

# Influence of Geological Substrate on the Structure and Diversity of Dinaric Mixed Beech–Fir–Spruce Forests: A Case Study from Mt. Konjuh

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## ABSTRACT

This study explored the relationships between geological substrate and the structural and compositional attributes of mixed beech (*Fagus sylvatica* L.), fir (*Abies alba* Mill.), and spruce (*Picea abies* [L.] Karst.) forests on Mt. Konjuh in northeastern Bosnia and Herzegovina. Research was conducted on 81 experimental plots established across three dominant substrates: limestone, peridotite, and chert. Stand structure, diversity, and spatial organization were assessed using the Shannon diversity index, Pretzsch's species profile index, Gini coefficient, and the Clark–Evans and Fuldner indices. The analyses revealed consistent differences among substrates, suggesting that geological conditions influence forest structure and diversity. Higher diversity and vertical heterogeneity were generally associated with limestone, while stands on peridotite and chert exhibited simpler but more balanced structures. All forest types displayed a reverse J-shaped diameter distribution, indicating uneven-aged composition and ongoing natural regeneration. Spatial patterns showed a tendency toward clustering of beech and spruce and higher species mingling on limestone. Overall, mixed beech–fir–spruce forests on Mt. Konjuh appear to be stable ecosystems whose structure and diversity are shaped by an interplay of geological, edaphic, and ecological factors. The results highlight the relevance of site-specific and adaptive silvicultural approaches that account for local variability in substrate and stand conditions.

**Keywords:** mixed forests; geological substrate; structural diversity; spatial structure; Mt. Konjuh

## INTRODUCTION

Mixed forests of beech (*Fagus sylvatica* L.), silver fir (*Abies alba* Mill.), and Norway spruce (*Picea abies* [L.] Karst.) represent one of the most important forest types within the temperate zone of Europe. They cover more than 10 million hectares across an altitudinal range of 600–1,400 m a.s.l., predominantly in mountainous regions characterized by a moderately humid climate (Brus et al. 2012, EUFORGEN 2017). In Bosnia and Herzegovina, these forests occupy approximately 562,500 ha, accounting for about 22% of the country's total forest area (Matić et al. 1971). Thus, they represent its most significant forest resource—both economically and ecologically. Their

distribution follows the Dinaric Mountain range from northwest to southeast (Stefanović et al. 1983), occurring on a broad spectrum of geological substrates and soil types. Based on taxonomic and ecological characteristics, eight principal types of mixed beech–fir–spruce forests have been identified (Čirić et al. 1971). Owing to the wide range of edaphic and climatic conditions, these forests exhibit pronounced differentiation in both floristic composition and structural organization, with edaphic factors—particularly soil chemistry and water regime—playing a decisive role in their development (Beus 2011).

A defining feature of these forests is their capacity for natural regeneration (Višnjić and Prljača 2016), which results in predominantly uneven-aged structures where

trees of various sizes and ages coexist within small areas. The maintenance of such stands relies on the selection system, a silvicultural approach designed to sustain continuous growth and preserve natural stand structure (Bončina et al. 2014). Originating in Central Europe during the 19th century as an alternative to clear-cutting (Schütz 2001), the selection cutting system gradually became the dominant management approach for uneven-aged forests in both Alpine and Dinaric regions (Diaci 2006). In Bosnia and Herzegovina, it has been practiced for more than a century (Čilaš et al. 2023), and for a long time served as the only management system for mixed forests, irrespective of their species composition. However, due to local variability in site conditions and management intensity, outcomes have differed widely—from stable, productive stands to cases of degradation (Pintarić and Izetbegović 1980).

Forest structure is a central concept in understanding forest ecosystem dynamics, encompassing the spatial arrangement of trees, species mixture, and dimensional distribution (Gadow and Hui 2002). It reflects the combined effects of natural processes and silvicultural interventions and, in turn, governs many ecological, productive, and social functions of forests (Pretzsch 2019). Continuous processes of regeneration, growth, and mortality constantly reshape stand structure, making it a dynamic indicator of ecosystem state and development (Gadow et al. 2012).

