

Effect of site productivity on structural diversity of *Pinus sylvestris*–*Fagus sylvatica* stands in the Central Rhodope Mountains, Greece

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Abstract

Although the relationship between site productivity and stand structure has been extensively studied, there is limited research specifically addressing how site productivity influences structural diversity in mixed stands. The aim of this work was to analyse the effect of site productivity on the structural diversity of the *Pinus sylvestris*–*Fagus sylvatica* stands in the central part of the Rhodope Mountains in north-eastern Greece. Data from 35 plots of 500 m², established in mixed *P. sylvestris*–*F. sylvatica* stands, representing two site productivity types, were used. For each plot, the tree diameters were classified into 4-cm diameter classes. Using diameter at breast height (DBH) data, the following diversity indices were calculated for each sampling plot: Richness, Gini-Simpson, Gini-Simpson equitability, and Berger-Parker index. In most cases, the studied distributions exhibited high diversity. Overall, in *P. sylvestris*–*F. sylvatica* stands of the study area, *F. sylvatica* diameter distributions tended to exhibit higher structural diversity in good-productivity sites than in medium-productivity sites, although this trend was not consistent across all developmental stages. Further research in mixed *P. sylvestris*–*F. sylvatica* forests, as well as in different other species mixtures, is needed to draw more robust conclusions.

Key words: European beech, productivity, diversity indices, Scots pine.

Introduction

Environmental factors significantly influence the growth, productivity, and diversity of forest ecosystems, and these factors are collectively referred to as site characteristics (Dafis 1986). Accurate assessment of site characteristics is cru-

cial for effective forest management, as it directly predicts forest productivity and outputs (Smith et al. 1997). Site productivity estimation can be conducted through long-term growth data or indirect indicators, such as dominant tree height and soil properties (Forrester and Bauhus 2016, Bottero et al. 2021). Modern techniques,

including remote sensing and advanced modelling (e.g., LiDAR, satellite imagery), have enhanced the precision and cost-effectiveness of these assessments (Melin et al. 2015, Ferraz et al. 2016, Müller et al. 2017).

Climate change further complicates forest management by altering precipitation patterns, and temperature regimes, and by increasing the frequency of extreme weather events, thereby significantly affecting forest structure and productivity (Anderegg et al. 2020, Brichta et al. 2024). For example, drought stress strongly influences the growth dynamics of key tree species, such as *Pinus sylvestris* L. (Scots pine) and *Fagus sylvatica* L. (European beech) (Gessler et al. 2020).

Forest stand diversity, particularly in mixed-species stands, is increasingly recognised as beneficial for maintaining productivity and stability compared to with monocultures (Jactel et al. 2017; Pretzsch et al. 2016, 2017). Mixed stands often demonstrate resilience through complementary interactions among different species, buffering against site-specific adversities and enhancing overall ecosystem services (Ampoorter et al. 2015; Jactel et al. 2017; Pretzsch et al. 2016, 2017). Consequently, understanding and quantifying structural diversity within these stands using appropriate diversity indices is essential for biodiversity conservation, ecosystem functioning, and resilience management (Lindenmayer and Franklin 2002, Forrester and Bauhus 2016, Thom et al. 2016, Grilli et al. 2017, Bourma et al. 2023, Michailidis et al. 2025, Milios and Kitikidou 2025a).

Several diversity indices, such as Richness, Shannon, Simpson, and the Gini coefficient, have been employed to quantify forest stand structural complexity and biodiversity, offering valuable insights

into forest ecosystem dynamics and informing conservation strategies (Chao et al. 2016, Marsh et al. 2018, Pommerening and Grabarnik 2019, Zhao et al. 2022). Recent studies emphasise that forests with complex structural attributes, such as diverse age classes, multi-layered canopies, and abundant deadwood, typically support higher biodiversity and contribute positively to ecosystem resilience (Silva Pedro et al. 2016, Betts et al. 2017).

