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RECENT STRUCTURAL CHANGES, SPECIES COMPOSITION AND INTERACTION IN AN OLD-GROWTH FOREST – AN EXAMPLE FROM BJELAŠNICA MT.

SUMMARY

This study examines the structural dynamics and species composition of the "Ravna Vala" old-growth forest on Bjelašnica Mountain, focusing on neighborhood effects on tree growth. Data from a permanent 1-hectare plot, measured 2012 and 2023, revealed that silver fir (*Abies alba* Mill.) constitutes nearly 73% of the total volume, while beech (*Fagus sylvatica* L.) dominates in tree numbers. The forest displays a reverse J-curve pattern, with significant mortality in smaller diameter classes. Using indices for species intermingling, aggregation, and competition, the study found that diameter at breast height (dbh) and the aggregation index significantly influenced growth, especially for silver fir and beech. Additional factors like the mixing index and competition index were significant for beech growth. These results underscore the complexity of species interactions and the importance of tailored management strategies. Future research should explore factors limiting fir regeneration and the link between disturbances and beech recruitment. Management practices that mimic natural disturbances, such as creating larger gaps, are recommended to enhance species diversity and forest resilience.

Keywords: Old-growth forest, species composition, tree growth, beech-fir, competition

INTRODUCTION

Old-growth forests can be defined as naturally regenerated stands composed of native tree species with minimal human impact, where ecological processes operate dynamically (Barton and Keeton, 2018; Sabatini et al., 2020). Currently, less than 1.5 million hectares are considered old-growth forests, predominantly located in the boreal zone (Sabatini et al., 2018). In the temperate zone of Europe, old-growth forests are exceedingly rare, covering less than 0.1% of the forest area, and are nearly non-existent for many forest types within the EU (Meyer et al., 2021). The Dinaric Alps is one of the European regions that still hosts old-growth forest stands (Motta

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et al., 2024). Historically, this mountain range served as a border between European Kingdoms and the Ottoman Empire, resulting in relatively low population densities over centuries. This low human density led to less intensive and less widespread deforestation and land use compared to other European mountain regions (Kaplan et al., 2009; Cagliero et al., 2023). One of the most prominent forest communities in this mountainous region consists of mixed stands of European beech (*Fagus sylvatica* L.), Norway spruce (*Picea abies* Karst.), and silver fir (*Abies alba* Mill.), which dominate not only managed forests that follow "close-to-nature" principles due to the long-term application of the selection (plenter) management system but also old-growth forests (Keren et al., 2014; Diaci et al., 2011; Čilaš et al., 2023).

Consequently, large, well-preserved forest patches have been conserved, attracting the attention of European foresters, ecologists, and botanists since the early 20th century (Motta et al., 2024). Studying old-growth forests is crucial for understanding forest ecosystem dynamics and developing effective forest management strategies. In central Europe, the current forest structure and composition are largely the result of human activities, whereas old-growth forests are shaped by infrequent, stand-replacing disturbances in the absence of human interference (Nagel et al., 2010). Excluding human activities provides valuable insights into trends in tree species occurrence and changes linked to factors such as climate and air pollution. For instance, an increase in beech in old-growth forests began 60 years ago (Šafar, 1951) and has become more evident in recent decades. Conversely, a decline in fir has been observed in some old-growth forests of the Dinaric region (Diaci et al., 2022; Keren et al., 2014; Klopčič et al., 2010). The coexistence of beech, fir, and spruce is influenced by many factors, complicating the study of these dynamics. The spatial and temporal dynamics of some forest types are significantly affected by neighbourhood effects (Frelich and Reich, 1999). The neighbourhood effect can be measured using various competition indices, with growth response yield or increment as a function of density being common measures (Balandier et al., 2006). However, this method does not fully capture competition due to spatial and temporal variation, plant immobility, and phenotypic plasticity. An alternative approach involves studying plants individually, focusing on their interactions with specific neighbours rather than overall population density, with diameter at breast height (dbh) serving as a key indicator of growth and resource utilization (Antúnez et al., 2023; Stoll and Weiner, 2000).

The aim of this study was to investigate the recent structural dynamics and tree species composition resulting from past disturbances and to assess the impact of neighbourhood factors on tree growth. Specifically, we aimed to:

- (I) Evaluate the recent structural dynamics and compare it to other old-growth forests in the Dinaric region.
- (II) Analyse tree distribution within the stand as a consequence of nonhuman activities
- (III) Determine the influence of neighbourhood parameters (e.g. neighbour dbh, tree species, distance, etc.) on tree growth and identify the key drivers.