Studies of mixed beech–fir–spruce forests across Europe have shown that, despite regional differences, they often display similar structural patterns: a reverse J-shaped diameter distribution, high tree density, and large growing stock, frequently exceeding 350 m<sup>3</sup>·ha<sup>-1</sup> (Pretzsch et al. 2015, Hilmers et al. 2018, Torresan et al. 2020). Nonetheless, variation in species composition and horizontal distribution substantially influences both diversity levels and structural complexity among stands.

Diversity, a fundamental component of biodiversity, encompasses not only the number of species but also their relative abundance and interactions (Konnert 1992, Hattemer 1994, Višnjić et al. 2013, 2017, Bartsch et al. 2020). It is shaped by a multitude of factors, including energy availability, habitat complexity, disturbance regime, stress conditions, ecosystem stability, and habitat area (Hansen and Rotella 1999). Among these, geological substrate plays a particularly influential role because it determines the chemical and physical properties of the soil (Kruckeberg 2004), such as texture, nutrient content, and water-holding capacity (Troeh and Thompson 2005, Vojniković 2021). This heterogeneity enhances the number of ecological niches and supports the coexistence of a wider range of plant species (Levine and HilleRisLambers 2009).

Floristic and vegetation studies of beech and fir forests on different substrates in Serbia and Montenegro (e.g., granodiorites, serpentinites, and eruptives) by Novaković-Vuković et al. (2016, 2022) revealed clear differences in floristic composition and diversity indices among the examined stands, emphasizing the importance of edaphic variation in shaping forest diversity.

Given the complex interactions among structural characteristics, site factors, and regeneration processes, mixed beech–fir–spruce forests are intricate ecological systems of exceptional significance. Their understanding requires an integrated approach that links structural indicators with ecological and edaphic variables. Therefore, the objective of this study is to analyze the structural characteristics of mixed beech–fir–spruce forests on different geological substrates and to assess how structural variation influences the diversity of trees and ground vegetation.

