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Effect of Species Composition on Growth and Yield in Mixed Beech–Coniferous Stands

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Abstract: *Research Highlights*: In mixed stands, competitive and supportive relationships occur between trees, illustrated by their dendrometric characteristics. *Background and Objectives:* We investigated the effect of species composition on growth and yield in mixed beech–coniferous stands in the Romanian Carpathians. *Materials and Methods*: We selected sites with similar trophicity levels, as determined by the site mapping method. Under the same site conditions, we generated models to determine, for each species (spruce, fir, and beech), the main parameters of the site index, including mean height, dominant height, standing volume yield, and mean annual volume increment for different compositional species proportions (p_{sp}) and categories of proportions (i.e., low p_{sp}, between 10 and 50%, and high p_{sp}, ranging between 60 and 90%). *Results*: Overall, up to the age of 100 years, mixed stands with low p_{sp} had enhanced tree height growth, characterized by mean values 2.2% higher for spruce and 4.8% higher for fir and beech. Dominant height showed similar values, regardless of p_{sp}. Mixed stands in which the p_{sp} increased (i.e., p_{sp} > 50) were more productive, with the mean yield differences at the age of 100 years ranging from +1.7% (for fir) to +3.8% (for spruce and beech), increasing to +6% at 140 years. *Conclusions*: When setting management targets, the management of mixed forests should be based on an understanding of the relationship between the site, species ecological requirements, and their yield potential. Mixed stands can influence individual tree growth and stand yield through p_{sp}.

Keywords: mixed stand; soil trophicity; mean height; dominant height; species composition; mean annual volume increment

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1. Introduction

Mixed coniferous–beech stands have complex structures and fulfill multiple protection and production functions. In mixed stands, competitive and supportive relationships arise between trees, thus the structural conditions promoted by management decisions can influence the growth and development of each stand species. Several studies have investigated pure and mixed stands in terms of yield [1–5], stand growth, stock [2,6], and density [3,4,7,8]. The findings from these studies have suggested that mixed stands can be more productive than monocultures of the same species, they show higher increases in basal area and volume, and generally higher values of the dendrometric characteristics of the mean trees of the stands [9]. However, the effects of mixing tree species depend on the proportions of tree species and on their spatial structure in the mixed stand [10]. The dynamics of various types of species interactions are influenced by the species mix and the site conditions, which determine the species synergy effect [11]. Species mixing can significantly increase stand density, growth rate, and stand production, respectively [10]. Therefore, growth models of individual trees can be used in different scenarios to analyze under which specific conditions (e.g., species proportions, stand structure, interspecific competition) growth is affected at the stand level [12]. Species mixing can alter the growth and productivity of individual trees [13]. Consequently, at the level of individual trees in spruce-beech mixtures, beech is more resilient in pure stands and spruce is favored by mixing, but at the stand level the difference of growth loss is not significant [14]. The presence of spruce in upland mixtures keeps stand productivity high [15]. The study of the interaction between mixing effects and site conditions based on a dataset from long-term plots which covers a wide range of site conditions [16] demonstrates that spruce growth in poor soils could be accelerated by promoting beech in mixtures and beech growth could be enhanced by promoting spruce in mixtures, especially in excellent sites.

Regional climate-growth relationships showed differences between mixed beech-fir and pure beech-fir compartments [17]. The effects of drought are mitigated in mixtures (e.g., spruce with beech) compared with monospecific spruce stands [18]. Investigations at regional level show the importance of knowing the climatic conditions to promote the most suitable species in mixtures [19]. Climate change can intensify the decline of some species (e.g., fir and spruce in the Dinaric Mountains), so several management scenarios should be considered to ensure stand stability [20]. Mixtures have become relevant for achieving management objectives and the best option for the future [21]. For the achievement of management objectives, coefficients for density change of mixed stands and silvicultural prescriptions have been defined in order to predict structural parameters of stands with different proportions of species participation in the composition [22].