MATERIAL AND METHODS

The research was conducted on a permanent 1 ha plot within a pristine forest reserve „Ravna vala“ on Bjelašnica mountain. The forest reserve „Ravna vala“ is located around 30 km south west from Sarajevo, with an altitude range from 1280 to 1450 m. The total area is around 45 ha. „Ravna vala“ belongs to *Abieti – Fagetum illyricum* community with Beech and Fir as dominant tree species and Norway spruce (*Picea abies* Karst) and Sycamore (*Acer pseudoplatanus* L.) can also occur. The dominant parent substrate is limestone and dolomite, where moraine deposits are also present. This results in soils with variable depth. Most common soil types are rendzina, calcomelasol and calcocambisol. Climate is continental with strong mountain influence (Lučić, 1966). Average annual temperature is 6°C, and annual precipitation sum is 1600 mm. The data was collected on a permanent 1 ha plot within the reserve. The plot was further divided into 10 x 10m grid where for all trees above 5 cm following attributes were recorded: tree species, diameter at the breast height (dbh), height, height to the live crown, x and y coordinates using the pollard method (later recalculated on whole plot). For purpose of this study we used the data from the last two measurements in 2012 and 2023. To assess the tree species composition and interaction Fuldner's intermingling index (Fuldner 1995) and Clark-Evans aggregation index (Clark and Evans 1954) were calculated. To assess the influence of competition Hegyis index was also calculated using the *pairwise* function from the *sipplab* R package (Garcia 2014). Trees close to the edge were excluded using the *edge* function from the same package. As influence radii 6 meters was chosen since smaller radii tend to spatial autocorrelation (Pedersen et al. 2013) and with larger radii it is difficult to spot direct competitive differences. In our analysis we used the competition values from the end of period since Wilcoxon signed rank test showed no statistical differences. Additionally, we identified for each tree his closest neighbour. All these factors were used in analysis of variance (ANOVA) to assess the tree species interaction. The interaction was represented through dbh increment which was calculated as the difference of dbh between two periods (2023 and 2012).

RESULTS

The total volume in 2023 was approximately 746 m³/ha, with silver fir contributing the majority share at 72%, followed by beech at 20%, sycamore at 6%, and spruce at 2%. The total number of trees was 746, with beech trees constituting more than 70% of the total tree count. Compared to the data from 2012, there is a notable reduction in both the total volume and the number of trees. This reduction is particularly pronounced for silver fir in terms of volume and for beech in terms of tree numbers (table 1).

The forest structure illustrated in Figure 1 exhibits a reverse J-curve pattern, characteristic of an uneven-aged forest stand. Comparative analysis between the years 2012 and 2023 reveals minimal variation in forest composition over this period. Notably, there is a significant mortality rate observed among the smallest diameter class (dbh < 10 cm). As tree diameter increases, mortality rates decrease progressively across the dbh classes.

Table 1. Comparison between the last two measurements

Tree species	2012				2023			
	dbh	G (m ² /ha)	V (m ³ /ha)	n	dbh	G (m ² /ha)	V (m ³ /ha)	n
Silver fir	51.21	42.6	594.1	163	50.98	39.58	548.05	154
Beech	11.83	12.91	157.14	612	12.41	12.6	156.12	543
Spruce	22.83	1.26	13.52	21	23.2	1.25	13.5	20
Sycamore	23.23	3.02	45.87	36	27.33	3	45.79	29
Total	27.28	59.79	810.63	832	28.53	56.43	763.46	746

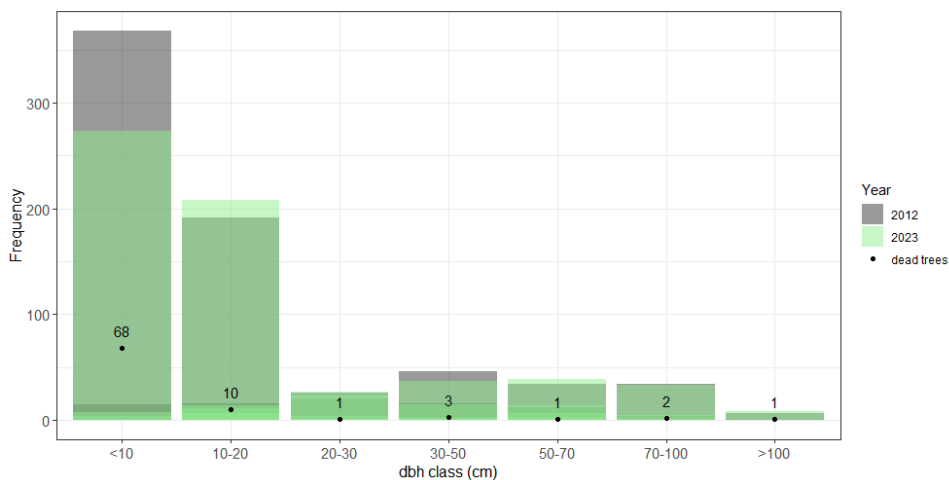
**Figure 1.** A comparison of dbh structure between two measurements in 2012 and 2023