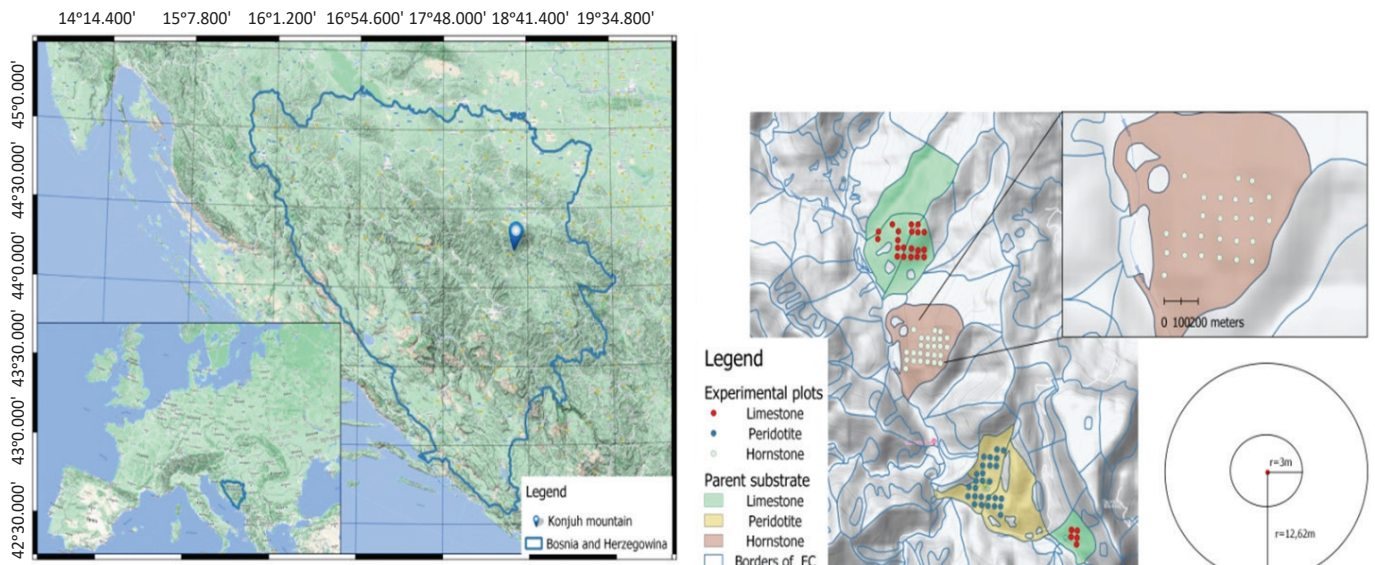
## MATERIALS AND METHODS

### Study Area

The study area is located in northeastern Bosnia and Herzegovina, on Mount Konjuh (44°18'32" N, 18°30'57" E), within the Forest Management Unit "Gornja Drinjača" of the Forest Management Area "Konjuh" (Figure 1). It lies within the Central Bosnian ophiolite zone and features hilly to mountainous terrain. The geology is diverse, dominated by serpentinitized peridotites, eruptive rocks, and cherts, with a smaller proportion of limestone. Soils are mainly eutric and dystric cambisols, locally accompanied by pseudogleys and pockets of calcomelanosols and calcocambisols. This heterogeneous substrate and complex relief create a pronounced vegetation mosaic (Stefanović 1983): pine and sessile oak forests prevail on warmer slopes, while cooler, more humid sites support beech–fir and beech–fir–spruce forests. In our study, all study plots are located in uneven-aged mixed stands of beech, fir, and spruce, representative of the prevailing stand structure in the study area. The moderately mountainous climate, with a mean annual precipitation of 1,219 mm and an average temperature of 7.4°C (Višnjić 2006), provides favorable conditions for the development of these mixed forests.

### Field Measurements

Data collection was conducted on 81 circular sample plots (radius 12.62 m; area 500 m<sup>2</sup>), evenly distributed across three geological substrates—peridotite, limestone, and chert (27 plots each)—and spaced 100 m apart in a regular square grid arrangement to ensure uniform coverage. A complete inventory was carried out on each plot, recording tree species, diameter at breast height (DBH > 5 cm), and total height. For spatial structure analysis, an additional square plot of 100 × 100 m (1 ha) was established per substrate, within which all trees with a DBH > 5 cm were mapped using the orthogonal method. For each tree, diameter at breast height, total height, and height to the live crown (HLC) were measured. Tree spatial arrangement was quantified using the Clark–Evans aggregation index (Clark and Evans 1954), calculated from nearest-neighbor distances. Since the Clark–Evans index is a distance-based method, no angle threshold or angle-based sampling design was applied. Simultaneously, vascular plant diversity was surveyed on 400 m<sup>2</sup> plots (27 per substrate) using the Braun–Blanquet cover–abundance scale.



**Figure 1.** Location of the study area on Mount Konjuh in northeastern Bosnia and Herzegovina, showing the distribution of sample plots across the three geological substrates: peridotite, limestone, and chert.

### Data Analysis

Phytosociological data were processed in Turboveg 2.38 (Hennekens and Schaminee 2001), while structural and ecological indices were calculated in R (R Core Team 2024) using the packages *vegan* (Oksanen et al. 2022), *spatstat* (Baddeley et al. 2015), *ineq* (Zeileis 2014), and *dplyr* (Wickham et al. 2023). Species diversity was quantified using the Shannon index (Shannon 1948), computed with *diversity()* from *vegan* based on both stem number and basal area, with evenness expressed as the ratio between observed and maximum diversity. Floristic similarity among plots was assessed using the Sørensen index implemented in *vegdist()*. Horizontal structural diversity of tree diameters was expressed by the Gini coefficient (*Gini()*, *ineq*), while species mingling was evaluated using Fuldner's mingling index (1996), based on the four nearest neighboring trees. Spatial tree patterns were analyzed in *spatstat*, and vertical structure was quantified using the species profile index (Pretzsch 2019), combining Shannon's formulation with species distribution across height layers ( $\leq 50\%$ ,  $50\text{--}80\%$ ,  $> 80\%$  of maximum stand height). The Clark–Evans aggregation index (Clark and Evans 1954) was applied to characterize tree spatial arrangement, comparing observed to expected nearest-neighbor distances ( $R < 1$  = aggregated,  $R \approx 1$  = random,  $R > 1$  = regular; *clarkevans.test()*, *spatstat*). Regeneration counts from 3 m radius subplots were converted to individuals per hectare, and understory vegetation diversity was analyzed using the same set of indices as for trees.