Recent methodological advancements also highlight the importance of structural spatial heterogeneity as a key metric for comparing biodiversity across forest stands. Milios and Kitikidou (2025b) propose a straightforward statistical approach, using variance comparisons of the Gini-Simpson index, to effectively quantify differences in structural spatial heterogeneity between forests with varying characteristics. Their method, applied to *Fagus sylvatica* stands in the Rhodope Mountains, Greece, revealed significant differences in spatial diversity heterogeneity between medium- and high-productivity sites, providing valuable insights for biodiversity management and ecological resilience.

Despite these insights, gaps remain regarding how site productivity influences structure diversity within mixed-species stands, as most previous research has primarily focused on general stand structure analysis rather than on diversity aspects. In particular, mixtures of *Pinus sylvestris* and *Fagus sylvatica* have not been thoroughly investigated in terms of their structural diversity. *F. sylvatica*, a shade-tolerant species, tends to dominate and gradually replace the pioneer species *P. sylvestris*, while the climax community in the area expected to be composed of *F. sylvatica*–*Abies borisii-regis* Mattf. (Milios 2000a).

Earlier descriptions of these stands (Milios 2000a,b) characterised overall stand structure but did not quantify the diversity of diameter structures or evaluate its relationship with site productivity, leaving an important gap that the present study addresses. Therefore, this study aims to fill this specific knowledge gap by analysing how site productivity affects the structural diversity of mixed *Pinus sylvestris*–*Fagus sylvatica* stands in the central Rhodope Mountains of north-eastern Greece. By exploring these relationships, the findings are expected to enhance our understanding of biodiversity management and the resilience of mixed-species forest ecosystems in the face of environmental change.

The working hypothesis in this work is that, within a given developmental stage, stands on high-productivity sites would display higher structural diversity, expressed as more numerous and more evenly occupied DBH classes, than stands on medium-productivity sites. We expected this pattern to be particularly pronounced for the shade-tolerant *Fagus sylvatica*, whose growth plasticity allows it to exploit favourable growing conditions. In contrast, we anticipated weaker productivity-related differences in the DBH distributions of the pioneer *Pinus sylvestris*.

Materials and Methods

Study area

The study area is the central part of the Rhodope Mountains in the region of Xanthi in north-eastern Greece, with geographical coordinates of 24°42′ – 24°46′ E and 41°19′ – 41°22′ N (Fig. 1). The altitude ranges from 1100 to 1725 m a.s.l. and the soils are classified as acid brown

(Milios 2000a,b). The mean annual temperature varies from 5.42 °C to 8.49 °C, and the mean annual precipitation ranges from 660 mm to 754 mm (WorldClim, undated). In the area, there are various mixed-species forest formations, while the *P. sylvestris*–*F. sylvatica* stands are one of the main mixtures in the area (Milios 2000a,b).

Research procedure

In this study, data from Milios (2000a) were used. Specifically, data from 35 rectangular plots (20 × 25 m; 500 m²) established in mixed *P. sylvestris*–*F. sylvatica* stands growing in two site productivity types were analysed. No new field measurements were taken; all plot data were originally collected by Milios (2000a,b) and are re-analysed in the present study. The plots were established at altitudes ranging from 1230 to 1435 m a.s.l. Site type A represents high-productivity sites (good site quality), and site type B represents medium-productivity sites (moderate site qualities) (Milios 2000a,b). In each plot, the DBH of all trees was recorded. Details on how the developmental stages were created, and other relevant information on the *P. sylvestris*–*F. sylvatica* stands, are provided in Milios (2000a,b). Milios (2000a) described the plots and the development stages in mixed stands, reporting classical stand structure variables (mean diameter, height, basal area, age distribution) and general successional patterns. In Milios (2000b), these structural characteristics and dynamics are presented in greater detail; however, neither Milios (2000a) nor Milios (2000b) provide any quantification of structural heterogeneity or diversity.

