NE and CO shapes in all inventories. CO patterns in beech were often observed due to a few widely scattered large trees. It seems that they have filled some of the space made available by the conifer decline.

4.3. Historical Evidence and Possible Causes of Beech Progression

Coexistence of spruce, fir and beech is a complex subject [12,13,17,19,46]. It is driven by the interaction of many factors, anthropogenic and natural. While small scale endogenous disturbance favours fir, intermediate disturbance promotes beech, spruce and admixed broadleaved species [5,19]. Regarding site conditions, conifers are for example more susceptible to competition from ground vegetation than broadleaves and are therefore more successful in the regeneration on rockier sites or acidic soils and on CWD with less abundant ground flora [16]. Besides the natural drivers of stand composition in old-growth forests, the influence of indirect anthropogenic factors may also be strong [3,7,33,70]. Air pollution, over-browsing and position within the agricultural landscape may change natural processes [71].

Factors influencing coexistence act at different spatial scales from tree neighbourhood effects, through the regional impact of diverse deer densities and air pollution to the larger scale impact of climate change. Moreover, species coexistence in mixed mountain forests should also be observed from a long-term perspective since all three species are long-lived and reach ages up to five centuries and more. Many dominant trees in old-growth forests originated two to four centuries ago [42,47,72]. At that time, the densities of ungulates in the Dinaric Mountains were significantly lower, with some species even going extinct due to poaching [14], and the climate was cooler (little ice age, 16th–mid 19th century period; see [73–75]). In managed forests, conifers were favoured and beech treated as a non-commercial species. It was often felled as firewood or for charcoal and potash production [9]. This type of forest exploitation did not require sophisticated logging infrastructure and has affected some remote old-growth forests [15]. Before the last century, a cooler climate, unregulated logging of beech, and low densities of ungulates favoured regeneration of conifers.

During the last century, a new constellation of factors has evolved which have given an indirect competitive advantage to beech. Compared to the mid 19th century, warmer climate conditions were already being reported at the beginning of the 20th century [75,76]. Warm spells induced a diffuse decline of conifers in mixed mountain forests on extreme sites and at the limits of their geographic range [4]. After WWII, modern silviculture was introduced in former Yugoslavia, which included beech as a valuable species, while forest grazing was prohibited [77]. In the 1950s, with the onset of accelerated industrialization, air pollution began to be a factor that negatively affected conifers, especially silver fir [21,78]. This species was also weakened by increasing ungulate densities [14]. Higher temperatures and longer vegetation periods coupled with nitrogen deposition may have also contributed to more exuberant ground vegetation [23,79], which represents a greater obstacle for the development of conifer seedlings than those of beech [16].

In BiH, air pollution was less pronounced compared to other parts of Yugoslavia [36], and game densities were never considered to be excessive. Red deer in particular was extremely rare, while roe deer and chamois densities even then rarely exceeded one animal per square kilometre [15,35]. On the other hand, the consequences of climate fluctuations at the beginning of the 20th century in BiH received a great deal of attention in the scientific literature (comp. Safar [4] and references therein).

Bark beetle outbreaks on fir and spruce in the Dinaric Mountains were already reported in 1923 and 1924 [38]. A new wave of outbreaks started after the extremely hot and dry summer of 1928, which was followed by a harsh winter (compared to meteorological data in Brunetti *et al.* [76], Böhm *et al.* [80] and Kress *et al.* [81]). This resulted in a patchy and diffuse decline of conifers on south-exposed and shallow soil sites, which was later followed by a large-scale bark beetle outbreak on conifers: spruce, fir and Scots pine (*Pinus sylvestris* L.), with the exception of black pine (*Pinus nigra* J.F. Arnold; see [32,37]). Some authors shared the opinion that bark beetle outbreaks were partially caused by unregulated felling and improper handling of felling residues [38,82]. According to Popovic [39], in 1928 only individual conifers at the most exposed sites were weakened by the drought and consequently infested by bark beetles, but at the beginning of 1929, groups of 10–15 trees were already being attacked, and by the end of 1929, this increased to circular patches of 100 trees or more. In 1930, the size of patches reached 1000–5000 trees. Healthy trees were also attacked, but not small trees and saplings. At the start of the outbreak, its upper borderline was at about 1200 m, but by 1930 it reached an altitude of 1400 m a.s.l. Tregubov [39], an early researcher of old-growth forests in the Lom region, also mentioned these events.