## RESULTS AND DISCUSSION

### Structural Characteristics

The structural characteristics of the studied mixed beech–fir–spruce stands varied markedly across geological substrates. To quantify these differences, key stand indicators—tree number ( $N$ ), quadratic mean diameter ( $D_g$ ),

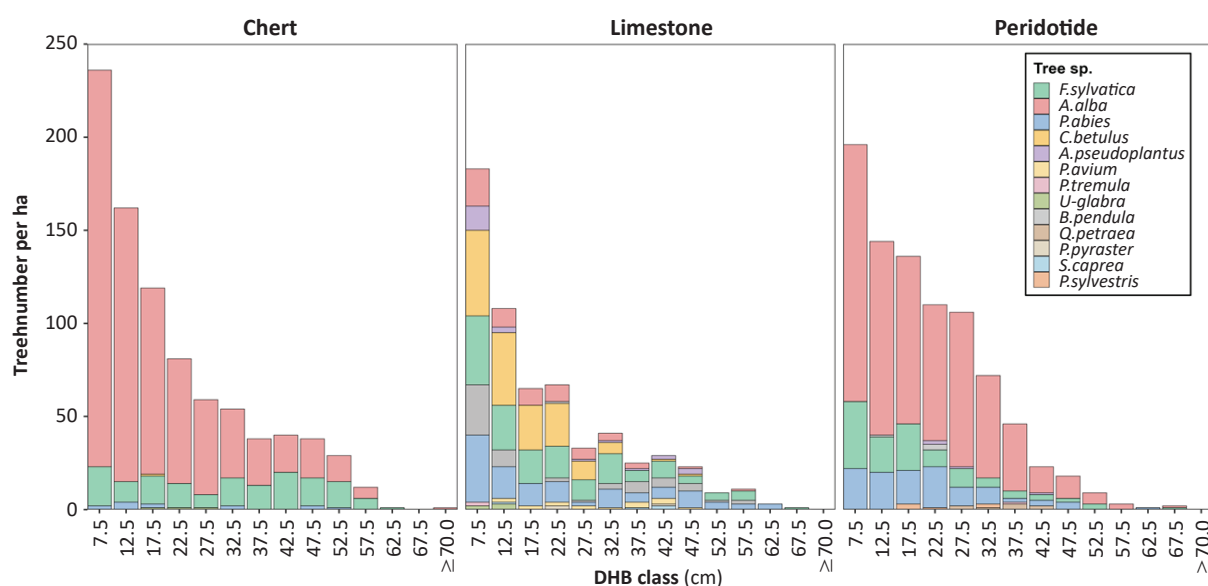
mean height ( $H$ ), basal area ( $G$ ), and growing stock volume ( $V$ )—were analyzed by species and substrate (Table 1).