Different factors were used to classify the plots into good productivity sites (site type A) and medium productivity sites

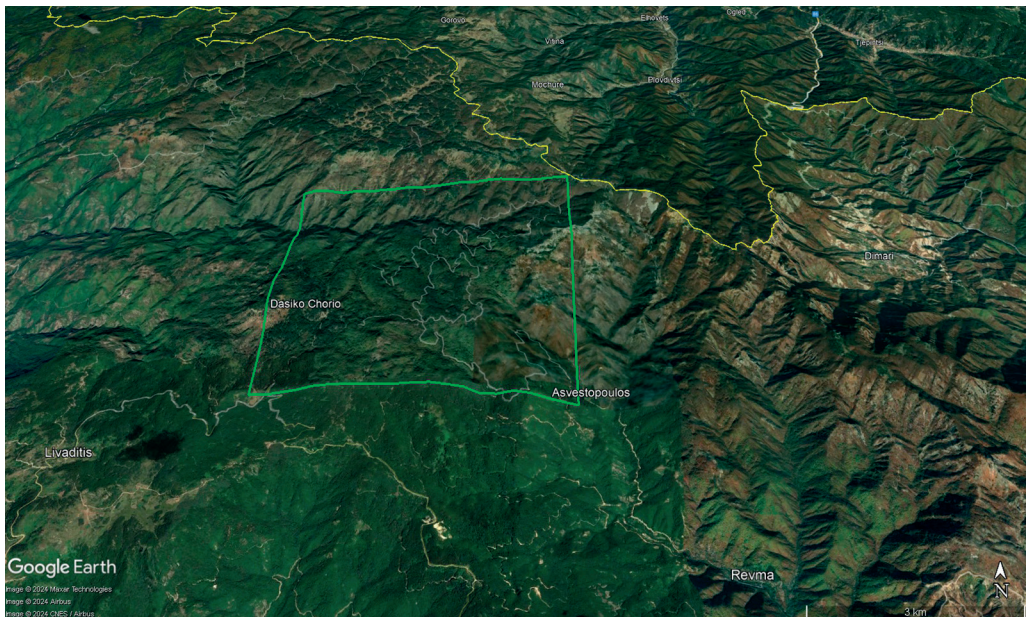
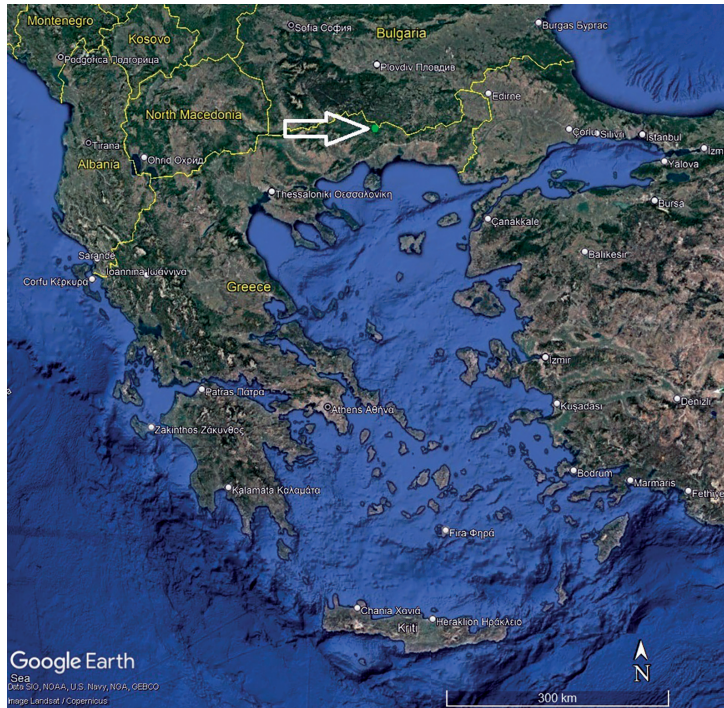


Fig. 1. Location of the study area in Greece and in the Greek part of the Rhodope Mountains (Xanthi region, north-eastern Greece), with the study area delineated (source: Google Earth Pro).