Thus, stand management is based on knowledge of the relationship between site and mix species requirements. Knowing the productive potential of the site requires an analysis of site conditions (geological, geomorphological, climatic, edaphic) directly [23–25] and indirectly, through indicator plants [26–28] and the dendrometric characteristics of trees [29,30]. Of these characteristics, stand height is an indicator of site productivity at a reference age [31,32], acknowledged for the management of even-aged stands [31,33]. The dominant height (h_{dom}) (the average height of the 100 largest tree diameters per hectare at a given age) [25] relative to stand age is not influenced by stand density and the management measures applied, and is considered an indicator of site productivity [34–37]. Another criterion for assessing the site productivity potential is the mean annual increment (MAI) of the volume of the total yield [38], i.e., its maximum size or the size of the MAI at a reference age. Volume increment depends on stand density and composition [39]. Relatively recent studies have also pointed to basal area increment as an indicator for quantifying site productivity in mixed multi-aged stands [40] or carbon increment [41], as well as to other indicators such as tree height with mean basal area (h_g), mean form-height or the ratio of the mean volume tree to its basal area [42]. MAI inferred from standing volume yield (V) can also characterize site productivity. It is clear that, at stand level, the higher proportion of coniferous trees contributes to increased production and growth of mixed stands.

In the case of mixed multi-aged stands, height is the measure of the effect of species mixing. However, it can become relevant only at the level of the generations of trees within the species that make up the mixture. In our study, we used the determination of indicators (i.e., h_g, h_{dom}, V, and MAI) at the level of tree generations. In addition, V and MAI can characterize site productivity under normal stand density conditions. Thus, in the case of stands which underwent silvicultural operations, the volume of harvested trees must also be taken into account. We inventoried the stands after a decade of forest management planning, when the stands were already structurally closed (i.e., stocking degree 1.0) following silvicultural operations. For all the stands, the V values characteristic of the generations/species in the mixtures were corrected to the hectare of forest under the assumption that each generation in the mixture would form a hypothetical pure, even-aged stand with normal stocking density (i.e., 1.0). Therefore, each productivity indicator incorporates the effect of the species mixture. MAI, resulting from V, was entered into the calculations still with normal values. The effect of stand structure, including of the variation in species composition and mixing pattern, can be highlighted against the background of the same site conditions. Accordingly, if the investigated stands are located in trophically equivalent sites, then the values of the stand productivity indicators (i.e., h_g, h_{dom}, V, and MAI) are the result of the structure conditions.

The aim of this study was to determine the effect of the proportion of participation (p_{sp}) of species (i.e., spruce, fir, and beech) on their growth and production in beech and coniferous mixed multi-aged stands located in sites with the same trophicity level. The findings are grounded on values of the main indicators (i.e., h_g, h_{dom}, V, and MAI) which estimate the site-index (SI) for different proportions of species participation in the mix. However, the results we have obtained are based on data that are sometimes insufficient to obtain definitive values of the indicators, which is why this study was also intended to experiment with a working method to be developed through further research.

2. Materials and Methods

Study area. The study was carried out in the Călimani–Gurghiu Massif in the Eastern Carpathians of Romania, in the Fâncel Forest District (46°47′59″ N, 25°9′22″ E) (Figure 1). The forests were located at altitudes of between 700 and 1600 m, on volcanic bedrock. The geomorphological factors varied throughout the studied stands, the slope frequently ranged from 25 to 35°, and the most common exposures were sunny or partially sunny. The average annual temperature was around 5 °C, the potential evapotranspiration around 500 mm, and the average annual precipitation around 1000 mm. The most common species of fir in the study area were beech, spruce, fir, and other deciduous (OD) trees, such as sycamore, Norway maple, hornbeam, wild cherry, elm, and European ash. The surveyed stands were located on an altitudinal gradient of between 1000 and 1350 m. They were between 10 and 140 years old and had been covered with silvicultural interventions (tending operations) of moderate intensity. The stands were generally multi-aged structures. In the stands, species occurred in different proportions and came from natural regeneration. However, there were stands where spruce had also been introduced through planting in order to complement the natural regeneration. Through management of the studied forest, the group shelterwood system, with its long regeneration period, was being promoted.