The next important period of high summer temperatures and drought was in the late 1940s and early 1950s (comp. to Brunetti *et al.* [76], Böhm *et al.* [80] and Kress *et al.* [81]). For these events, reports of bark beetle outbreaks in the Perucica old-growth forest are available. According to Eic [41] and Golubovic [33], in the fir dominated part of Perucica, 20,000 m^3 of infested conifer logs were cut down, which represented about 10% of the exploitable timber. Logs were not properly handled, increasing the potential for beetle infestations. Eic [41] further stated that the increased infection was also due to fires in neighbouring forests after heavy forest exploitation.

The combination of the bark beetle outbreaks in the early 1920s, the severe climatic event in 1928 followed by the droughts of the late 1940s and early 1950s, and anthropogenic disturbances [4] had weakened the competitive strength of conifers and probably induced a large-scale synchronous regeneration wave of beech (Figure 6), which had already been observed by the early researchers of old-growth forests [4,46].

Figure 6. A dense, ubiquitous small tree layer of beech with scattered conifer seedling clusters below is typical for a large part of the Janj reserve (November 1, 2012; photo: J. Diaci).

Beech seed crops are not as frequent as those of conifers [83]; however, beech mast years have become more frequent in the last century, possibly due to temperature increases, climatic extremes and increased atmospheric nitrogen [22]. Regarding disturbance events in BiH from the 1920s to the early 1950s, it is also important that early summer drought is a strong masting predictor for beech [84]. Large-scale synchronous regeneration of beech has probably delayed the regeneration of conifers, lasting for several decades [19]. Documented climatic events, likely coupled with anthropogenic disturbances, are indicated in this study by the following: (1) beech dominance among small trees in all inventories and its increase overall dbh classes in recent inventories; (2) the future decrease of the beech middle-story modelled with transition probabilities; (3) the IQ shape of dbh frequency distribution in the 1950s for conifers in all old-growth forests and (4) changes in dbh frequency distributions. Other recent studies have also suggested these events, e.g., the disturbance study in Motta *et al.* [47] and gap age analysis in Bottero *et al.* [48].

5. Conclusions

The recent forest structure of the Janj old-growth forest in comparison to other Dinaric and European mixed mountain forests is characterized by a high growing stock and a large proportion of conifers, particularly spruce. The former may be due to site quality, dominant conifers, and the absence of large disturbances in recent decades. The high share of conifers in comparison to other Dinaric mixed old-growth forests in Slovenia and Croatia could be attributed to the higher altitude and continental climate. However, other Bosnian mixed old-growth forests (Igman, Lom and partly Perucica) are in a similar altitudinal belt and exhibit fewer conifers; therefore, past natural or anthropogenic disturbances may have also influenced the high share of conifers. This seems likely since spruce dbh distribution changed in time and the recent distribution does not show sustainable recruitment.

With respect to tree height and diameter size, beech is slightly inferior to both coniferous trees, but many changes in structural parameters indicate its progression (e.g., increasing abundance within small trees; changes in dbh distributions, GS and BA; neighbourhood effects). The causes of conifer regression are likely associated with climatic extremes, especially high summer temperatures and droughts, which have weakened their vitality and influenced bark beetle infestations. However, many anthropogenic disturbances may have accelerated this process (unregulated and sanitary fellings in old-growth forests and in the near vicinity, burning of slash and clearing of land for fields and pasturing, building of logging infrastructure). Some evidence suggests that the sequence of droughts, bark beetle infestations, and anthropogenic disturbances during the 1920s, 1940s and early 1950s had diffusely opened the canopy layer of the three analysed old-growth forests in BiH, reduced conifer and increased beech seed potential, and thus triggered a wave of beech regeneration. Conifers did regenerate below the dense beech seedling and sapling layer, but with a certain delay, thus their density and competitive ability probably decreased with each wave of drought and proliferous beech regeneration.

The results of this study indicate conifer decline in some Bosnian old-growth forests. It seems that the decline was not continuous but rather followed extreme climatic events (summer droughts and harsh winters), most likely in conjunction with bark beetle outbreaks and anthropogenic disturbances. This hypothesis deserves in-depth research in the future. If confirmed, it could contribute to a better understanding of future changes in forest composition due to climate change.

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Author Contributions

Initial ideas and financing of the research: Jurij Diaci, Renzo Motta and Srdjan Keren; data compilation and evaluation: all authors; manuscript drafting: Srdjan Keren and Jurij Diaci; all authors contributed to revising successive drafts.