(site type B). These factors included the plot's position on the slope, the height of the tallest trees in relation to their age, soil characteristics, soil topography, and the exposure (Milios 2000a). Good-productivity sites are typically located on lower or less steep slope positions, where soil depth, moisture availability, and nutrient retention are generally higher. In contrast, medium-productivity sites usually occur higher up or on steeper slopes with shallower soils, reduced moisture availability, and higher erosion rates. Topography also plays a role in site quality classification: good-productivity sites are generally situated in slightly concave areas where the soil is deeper. Regarding exposure, good-productivity sites mainly face north, where moisture conditions are more favourable, whereas medium-productivity sites tend to face south, where conditions are generally warmer and drier (Dafis 1986). Site classification was verified using site index curves developed for *P. sylvestris* growing in mixed *P. sylvestris*–*F. sylvatica* stands in the area (Milios et al. 2018), confirming that sites classified as good-productivity (type A) supported taller trees of a given age, compared with those classified as medium-productivity (type B).

P. sylvestris–*F. sylvatica* stands exhibit three main developmental stages (phases) based on the establishment pattern of *F. sylvatica* in relation to *P. sylvestris*. These stages appear on both site types (Milios 2000a,b) and are summarised in (Table 1). In stage 1, *F. sylvatica* established beneath the canopy of *P. sylvestris*, with its establishment delayed by several decades compared with *P. sylvestris*. In site type A, 8 plots were established (pine–beech 1A), and in site type B, 4 plots (pine–beech 1B) (Milios 2000b). In stage 2, a few *F. sylvatica* individuals co-existed with *P. sylvestris*, and the estab-

lishment of *F. sylvatica* continued over an extended period. In site type A, 7 plots were established (pine–beech 2A), and in site type B, 6 plots (pine–beech 2B) (Milios 2000b). In stage 3, the establishment of *F. sylvatica* occurred simultaneously with that of *P. sylvestris*. In site type A, 5 plots were established (pine–beech 3A), and in site type B, 5 plots (pine–beech 3B) (Milios 2000b).

Only a few trees of species other than *P. sylvestris* and *F. sylvatica* were observed in the stages analysed at both site types (Milios 2000a). Logging in the study area affected stand structure in both site types in a similar manner. The analysed stands belong to the same management unit and have been subjected to comparable thinning and harvesting regimes in terms of timing, intensity and silvicultural system, without systematic differences between site type A and site type B. Additionally, the age structure of the species was considered not to differ significantly between the two site types within each analysed stage.

For each plot, the tree DBHs were classified into 4 cm diameter classes (4–7.99 cm, centred at 6 cm; 8–11.99 cm, centred at 10 cm; and so on), following the class width used in the original DBH figures published for these plots (Milios 2000b). This class width provides sufficient resolution to capture differences in stand structural patterns while limiting overly sparse classes, which can affect diameter-class diversity indices based on proportional abundances. In this study, 'structural diversity' refers specifically to diameter-based structural diversity quantified from DBH-class distributions; vertical or spatial structural attributes were not assessed. This classification was carried out separately for *P. sylvestris* individuals, *F. sylvatica* individuals, and for all trees

Table 1. Characteristics of *P. sylvestris*–*F. sylvatica* stands (Milios 2000a,b).