Figure 2 illustrates a significant contrast between beech and silver fir, the two most prominent species. The dbh distribution of beech exhibits a characteristic reverse J-shaped curve, typical of uneven-aged or mixed-species forest stands. In contrast, silver fir demonstrates a more normal distribution, akin to even-aged stands. Notably, there were no significant differences observed in the dbh distribution of beech between the two measurements except a decrease in numbers in the lowest dbh class. However, for silver fir, a discernible shift to the right, indicative of negative skewness, suggests a decline in older silver fir trees over time. Moreover, sycamore and spruce exhibit distinct patterns across dbh classes. Sycamore distribution appears bimodal, indicating the presence of two distinct age cohorts. In contrast, spruce demonstrates a positive skewness. But the total number of spruce and sycamore trees is not enough to have concrete conclusions.

Relative risk, a common term used in medical studies such as epidemiology represents the ratio of the outcome among the exposed group to the risk of the outcome among the unexposed group. In the context of spatial data analysis, relative risk can be interpreted as the probability of occurrence of one type, while considering the occurrence of other types. Specifically, it measures the likelihood of one tree

species occurring relative to the occurrence of another species within the same spatial context. Higher values of relative risk indicate 'hot spots' where the occurrence of a particular tree species is more probable, suggesting favorable conditions for its growth and development. Conversely, lower values indicate less favorable conditions.