Analysis of these indicators revealed pronounced variations in stand characteristics depending on the underlying geology. The total number of trees was highest on peridotite ( $601 \text{ trees}\cdot\text{ha}^{-1}$ ) and lowest on limestone ( $428 \text{ trees}\cdot\text{ha}^{-1}$ ). The largest average dimensions occurred on chert ( $D_g = 37.9 \text{ cm}$ ;  $H = 25.9 \text{ m}$ ), while the smallest were recorded on peridotite. Total basal area and volume were also highest on chert ( $G = 35.8 \text{ m}^2\cdot\text{ha}^{-1}$ ;  $V = 485 \text{ m}^3\cdot\text{ha}^{-1}$ ). Across all substrates, silver fir dominated both in stem number and growing stock, whereas spruce and beech were less frequent but attained larger dimensions. The variation among substrates may reflect differences in site conditions mediated by geological and edaphic factors, as well as by past management. Bedrock influences soil development and the physical and chemical environment of roots, thereby shaping water and nutrient availability, although these effects are often indirect and context-dependent (Vestin et al. 2013, Richter and Billings 2015). Previous studies have shown higher forest growth on more weatherable, or nutrient-rich substrates such as limestone or shale compared to granitic or sandstone bedrock (Jiang et al. 2020, Basnet et al. 2024). In addition to these geochemical effects, differences in historical use and management intensity may have modified stand composition and structure, potentially amplifying or masking substrate-related trends. The observed structural variation therefore likely results from the combined influence of geological substrate, soil formation, climatic factors, and long-term management history.

Across all geological substrates, the diameter structure follows a negatively exponential curve, indicating an uneven-aged stand structure (Schütz 2001). On chert and peridotite, fir predominates, while beech occurs across all diameter classes, particularly the intermediate ones. Spruce is more abundant on limestone and peridotite, where it reaches larger diameter classes. On limestone,

**Table 1.** Stand-level indicators describing the structure of mixed beech–fir–spruce forests across three geological substrates (limestone, peridotite, and chert) on Mt. Konjuh where N is tree number per ha, Dg quadratic mean diameter (cm), H is the mean height (m), G is basal area ( $\text{m}^2 \cdot \text{ha}^{-1}$ ), and V is the growing stock ( $\text{m}^3 \cdot \text{ha}^{-1}$ ).

Supstrate	N (trees·ha <sup>-1</sup> )	Dg (cm)	H (m)	G (m <sup>2</sup> ·ha <sup>-1</sup> )	V (m <sup>3</sup> ·ha <sup>-1</sup> )
Limestone					
Beech	96 ± 139	33.9 ± 14.1	22.7 ± 9.0	7.8 ± 12.4	113.0 ± 197.0
Silver fir	183 ± 188	34.3 ± 14.2	21.1 ± 8.4	10.1 ± 10.3	119.0 ± 139.0
Spruce	85 ± 105	41.9 ± 16.0	27.2 ± 8.0	9.8 ± 10.8	135.0 ± 166.0
Other sp.	64 ± 15	26.9 ± 15.8	20.3 ± 7.4	3.5 ± 1.1	42.5 ± 15.7
Total	428 ± 200	34.3 ± 15.7	22.9 ± 8.5	31.2 ± 11.2	410.0 ± 188.0
Peridotite					
Beech	38 ± 42	21.9 ± 14.9	18.6 ± 9.0	1.7 ± 3.3	24.7 ± 55.7
Silver fir	425 ± 216	3.1 ± 9.6	25.6 ± 5.4	24.1 ± 12.8	291.0 ± 198.0
Spruce	104 ± 112	30.1 ± 15.5	22.4 ± 10.1	6.0 ± 6.7	76.3 ± 90.9
Other sp.	34 ± 13	34.0 ± 15.0	20.3 ± 8.0	3.4 ± 1.4	37.6 ± 17.1
Total	601 ± 219	31.4 ± 14.5	22.2 ± 8.5	35.3 ± 8.9	430.0 ± 173.0
Chert					
Beech	113 ± 103	41.0 ± 11.7	27.3 ± 6.1	9.6 ± 7.3	139.0 ± 114.0
Silver fir	344 ± 182	37.8 ± 5.5	26.1 ± 3.3	21.9 ± 12.1	290.0 ± 176.0
Spruce	34 ± 53	41.4 ± 15.1	27.7 ± 8.1	3.9 ± 7.4	53.0 ± 101.0
Other sp.	17 ± 8	21.7 ± 10.2	18.0 ± 6.5	0.4 ± 0.2	3.0 ± 1.4
Total	508 ± 196	37.9 ± 11.7	25.9 ± 6.2	35.8 ± 8.9	485.0 ± 138.0

**Figure 2.** Diameter distribution of trees by species and geological substrate.

a higher proportion of other broadleaved species, such as sycamore maple and hornbeam, indicates a more heterogeneous species composition.