Stage	Stands type	<i>P. sylvestris</i>				<i>F. sylvatica</i>				Total basal area, m ² ·ha ⁻¹
		Age	Mean DBH, cm	Mean height, m	Basal area, m ² ·ha ⁻¹	Age	Mean DBH, cm	Mean height, m	Basal area m ² ·ha ⁻¹	
1	Pine–beech 1A	76–90 years, except for some younger individuals	44.13	25.72	24.47	35–55 years	11.54	11.16	10.27	34.74
	Pine–beech 1B	105–125 years, except for some younger individuals	32.30	22.28	27.34	45–75 years	7.77	7.62	4.25	31.59
2	Pine–beech 2A	76–95 years	40.93	25.64	21.51	Unevenly aged; oldest 70–90 years	14.15	13.59	14.88	36.39
	Pine–beech 2B	100–120 years, except for some younger individuals	33.29	21.94	21.51	Unevenly aged; oldest 75–110 years, few older individuals	11.42	10.81	13.72	35.23
3	Pine–beech 3A	89–123 years	48.64	27.75	17.00	Two age groups: main 85–107 years, few older; second 20–40 years	28.08	19.80	26.38	43.38
	Pine–beech 3B	120 years, except for a few younger individuals	41.43	22.38	22.15	Two age groups: main 83–112 years, few older; second 25–40 years	15.84	12.90	16.09	38.24

present in each plot, regardless of species. The corresponding DBH class distributions were then created for each plot.

For all plots in each stage, Milios (2000b) published the distributions of DBH. Consequently, figures are available showing the total DBH distributions for the three stages in both good- productivity sites (site type A) and medium-productivity sites (site type B). Using these DBH distributions, the following diversity indices were calculated for each sampling

plot (Table 2): Richness, Gini-Simpson, Gini-Simpson equitability (Jost 2006, Kitikidou et al. 2022), and Berger-Parker index (Berger and Parker 1970, Kitikidou et al. 2022).

To calculate the value of each index for the DBH distributions of each plot, the template of Kitikidou et al. (2022) was used. For the Richness index, only the number of DBH classes was considered, whereas for the other three indices, both the number of classes and the abundance

Table 2. Biodiversity indices used for each sampling plot.

No	Index	Formula	Meaning
1	Richness	$R = \text{number of classes}$	Higher R indicates greater diversity (Jost 2006, Kitikidou et al. 2022).
2	Gini-Simpson	$GS = 1 - \sum_{i=1}^R p_i^2$	Values closer to 0 indicate lower diversity (Jost 2006; Kitikidou et al. 2022).
3	Gini-Simpson equitability	$GSE = \frac{GS}{1 - \frac{1}{R}}$	Values closer to 0 indicate lower diversity (Jost 2006, Kitikidou et al. 2022).
4	Berger-Parker index	$BP = \max p_i$	Values closer to 0 indicate greater diversity (Berger and Parker 1970, Kitikidou et al. 2022).

Note: p_i = proportional abundance of the i -th class.

of trees in each class are were taken into account (Berger and Parker 1970; Jost 2006; Kitikidou et al. 2022, 2024). Diversity is considered higher when there are more classes and the trees are distributed more evenly among them, meaning that no single class, or only a few classes, dominate the distribution (Berger and Parker 1970, Jost 2006).

Statistical analysis

The t-test and the Mann-Whitney test were used to compare the diversity index values between the two site types in each stage (Kim 2015, Fay and Malinovsky 2018). The t-test was applied when the data met the assumptions of normality and homogeneity of variance. Normality was evaluated with the Lilliefors (Kolmogorov-Smirnov) test and homogeneity of variances with Levene's test. If these assumptions were not met, the non-parametric Mann-Whitney test was used. All analyses were conducted in IBM SPSS Statistics for Windows, Version 21.0 (IBM Corp. 2012). The group means and standard deviations reported in Tables 3–5 provide a simple indication of the magnitude of differences between site types.

Results and Discussion

In stage 1, for the DBH distribution of *F. sylvatica*, the pine–beech 1A stands (high-productivity, site type A) exhibited significantly higher values ($p < 0.05$) for the Richness and Gini-Simpson indices, and significantly lower values ($p < 0.05$) for the Berger-Parker index compared with the pine–beech 1B stands (site type B) (Table 3). No other comparisons in stage 1, showed statistically significant differences.