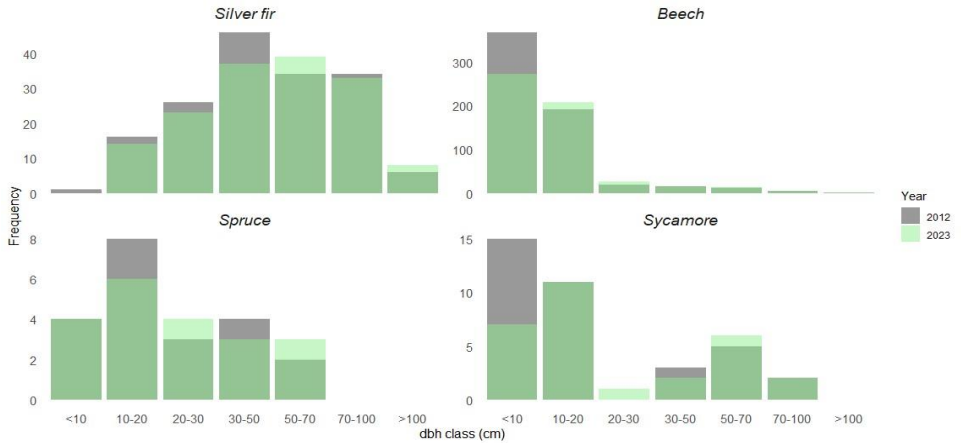


Figure 2. dbh distribution per tree species

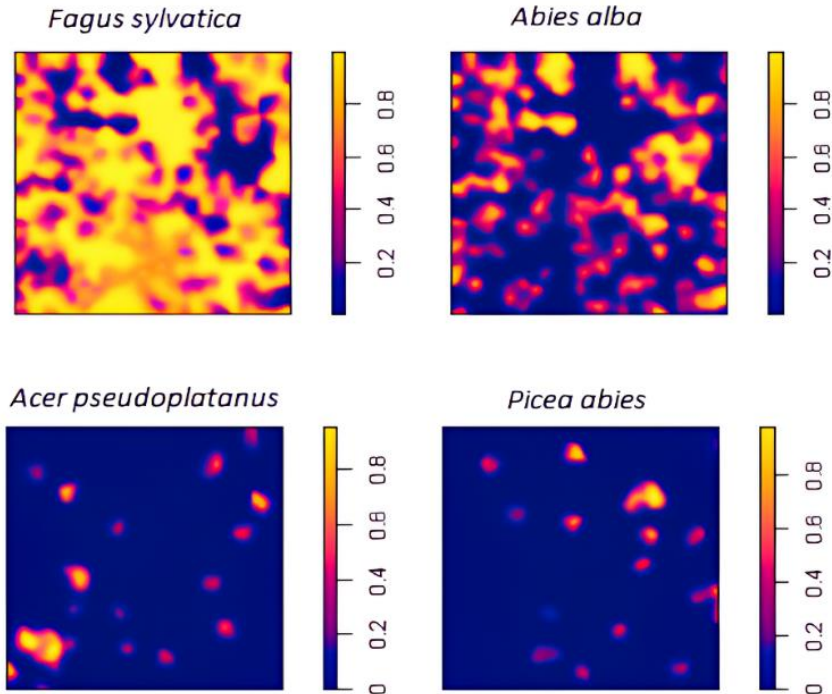


Figure 3. Relative risk analysis as heat map

The analysis reveals that beech trees are the most favored species, occupying a substantial portion of the plot. Favorable conditions for silver fir are primarily observed in clustered groups, while spruce and sycamore tend to thrive in smaller groups or as individual specimens. Interestingly, there are distinct 'hot spots' for spruce and sycamore, particularly in areas of the plot that are less suitable for beech. The analysis of Fuldner's index revealed notable variations in species aggregation among the studied tree species. Spruce exhibited the highest index value at 0.94, followed by silver fir at 0.70 and sycamore at 0.66. Conversely, beech demonstrated the lowest index value at just 0.24. Similar trends were observed for the Clark-Evans aggregation index, although silver fir showed slightly higher values. When examining the index values per dbh class, a clear pattern was not evident, with Pearson correlation coefficients (PCC) consistently below 0.3, except for sycamore in both cases. Notably, for spruce, there was a slight negative trend observed with increasing dbh. However, upon closer examination of the data, it becomes apparent that while values were lower at smaller dbh classes, the increase did not follow a linear trend with increasing dbh.

Table 2. Tree species intermingling and aggregation per tree species, where M – Fuldner's index, R – aggregation index according to Clark – Evans, n – number of trees, PCC- Pearson correlation coefficient

Measure	Tree species							
	Beech		Fir		Norway spruce		Sycamore	
	mean	PCC	mean	PCC	mean	PCC	mean	PCC
M	0,24	0,155	0,7	0.144	0,94	-0,079	0,66	0,641
R	0,91	0,279	1,3	0.062	1,24	0,274	0,96	0,457

Additionally for each tree species his closest neighbour was identified as shown on the Sankey diagram (fig 4). The Sankey diagram provides a visual representation of the spatial distribution and proximity relationships between different tree species within the study area. Our analysis revealed a predominant clustering of beech trees, with the majority having other beech trees as their nearest neighbors, followed by silver fir. Silver fir and sycamore trees exhibited mixed proximity patterns, with flows indicating both intra-species and inter-species clustering, highlighting a more heterogeneous distribution within the stand.

Multifactorial ANOVA was employed to investigate the influence of various factors and their interactions on dbh increment. Overall, the analysis identified dbh as the primary determinant of tree growth, exhibiting substantial effects, along with the aggregation index and its interaction with dbh, both of which were statistically significant ($p < 0.01$). Further, significant interactions were observed between dbh and the competition index ($p = 0.006$), suggesting a notable modulation of growth by competitive dynamics. Moreover, complex interactions involving multiple factors, such as dbh, neighbour tree species, and neighbour dbh, were significant ($p = 0.048$), as was the interaction that additionally included the aggregation index ($p = 0.048$). For silver fir only dbh and aggregation index were found to have a

significant impact on tree growth ($p < 0.01$). For beech multiple individual factors affected the growth significantly: dbh, aggregation, mixing ($p < 0.01$) and competition index ($p = 0.02$) and also the interaction between dbh:competition, aggregation: competition, mixing:competition and dbh:aggregation:mixing had a significant impact ($p < 0.05$). For spruce dbh and mixing index were significant where for sycamore only dbh was significant ($p=0.02$).