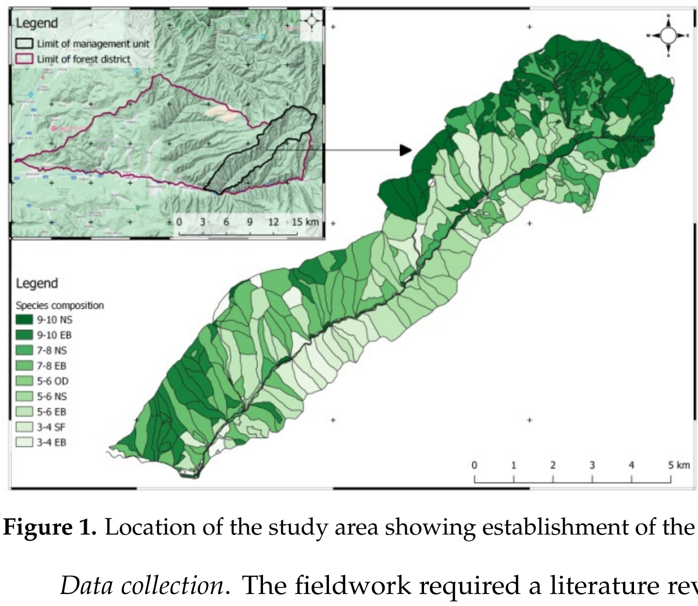


Figure 1. Location of the study area showing establishment of the investigated management unit.

Data collection. The fieldwork required a literature review of the area's physicogeographical conditions based on existing geological, geomorphological, and pedological maps. According to the management information, the forest district was stratified in relation to the main geomorphological factors (altitude, exposure, and slope), and in terms of the composition and age of the stands. In the four management units of the forest district, Management Unit IV Fâncel comprised the largest area of mixtures, reflecting the diversity of site conditions found in the montane mixed coniferous–beech stands in the area (Table 1).

Field observations were made using the site mapping method on an experimental area of 4647.36 ha, which represents this unit.

Table 1. Species and slope distribution in relation to altitude.

Altitude (m)	Species (%)				Total
	Beech	Fir	Spruce	Other Species	
600–800	10	5	1	14	6
801–1000	42	39	10	38	27
1001–1200	36	37	24	18	30
1201–1400	12	18	42	20	26
1401–1600	-	1	23	10	11
Total (%)	100	100	100	100	100
Density	0.73	0.76	0.74	0.81	0.75
Area (ha)	2004.90	303.48	2063.61	275.37	4647.36
Total (composition) (%)	43	6	45	6	100

Slope (°)	<5	6–15	16–25	26–30	31–35	36–40	Total
Area (%)	-	1	13	32	37	17	100

Identification of the characteristics and estimation of the forest sites' productivity was carried out directly, based on a survey of the site components, and indirectly, by means of indicators of the herbaceous flora and the stand yield [30,43,44]. The fieldwork consisted of recognizing and characterizing primary site units. A total of 429 subplots, based on the site conditions and stand structure, were constituted within the experimental area. In this case, 81 soil profiles (35 main soil profiles and 46 control profiles) were placed in the management unit. Samples were collected from the 35 main soil profiles and analyzed in the laboratory in order to determine the soil physicochemical properties. From the 429 stands, 115 were selected, consisting of spruce, fir, and beech, and being multistoried, located on eutrophic soils, systematically covered with moderate-intensity interventions, and stands in which the p_{sp} was between 10 and 90%. Sample areas, ranging from 0.05 to 1.0 ha, were placed in each mixed stand in order to investigate stand structure [45,46]. Measurements of tree dimensions (diameter and height) were taken from the 7798 inventoried trees. Within each stand, for each species, the trees were grouped by dimensional class, allowing the tree generations to be captured at the species level. The height and diameter of the mean tree (h_g and d_g, respectively), when considering the basal area, were determined at the generation level. In addition, the mean tree and its dimensions (d_g and h_{dom}) were established for the dominant-story trees. The proportion of tree generation in the stands (i.e., species and generation stand composition) were determined by species, based on the proportion of their basal areas in the stand. Where two generations were identified in the same species, the age was determined for each generation separately based on core samples extracted from the mean trees characterizing each generation. Data processing included the species-specific tree generations found in the 115 stands, along with their ages and dendrometric parameters. Stands derived from natural regeneration with ages of between 10 and 140 years were studied. In these locations, 21% of the spruce stands came from completed natural regeneration (from plantations).