In stage 2, no statistically significant differences were observed between the two site types (Table 4).

In stage 3, the pine–beech 3B stands exhibit significantly higher values ($p < 0.05$) for the Richness index in the *P. sylvestris* and total DBH distributions compared with the pine–beech 3A stands. Conversely, in the DBH distribution of *F. sylvatica*, the 3A stands showed significantly higher values for the Gini-Simpson and Gini-Simpson equitability indices, and lower values for the Berger-Parker index compared with the 3B stands. In the total DBH distribution, the 3A stands also displayed higher Gini-Simpson equitability and lower Berger-Parker index values than the 3B

Table 3. Comparisons of diversity indices in stage 1.

Stands	Species' DBH	Richness, mean $\pm$ S.D.	Gini-Simpson, mean $\pm$ S.D.	Gini-Simpson equitability, mean $\pm$ S.D.	Berger-Parker index, mean $\pm$ S.D.
Pine-beech 1A	<i>P. sylvestris</i>	4.50 ^a $\pm$ 0.926	0.72 ^a $\pm$ 0.096	0.94 ^{1a} $\pm$ 0.077	0.38 ^a $\pm$ 0.123
	<i>F. sylvatica</i>	5.63 ^a $\pm$ 0.518	0.75 ^a $\pm$ 0.033	0.92 ^a $\pm$ 0.036	0.33 ^a $\pm$ 0.051
	Total	9.75 ^a $\pm$ 0.886	0.81 ^a $\pm$ 0.018	0.91 ^a $\pm$ 0.019	0.28 ^a $\pm$ 0.027
Pine-beech 1B	<i>P. sylvestris</i>	6.25 ^a $\pm$ 2.986	0.73 ^a $\pm$ 0.128	0.90 ^{1a} $\pm$ 0.059	0.37 ^a $\pm$ 0.151
	<i>F. sylvatica</i>	3.75 ^b $\pm$ 0.957	0.57 ^b $\pm$ 0.094	0.79 ^a $\pm$ 0.095	0.55 ^b $\pm$ 0.114
	Total	9.50 ^a $\pm$ 1.291	0.77 ^a $\pm$ 0.086	0.86 ^a $\pm$ 0.098	0.38 ^a $\pm$ 0.144

Note: Means for the same species' DBH that share the same letter are not statistically significantly different at $p < 0.05$. S.D. = standard deviation. Comparisons were made using the t-test, except for those indicated with ¹, which were made using the Mann-Whitney test.

Table 4. Comparisons of diversity indices in stage 2.

Stands	Species' DBH	Richness mean $\pm$ S.D.	Gini-Simpson mean $\pm$ S.D.	Gini-Simpson equitability mean $\pm$ S.D.	Berger-Parker index mean $\pm$ S.D.
Pine-beech 2A	<i>P. sylvestris</i>	4.29 ^a $\pm$ 0.951	0.72 ^a $\pm$ 0.071	0.96 ^a $\pm$ 0.016	0.37 ^a $\pm$ 0.099
	<i>F. sylvatica</i>	7.00 ^a $\pm$ 0.817	0.79 ^a $\pm$ 0.016	0.93 ^a $\pm$ 0.031	0.31 ^a $\pm$ 0.062
	Total	10.00 ^a $\pm$ 0.816	0.84 ^a $\pm$ 0.015	0.94 ^a $\pm$ 0.017	0.26 ^a $\pm$ 0.040
Pine-beech 2B	<i>P. sylvestris</i>	5.83 ^a $\pm$ 2.401	0.72 ^a $\pm$ 0.176	0.91 ^a $\pm$ 0.081	0.40 ^a $\pm$ 0.184
	<i>F. sylvatica</i>	7.00 ^a $\pm$ 1.095	0.72 ^a $\pm$ 0.101	0.84 ^a $\pm$ 0.126	0.41 ^a $\pm$ 0.149
	Total	10.50 ^a $\pm$ 1.049	0.80 ^a $\pm$ 0.059	0.88 ^a $\pm$ 0.073	0.32 ^a $\pm$ 0.122

Note: Means for the same species' DBH that share the same letter are not statistically significantly different at $p < 0.05$. S.D. = standard deviation. Comparisons were made using the t-test.

stands. No other comparisons in stage 3 were statistically significant (Table 5).