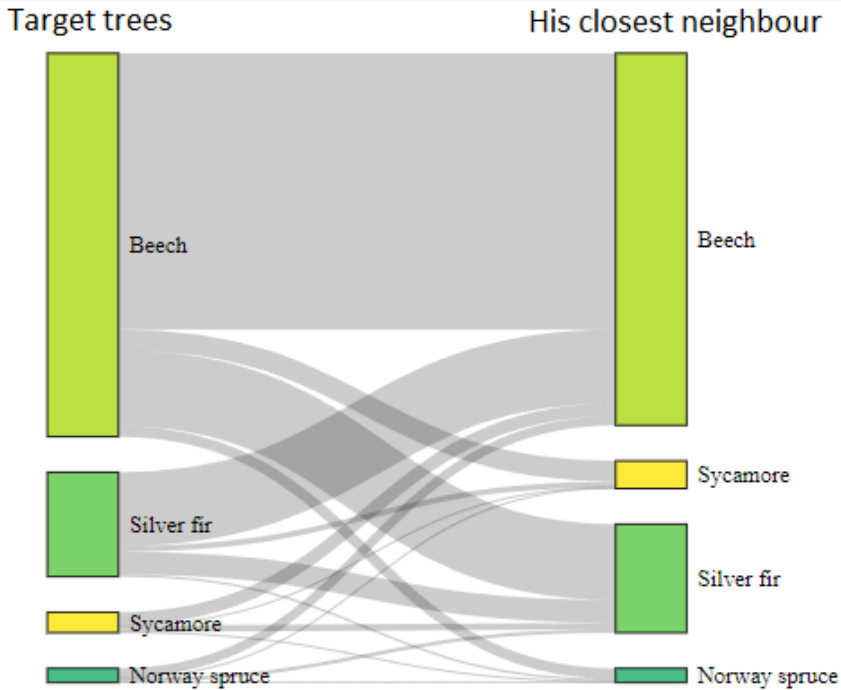


Figure 4. Sankey diagram representing the relationship between each tree and their neighbour

DISCUSSION

The total volume was estimated at approximately 746 m³/ha, which is comparable to the estimates for Lom (Motta et al., 2024) and Čorkova Uvala (Saniga et al., 2011) old-growth forests. However, it is lower than in Janj, Perućica, and Biogradska Gora (Motta et al., 2024), where the total volume exceeds 1000 m³/ha. The only old-growth forest with a lower total volume than this study was Plješevica (Višnjić et al., 2009). Tree species composition according to growing stock comprised one of the highest shares of silver fir (73%) compared to other old growth forest in this region (Anić and Mikac, 2008; Keren et al., 2017; Motta et al., 2015, 2014, 2011; Višnjić et al., 2017, Curovic et al., 2020). Low percentage of beech was also found in the old growth forest Janj (cca 20%) and Biogradska gora (cca 25%). The share of spruce was the lowest compared to other old growth forest, where the share of sycamore was similar. In terms of tree density, it had the highest number of

trees per hectare compared to other old growth forest (Kral et al. 2010, Kucbel et al. 2010, Saniga et al. 2011, Parabekova et al. 2018, Motta et al., 2024). Beech was found to be the dominant tree species with 73% similar to Janj (63%) and Lom (60%). The contrast in fir and beech share in terms of volume and number is related to the structure of each tree species as shown in figure 2. Beech is dominant in lower dbh classes where the tree distribution of fir can be described as a negative skewed also dominantly present in higher dbh classes. Similar distribution between beech and fir have been found also in other old-growth forests of this region: Janj and Lom (Govedar et al., 2021), Plješevica (Višnjić et al., 2009), Perućica (Palandrani et al., 2021) and Biogradska gora (Čurović et al. 2011).

Compared to the last measurement in 2012, a slightly reduction in volume and tree number was evident. The reduction in volume was due to mortality of fir trees. High mean dbh and the negative skewed distribution indicate a late optimal or early decay phase for fir where a reduction in numbers for beech is due to competition and light availability. A long-term decay of coniferous and progression of beech in understory was recorded in other old growth forest of this region. For instance, the study by Keren et al. (2014) showed a decrease in spruce and fir tree density across all three analyzed reserves (Janj, Lom, and Perućica), while the proportion of beech increased. In contrast, the share of fir in basal area increased in Janj, remained stable in Lom, and decreased in Perućica. The proportion of beech in basal area also increased. To explain these changes in species composition within spruce, fir and beech stands is difficult (Šafar, 1951.; Nagel et al., 2010) since it depends on many factors. These factors can be related to human activities or natural disturbances. For deeper understanding long-term data is required. An increase of beech on plot is also to be expected in future as revealed by relative risk analysis. Most parts of the plot were identified as the most suitable growing conditions for beech. Similar prediction have arisen in some early studies of beech – fir old growth forests (Šafar 1951, Pintarić 1982) and the issue about the regeneration of fir came up. The study of Ivojević et al., (2018) revealed a dyeback of fir samplings with the increase of its size. The highest number was present at the smallest height class and lowest in the highest class, which was contrary to the managed stand. This implies deeper studies into the regeneration of fir to identify the obstacles of fir which promotes beech regeneration. Fir had the highest value of Clark-Evans aggregation index (1.3) indicating a tendency to a regular distribution on the plot, followed by spruce, sycamore and beech (see table 2). The lowest values were in the lower dbh classes, where trees are more clumped and with increase of dbh trees are more regularly distributed. Although, the correlation coefficients are not high, similar observations were found in other old growth forests (Bilek et al., 2011; Parobeková et al., 2018; Wang et al., 2020). This is also in accordance with the classical Janzen-Connell spacing effect predictions which states that the spatial distributions of adult trees would become more regular than those of juveniles because of the differential attack rates between adults and juveniles by pathogens or herbivores (Janzen 1970, Connell 1971). The aggregation index was statistically correlated with mingling index showing a moderate positive correlation (0.37). In lower dbh classes trees were more