Conflicts of Interest

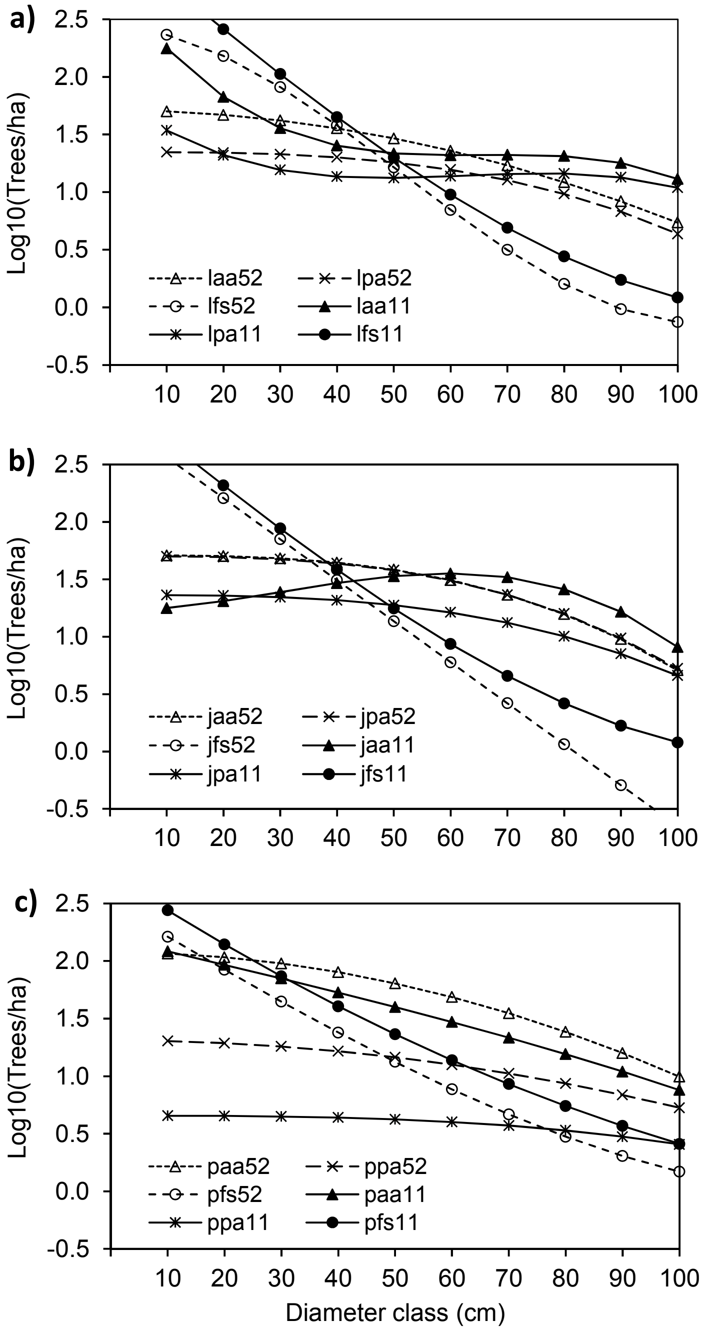
The authors declare no conflict of interest.

Appendix

Table A1. Heights of thickest trees of major tree species in old-growth Janj.

Species	European beech		Silver fir		Norway spruce	
No	dbh	height	dbh	height	dbh	height
1	48	31.2	72	38.6	68	37.9
2	48	30.4	73	40.3	70	36.3
3	51	31.5	74	34.7	70	35.5
4	53	30.5	74	38.4	71	37.5
5	54	40.8	75	41.0	74	37.4
6	56	33.4	80	42.3	75	40.1
7	57	32.1	81	45.0	75	41.8
8	58	30.0	85	42.0	75	43.0
9	58	33.0	86	35.3	77	36.3
10	58	39.0	94	39.4	77	34.6
11	59	36.0	96	49.5	78	39.3
12	59	37.2	98	39.0	83	46.2
13	60	32.5	99	44.5	85	43.5
14	60	39.2	108	50.5	91	41.9
15	69	35.6	110	48.5	92	44.9
16	70	35.6	110	46.2	95	44.5
17	72	35.5	117	47.5	96	43.4
18	79	35.4	117	44.8	99	44.3
19	83	44.7	120	46.5	100	45.5
20	92	41.6	124	44.8	110	45.0
Mean	62.2	35.3	94.7	42.9	83.1	41.0

Figure A1. Temporal changes in species-specific diameter distributions of old-growth forests (**a**) Janj, (**b**) Lom, (**c**) Perucica. Curves and lines represent the best regression models. The first letter indicates old-growth forest (e.g., l denotes Lom), the next two letters represent Latin species names (e.g., aa denotes *Abies alba*) and the following two numbers indicate the year of measurement (e.g., 11 denotes 2011).



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