Discussion

The studied distributions generally exhibited high diversity, as only two cases showed a Gini-Simpson index value below 0.7. The lowest observed value for the Gini-Simpson equitability index was 0.79, while in only three cases did the Berger-Parker index reach 0.4 or higher (tables 3–5). The closer the Gini-Simpson and Gini-Simpson equitability indices are to 0, the lower the diversity, whereas

values approaching 1 indicate higher diversity (Jost 2006, Kitikidou et al. 2022). Conversely, for the Berger-Parker index, values closer to 0 correspond to higher diversity, and the values closer to 1 indicate lower the diversity (Berger and Parker 1970, Kitikidou et al. 2022).

In almost all *P. sylvestris* DBH distributions, no significant differences ($p > 0.05$) in biodiversity index values were found between the good productivity sites (site type A) and the medium productivity sites (site type B) across the three stages of *P. sylvestris*–*F. sylvatica* stands. Only the pine-beech 3B stands exhibited significantly higher ($p < 0.05$) values for

Table 5. Comparisons of diversity indices in stage 3.

Stands	Species' DBH	Richness mean $\pm$ S.D.	Gini-Simpson mean $\pm$ S.D.	Gini-Simpson equitability mean $\pm$ S.D.	Berger-Parker index mean $\pm$ S.D.
Pine–beech 3A	<i>P. sylvestris</i>	3.40 ^a $\pm$ 0.894	0.67 ^a $\pm$ 0.096	0.98 ^a $\pm$ 0.021	0.38 ^a $\pm$ 0.073
	<i>F. sylvatica</i>	8.00 ^a $\pm$ 0.707	0.84 ^a $\pm$ 0.013	0.96 ^a $\pm$ 0.020	0.26 ^a $\pm$ 0.052
	Total	9.60 ^a $\pm$ 1.517	0.86 ^a $\pm$ 0.024	0.97 ^a $\pm$ 0.012	0.23 ^a $\pm$ 0.046
Pine–beech 3B	<i>P. sylvestris</i>	5.40 ^b $\pm$ 1.517	0.76 ^a $\pm$ 0.057	0.95 ^a $\pm$ 0.050	0.35 ^a $\pm$ 0.086
	<i>F. sylvatica</i>	9.00 ^a $\pm$ 0.707	0.78 ^b $\pm$ 0.037	0.88 ^b $\pm$ 0.033	0.39 ^b $\pm$ 0.048
	Total	12.00 ^b $\pm$ 1.581	0.85 ^a $\pm$ 0.025	0.92 ^b $\pm$ 0.027	0.30 ^b $\pm$ 0.046

Note: Means for the same species' DBH that share the same letter are not statistically significantly different at $p < 0.05$. S.D. = standard deviation. Comparisons were made using the t-test.

the Richness index than pine–beech 3A stands. This simply indicates that there were more *P. sylvestris* DBH classes in site type B than in site type A in stage 3, but it does not imply any difference in the evenness of tree distribution among the classes.

In stages 1 and 3 of the mixed stands, the comparisons of diversity indices indicated that the DBH distributions of *F. sylvatica* in mixed stands at good productivity sites (pine–beech 1A and 3A) exhibited higher diversity than the corresponding distributions at medium productivity sites (pine–beech 1B and 3B). This result is based on three of the four indices in each of the two stages: (Richness, Gini-Simpson, and Berger-Parker in stage 1, and Gini-Simpson, Gini-Simpson equitability, and Berger-Parker in stage 3) (tables 3 and 5).