Soil trophicity potential. Soils were analyzed according to their properties determined by field observations (altitude, exposure, slope, nature of parent material, physiological thickness) and through laboratory analysis. Analyses included the main physicochemical properties of the soils. According to the solidification factors and soil physical and chemical properties, eutricambisols and andic districambisols, as well as typical and dystric andosols, were identified in the monitored area. For this study, only the site type was included—-mixed mountain stands with high productivity, edaphic high eutricambisol/districambisol (eutrophic, euhydric), with *Asperula*/*Galium*–*Dentaria*. The soil trophicity level was the main soil indicator used to differentiate the site productivity using the direct method.

This was determined from the soil physicochemical properties derived from laboratory analysis and field measurements [30,43]. The relationship between the soil physicochemical properties was investigated by means of multiple regression and expressed in terms of a potential TI. Thus, the TI index sums of the values of humus content (HC) and base degree of saturation (V_B), and ranged from 32 to 180. In relation to the TI index, oligomesotrophic to eutrophic soils were identified in the management unit (Table 2) [43,44]. To highlight the influence of p_{sp} in the stand composition on species production, the analysis included only stands located on eutrophic soils with TI values varying between 81 and 120.

Table 2. Soil classification based on TI values.

TI	Soil	HC (%)	V_B (%)
31–50	oligomesotrophic (2%)	<6	20–30
51–80	mesotrophic (14%)	6–10	31–40
81–140	eutrophic (76%)	11–20	41–55
>140	megatrophic (8%)	>20	56–70

Note. HC = percentage humus in the A horizon and V_B (%) = base saturation at pH = 8.3.

Indicators characterizing the site index. The site index (SI), based on the indicators h_g, h_{dom}, V, and MAI, was expressed both in relation to the stand age and to the mean diameter (d_g). Tree volume, characterizing the V of the stands, was determined using the nationally established regression equation for forest species in Romania [47]:

$$\log v = a_o + a_1 \log d + a_2 \log d^2 + a_3 \log h + a_4 \log^2 h \quad (1)$$

where v = tree volume, d = diameter, and h = height. The regression coefficients in Equation (1) are: (for fir) $a_0 = -4.46414$; $a_1 = 2.19479$; $a_2 = -0.12498$; $a_3 = 1.04645$; $a_4 = -0.016848$; (for spruce) $a_0 = -4.18161$; $a_1 = 2.08131$; $a_2 = -0.11819$; $a_3 = 0.70119$; $a_4 = 0.148181$; and (for beech) $a_0 = -4.11122$; $a_1 = 1.30216$; $a_2 = 0.23636$; $a_3 = 1.26562$; $a_4 = -0.079661$. The MAI was inferred from the stand volume calculated at the tree generation level.

The relationships between the dendrometric indicators (i.e., h_g, h_{dom}, V, and MAI) and age/diameter were expressed by polynomial models. The models were developed for the individual species (spruce, fir, and beech). In this case, 32 regression equations are presented here, by species, for either of two trophicity levels of eutrophic soils encountered in the mixed stands (i.e., TI = 81–100 and 101–120). The dataset processed in relation to the species/generation p_{sp} every 10 to 10%. In the case of some proportions, especially in fir, there were insufficient data to characterize the influence of each p_{sp} on the species yield, with the proportions being clustered into two categories—10%–50% and 60%–90%. The developed models enabled quantification of the dendrometric parameters (h_{dom}, h_g, V, and MAI) for different ages or d_g for each species included in the mixed stand in relation to the p_{sp}.