### Species Diversity

The analysis of variance (one-way ANOVA) revealed statistically significant differences in tree-layer diversity among the geological substrates (Table 2). Species richness was highest on limestone ( $3.80 \pm 1.37$ ) and significantly higher than on chert ( $2.50 \pm 1.22$ ;  $p < 0.001$ ). The Shannon index based on tree number likewise reached its highest

mean value on limestone ( $0.94 \pm 0.41$ ), followed by peridotite ( $0.69 \pm 0.27$ ) and chert ( $0.61 \pm 0.38$ ). In contrast, diversity indices calculated from basal area and the evenness index showed no significant differences among substrates ( $p > 0.05$ ), suggesting a comparable proportional distribution of species within the stands.

In the vascular flora layer, differences among geological substrates were not statistically significant ( $p > 0.1$ ). Nonetheless, species richness was highest on limestone ( $37.14 \pm 13.9$ ), followed by peridotite ( $35.66 \pm 9.94$ ), and lowest on chert ( $30.96 \pm 8.69$ ). Comparable results were

**Table 2.** Analysis of variance for diversity indicators by different substrates with LSD test, where I refers to the mean value of the observed indicator and SD is the standard deviation.

Indicator	Substrate	I	SD	ANOVA	LSD test
Tree layer					
Number of tree species	Limestone	3.80	1.37	p < 0.05	*
	Peridotite	3.30	0.83		*
	Chert	2.50	1.22		*
Shannon's index (based on tree number)	Limestone	0.94	0.41	p < 0.05	*
	Peridotite	0.69	0.27		*
	Chert	0.61	0.38		*
Shannon's index (based on basal area)	Limestone	0.74	0.37	p = 0.47	*
	Peridotite	0.64	1.34		*
	Chert	0.63	0.34		*
Evenness (based on tree number)	Limestone	69.12	23.29	p = 0.21	*
	Chert	64.02	29.66		*
	Peridotite	57.88	14.66		*
Evenness (based on basal area)	Chert	66.68	31.85	p = 0.23	*
	Limestone	55.40	25.51		*
	Peridotite	55.10	26.51		*
Vascular plants					
Number of species	Limestone	37.14	13.94	p = 0.11	*
	Peridotite	35.66	9.94		*
	Chert	30.96	8.69		*
Shannon's index	Limestone	2.84	0.61	p = 0.18	*
	Peridotite	2.80	0.47		*
	Chert	2.58	0.54		*
Evenness	Limestone	75.90	8.85	p = 0.20	*
	Chert	74.40	9.77		*
	Peridotite	712.00	10.96		*

reported by Beus and Vojniković (2010), who found greater species richness on limestone than on basic and ultrabasic substrates. Beus (1979) likewise noted that beech–fir–spruce forests on limestone are richer in species in both the tree and ground layers, particularly with respect to the presence of noble broadleaves. In contrast, forests on peridotitic–serpentinic soils exhibit a more specific floristic composition, characterized by a lower frequency of typical mesophilous species. Therefore, based on the analysis of site factors, floristic composition, and stand structure, Beus (1979) proposed that these communities represent a distinct syntaxonomic unit: *Abieti-Fagetum serpentinum*. The Shannon and evenness indices followed a similar pattern, with slightly higher values on limestone, indicating greater floristic diversity and a more balanced community structure on calcium-rich substrates.

### Structural Diversity and Spatial Pattern of Trees Distribution

The analysis of structural diversity revealed that stand complexity varied with the underlying geological substrate.