However, this pattern was not observed in the *F. sylvatica* breast height distributions of the mixed stands in stage 2, where no significant differences were found in the diversity indices (Table 4).

In mixed stands of stage 3, the higher ($p < 0.05$) value of the total breast height distributions in the Richness index for the pine–beech 3B stands compared to the pine–beech 3A stands is attributed to the

values observed in the *P. sylvestris* breast height distribution where the same pattern occurs (see above), while this is not the case for the *F. sylvatica* distribution. Respectively, the differences in the total breast height distributions between pine–beech 3A and pine–beech 3B stands in the Gini-Simpson equitability and Berger-Parker indices arise from the differences found in the *F. sylvatica* breast height distribution (Table 5).

In stages 1 and 3, the DBH distribution of *F. sylvatica* in the mixed stands was more diverse at the good productivity sites than at the medium productivity ones. This pattern is likely due to the growth plasticity of *F. sylvatica* (Milios 2000a, Milios and Papalexandris 2019). Ecologically, the stronger structural response of *F. sylvatica* is consistent with its shade-tolerant, late-successional status and its documented growth plasticity under varying resource availability. In contrast, the pioneer *P. sylvestris* appears to maintain broadly similar DBH distribution diversity across the studied productivity classes, suggesting a more constrained structural response under the current stand conditions. Owing to this plasticity and the more favourable growing conditions of high-productivity sites, greater DBH differentiation

occurred of among *F. sylvatica* trees in site type A, resulting in a higher number of DBH classes and a more even distribution of trees among them. In general, the tree dimension differentiation tends to increase with site productivity (Oliver and Larson 1996). Similarly, Petrou et al. (2023) reported that in at open *Pinus brutia* Ten. stands in central Cyprus, DBH distribution was more variable in medium-productivity sites than in low-productivity ones.

Forest practices that redistribute growing space and aim to modify growth dynamics (Anderson et al. 2018, Cannon et al. 2022, Hayford et al. 2023, Latterini et al. 2023, Stampoulidis et al. 2023, Pieter et al. 2024, Santelices-Moya et al. 2024) should enhance the diversity of DBH distributions of the species within the *P. sylvestris*–*F. sylvatica* stands, thereby increasing their structural heterogeneity and complexity. A plan of silvicultural interventions implemented at the appropriate stages of stand development can promote strong differentiation in tree dimensions. Such treatments – thinnings must exhibit various intensities on various spatial scales.

Thinning operations should target both the *P. sylvestris* and *F. sylvatica* components of the mixed stands. In medium-productivity sites, thinning regimes could therefore be designed to emulate some of the structural features observed in the more diverse *F. sylvatica* DBH distributions on good-productivity sites, for instance by maintaining a wider range of diameter classes and multiple cohorts of *F. sylvatica*. These suggestions remain qualitative and should be viewed as hypotheses for future silvicultural experiments rather than prescriptive guidelines. However, the removal of *P. sylvestris* trees will also have a strong impact on *F. sylvatica* trees growing in the understory

and midstorey layers. Thus, the proposed silvicultural treatments will influence the DBH diversity of the future stands and influence their overall biodiversity potential.

Conclusions

The studied DBH distributions generally exhibited high diversity. Taken together, our results indicate that productivity effects on stand structure are detectable mainly for *F. sylvatica*, whose DBH distributions in good-productivity sites tended to be more diverse than in medium-productivity sites, whereas *P. sylvestris* showed comparatively little differentiation among site-productivity classes. However, the greater diversity of *F. sylvatica* in good-productivity sites does not appear in all cases (stages), indicating that it results from a combination of factors that may vary on a case-by-case basis. These patterns should be interpreted with caution, given the limited number of significant differences and the observational nature of the data. More research is needed in forests of *P. sylvestris*–*F. sylvatica*, as well as in different mixtures to draw more robust conclusions.

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