clumped surrounded with same tree species resulting in lower values of Fuldners mingling indices. With a more random distribution the probability of different neighbour species is higher. Similar results were also found by (Li and Wei, 2024).

The key driver for dbh increment was dbh, aggregation index and its intereraction, all with high statistical significance. Additionally, dbh and competittion interaction and the interaction of dbh with multiple factors showed to be statistically significant. Thus, the main driver is the dbh of target tree. Thats why many dbh increment model are using dbh as the main predictor (Bayat et al., 2013; Ciceu et al., 2022; Manso et al., 2022; Schelhaas et al., 2018) where some additional predictors can be used. Aggregation value which on tree level is the distance to the closest neighbour showed to have a high impact on tree growth for booth beech and fir. The results of this study are contrary to the results of Antúnez et al., (2023) where distance of neighbors had a significant effect only when the dimension of those neighbors were larger than those of the refenece tree. The neighbour tree species and their dbh showed no significant impact on dbh increment. These findings doesnot align with the theory of Forrester and Bauhus, (2016) and similar studies (Chen et al., 2016; Di Maurizio et al., 2023; Fichtner et al., 2017; Searle and Chen, 2020). But even in these studies the effect varried depending on tree species and also on competition measure. In the study of Di Maurizio et al., (2023) growth response of most species to neighborhood dissimilarity was negatively influenced by increased competition, but on the other side the study of Searle and Chen, (2020) showed better growth with surrounded by dissimilar neighbors than those surrounded by similar neighbors under high competition intesity. This indicates additional considerations are required to describe the connection between tree growth, dissimilarity and competition. The contrast in findings between this study and previous mentioned can be due to different study plots. While previous studies were conducted in visual homogenous plots, our study was conducted in a heterogenous stand where different tree species occure in different sizes and distribution. In homogenous plots the effect of reference tree size may be equal, in a heterogenous stands the effect of reference tree size may be dominant, masking the effect of other factors. For instance the effect of hegyi competition index was significant for beech while for silver fir showed no significance. Overall, the competition index was only significant in interaction with the dbh of the reference tree, which indicates that the competition index was only relevant for smaller beech trees. Different indices affect the tree growth differently depending on the tree size. Therefore, its important to take into account the tree size distribution when analysing species mixing and interaction on tree growth. Similar suggestions can be found in the study of Madrigal-González et al., (2016).

CONCLUSIONS

The total volume was similar to Lom and Čorkova uvala but much lower than Janj, Peručica or Biogradska gora. Contrary, tree species compositions in this study are consistent with patterns observed in other old-growth forests in the region, with fir dominating the basal area and beech increasing in density. Fir's late-optimal or early-decay phase, alongside beech's competitive advantage, suggests a gradual shift

in species composition. The results suggest that beech will continue to dominate in the future, especially in conditions that favor its growth, as indicated by relative risk analysis. Fir regeneration remains a concern, as seen in lack of fir trees in lower dbh classes. The competition dynamics and tree size distribution were found to significantly influence tree growth, with dbh emerging as a key predictor. The lack of significant impact from neighboring species suggests that intra-species competition may be more critical in this context. Addressing the factors limiting fir regeneration is also crucial for maintaining species diversity and health and can give valuable insights for forest managers. On the other hand, management approaches that mimic disturbances, such as creating larger gaps, can promote beech regeneration. However, further investigations are needed to understand the relationship between these disturbances and beech recruitment fully.

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