Pretzsch's species profile index (A) reached its highest values on limestone (1.80), indicating greater vertical and horizontal heterogeneity and a more complex stratification pattern than on peridotite (1.50) or chert (1.45). The wider interquartile range on limestone further reflects higher structural variability among plots (Table 3). The elevated values of the species profile index (A) align with observations from studies of primary and near-natural mixed forests, where greater structural heterogeneity is commonly linked to enhanced ecological stability and resilience to disturbance (Pretzsch 2009). Such complexity is often associated with sites exhibiting pronounced topographic or edaphic variability, conditions typical of carbonate (limestone) substrates.

In contrast, the profile evenness index ( $A_{rel}$ ) was highest on chert (0.75), suggesting a more balanced distribution of individuals across height layers. The analysis of the Gini coefficient showed that diameter inequality ranged between 0.29 and 0.33, with peridotite exhibiting slightly greater variability in tree dimensions, and limestone

the lowest. No statistically significant differences were observed among substrates ( $p > 0.05$ ). Nevertheless, the observed range (0.29–0.33) is typical for mixed stands (Motta et al. 2015, Keren et al. 2020, Szmyt et al. 2020, Trifković and Ficko 2025). The somewhat higher inequality on peridotite (0.33) may reflect greater variation in tree dimensions, often associated with slow growth and long tree lifespans under nutrient-poor and ecologically demanding site conditions.

The spatial analysis based on the Clark–Evans aggregation index ( $R$ ) and Földner’s mingling index ( $M$ ) revealed clear differences in tree distribution among geological substrates. Beech and spruce exhibited aggregated spatial patterns on all substrates ( $R < 1$ ;  $p < 0.05$ ), whereas silver fir showed aggregation only on limestone ( $R = 0.75$ ) and a random or slightly uniform arrangement on peridotite and chert ( $R \approx 1$ ). High mingling values for beech ( $M = 0.8$ ) indicate pronounced interspecific mixing, typical of Dinaric mixed mountain forests where species coexist closely within small spatial scales, which is an important feature contributing to structural complexity and ecological

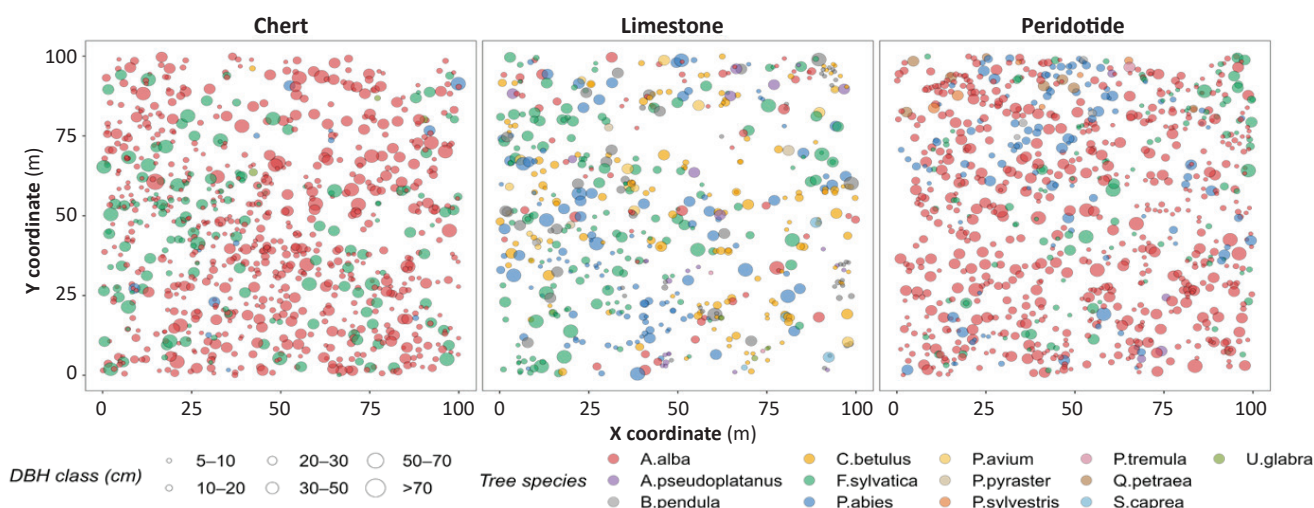
stability (Čilaš and Višnjić 2024). At the stand level, forests on limestone displayed a clustered but moderately mixed structure ( $R = 0.83$ ;  $M = 0.65$ ), while those on peridotite and chert showed patterns approaching randomness ( $R \approx 1$ ;  $M = 0.40$ ). Comparable spatial configurations have been described across various European mixed forests, where both managed and near-natural stands frequently exhibit random tree distributions at the hectare scale (Parobeková et al. 2018, Dukić et al. 2021, Keren et al. 2024). Management system plays a key role in these patterns: fine-scale selection cutting tends to produce random or uniform spatial arrangements, whereas group-selection interventions enhance local clustering (Lafond et al. 2014). The low mingling values for fir and spruce on peridotite and chert ( $M < 0.4$ ) likely reflect reduced neighborhood diversity and greater spatial segregation, consistent with strong intraspecific competition or adaptation to microsite-specific conditions. To visualize these spatial patterns more clearly, Figure 3 illustrates the horizontal distribution of trees by species and diameter classes on the 1 ha plots established on limestone, peridotite, and chert.