Soil trophicity and species composition influence on the site index. The SI (h_{dom}, h_g, V, and MAI) was investigated through F and χ^2 tests. The F test has been applied to explore the difference in significance between variances of distributions (experimental and theoretical). The distribution variance of the productivity indicators was compared through the variation in soil TI (81–100 and 101–120). The homogeneity of the indicator distributions for the two trophicity levels was tested by means of the χ^2 homogeneity test, according to the relationship:

$$\chi^2 = \sum_{i=1}^{m} \sum_{j=1}^{k} \left(a_{ij} - \frac{a_{i0} N_j}{N_0} \right)^2 \frac{N_0}{a_{i0} N_j} \quad (2)$$

where k = number of analyzed distributions, N_0 = total number of observations for the k distributions, $N_1, N_2, \ldots N_k$ = total number of observations, separated by distribution ($N_0 = N_1 + N_2 + \ldots + N_k$), a_{ij} = frequency corresponding to the I class and j distribution, where I takes values up to m and j up to k, and a_{i0} = sum of frequencies by class. The degrees of freedom are: f = (m − 1) (k − 1).

The applied statistical tests showed that the TI-index values approximated the same trophicity level characteristic of eutrophic soils. Thus, for the same site conditions, it was possible to analyze the differences in h_{dom}, h_g, V, and MAI, which were considered to be the effects of the variation in species composition and mixing pattern. This illustrates the variation in h_g and V for the reference ages of 40, 70, 100, and 140 years. The trend in these characteristics in relation to p_{sp} was expressed by linear models. Polynomial models generated for individual species were also used to determine the V and MAI for five mixtures for the reference values of age, d_g, h_g, and h_{dom}.

To assess the accuracy of the models, the values of the following statistical indicators were analyzed: root mean square error (RMSE); mean absolute error (MAE); mean absolute percentage error (MAPE); and the coefficient of determination (R^2). The values of these indicators gauged the accuracy of the model predictions in that the applied models fit the experimental data. In general, >90% of the variation in the values of the determined indicators (i.e., h_{dom}, h_g, V, and MAI) was explained by the models. In the case of the MAI, the models were accepted even at lower R^2 values (e.g., 0.79) because they captured the normal trend of MAI during stand development. The F test values, based on which differences in soil trophicity levels were determined, are presented in the Table S1.

3. Results

3.1. Soil Trophicity Potential and Productivity Indicators of Mixed Stands

The identified plant-accessible nutrient resource pool in soils varies in relation to humus type, humus content, and the properties of the soil's absorptive complex. The TI level for the analyzed soils ranged from 31 to 145. These values indicate a trophicity level specific to oligotrophic to megatrophic soils (Table 2). In soil profiles, trophicity decreases as HC decreases. Statistical analysis of the potential trophicity elements (i.e., HC and V_B) indicated a significant correlation between their values (Table 3):

Table 3. Parameters in the potential trophicity relationship.

TI (Equation)	Intercept	HC (%)	V_B (me%)	R^2	R^2 Adjusted
p-value	1.42×10^{-14}	3.94×10^{-31}	5.02×10^{-31}	0.426	0.422

By applying multiple regression, the potential trophicity can be written as:

$$\mathrm{TI} = 6.978HC + 3.147V_B - 127.49 \quad (3)$$

where HC = percentage humus in the A horizon and V_B (%) = base saturation at pH = 8.3.

Stand height and soil trophicity. Soils with a trophicity level of >80 are typical of higher-productivity sites. For stands located on soils with TI levels of 81–100 and 101–120, the models for h_g and h_{dom} predicted similar values. Among the three species (spruce, fir, and beech), an improvement in TI level from 81–100 to 101–120 at 100 years of age led to an increase in spruce h_g by 1.2 m. In fir and beech, the magnitude of h_g and h_{dom} showed no improvement in TI level. Contrastingly, on soils with higher TI levels (101–120), the models predicted even lower values for h_g in relation to age, ranging from −0.4 m (in beech) to −1.0 m (in fir) (Table 4 and Figure S1). No differences were observed in h_{dom} at 100 years as a result of TI level improvement for any species. Above 100 years, the respective differences slightly increased for beech, in the case of the h_g model (expressed in relation to age and diameter).