**Table 3.** Values of Pretzsch’s species profile index ( $A$ ), profile evenness index ( $A_{rel}$ ), and the Gini coefficient of tree diameter across different geological substrates.

Substrate	Species profile index ( $A$ )	Profile evenness ( $A_{rel}$ )	Gini coefficient
Limestone	1.80	0.67	0.29
Peridotite	1.50	0.63	0.33
Chert	1.45	0.75	0.30

**Table 4.** Clark–Evans aggregation index ( $R$ ) and Földner’s mingling index ( $M$ ) for spatial structure analysis of trees on the 1 ha plot.

Tree species	Limestone		Peridotite		Chert	
	$R$	$M$	$R$	$M$	$R$	$M$
Beech	0.82	0.59	0.79	0.81	0.89	0.83
Silver fir	0.75	0.79	1.00	0.25	1.00	0.20
Spruce	0.82	0.61	0.73	0.68	1.00	0.96
Stand level	0.83	0.65	0.97	0.40	0.99	0.32



**Figure 3.** Spatial distribution of trees by species and diameter class on limestone, peridotite, and chert substrates.

## CONCLUSIONS

The study demonstrated that geological substrate plays a key role in shaping the diversity and structure of mixed beech–fir–spruce forests on Mt. Konjuh. Stands on limestone showed the highest species richness, vertical heterogeneity, and spatial mingling, indicating greater structural complexity and ecological stability. In contrast, forests on peridotite and chert were simpler in structure, with lower diversity and weaker interspecific mixing, although chert supported a more balanced vertical profile. Diameter distributions followed a reverse J-shaped pattern across all substrates, confirming stable uneven-aged stand structures. Higher values of Pretzsch's species profile and mingling indices on limestone reflected greater spatial and vertical differentiation, whereas the range of the Gini coefficients indicated moderate inequality and well-developed structural diversity throughout. From a management perspective, these results suggest that silvicultural strategies should account for the substrate-related site potential. On limestone, where conditions favor species coexistence and complex canopy layering, selection systems that maintain multi-layered structures are most appropriate. On nutrient-poor peridotite and chert, management should focus on promoting stand stability and regeneration through lower-intensity interventions and the gradual enrichment of underrepresented species. Integrating geological and edaphic variability into forest

planning will enhance both productivity and resilience under changing climatic conditions.

### Author Contributions

BB handled conceptualization, methodology development, field investigation, original draft preparation, and project administration. ČV provided supervision, contributed to methodological refinement, validated results, and assisted with review and editing. MČ performed formal data analysis, curated datasets, prepared visualizations, and contributed to review and editing. SV and MLJ supported field investigation, supplied necessary resources, contributed to visualization, and assisted with manuscript review and editing. All authors approved the final manuscript.

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### Conflicts of Interest

The authors declare no conflict of interest

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