Mixed stand species growth on eutrophic soils. At lower TI levels (TI = 81–100), growth showed an increase at age 100 of 56 m^3 (6.1%) in spruce and 34 m^3 (5.5%) in beech. For fir alone, the improvement in TI level contributed to an increase in standing volume yield of 19 m^3 (+2.4%), which was maintained at greater ages. At 140 years (and at average diameter values of 54 cm), fir production increased by +20 m^3 (2%) (Table 4 and Figure S1).

Table 4. Yield indicators for mixed stands at 100 years of age on eutrophic soils (TI = 81–120).

Species	TI	Indicators			
		h_g (m)	h_{dom} (m)	V (m^3 ha^{-1})	MAI (m^3 yr^{-1} ha^{-1})
Spruce	81–100	30.2	33.3	970	9.7
	101–120	31.4	33.3	914	9.1
Fir	81–100	29.0	32.6	807	8.1
	101–120	28.0	32.6	826	8.3
Beech	81–100	27.0	30.7	657	6.6
	101–120	26.6	30.7	623	6.2

Note. The V and MAI values characterized the spruce, fir, and beech species in the mixed stands, although, for comparison, these are expressed under the assumption that the stands contained the same species at 100% density.

Mean volume increment and soil trophicity. The differences induced in the MAI values by variations in the TI level were also small (Table 4 and Figure S2). At 100 years, the improvement in TI level had a positive effect on growth in fir only, at +0.2 m^3 ha^{-1} yr^{-1} (+2.4%). On soils with a lower TI level (TI = 81–100), the MAI increased in beech by +0.4 m^3 ha^{-1} yr^{-1} (+5.5%) and in spruce by +0.6 m^3 ha^{-1} yr^{-1} (+6.1%), a tendency that was maintained at 140 years. Above 100 years (e.g., at 140 years and diameters of between 50 and 56 cm), spruce and fir showed a positive effect from the improvement in TI level, with an increase in MAI values of +0.3 m^3 ha^{-1} yr^{-1} (+4.5%).

A maximum MAI for spruce, fir, and beech on eutrophic soils (TI = 81–100 and 101–120) was reached at 70–75 years (Table 5 and Figure S2) when the mean stand diameters ranged between 28 and 32 cm. At these ages, the improvement in trophicity level (from TI = 81–100 to 101–120) induced growth differences of +0.1 m^3 ha^{-1} yr^{-1} in spruce (+1.5%) and −0.2 m^3 ha^{-1} yr^{-1} in fir and beech (−2.1 and −3.7%, respectively).

Table 5. Maximum mean annual volume increment.

Parameter		Species					
		Spruce		Fir		Beech	
		Age (Years)	Index (m^3 ha^{-1} yr^{-1})	Age (Years)	Index (m^3 ha^{-1} yr^{-1})	Age (Years)	Index (m^3 ha^{-1} yr^{-1})
TI	81–100	75	11.0	70	9.5	75	7.3
	101–120	70	11.1	70	9.3	75	7.1

The models for the analyzed dendrometric parameters are presented in the Table S1. The models explained between 75 and 98% of the variation in the dendrometric indicators and were significant ($p < 0.05$). The values from the $\chi^2{}_{exp}$ test showed that there were no significant differences between the model-predicted values under different TI-level conditions (TI = 81–100 to 101–120). The F test also showed that this different level in soil trophicity (i.e., TI = 81–100 to 101–120) did not influence the values of the analyzed yield indicators (i.e., h_g, h_{dom}, V, and MAI).

3.2. Influence of Species Composition on Stand Productivity

The effect of species p_{sp} on stand productivity was highlighted by the dendrometric parameters (h_g, h_{dom}, V, and MAI) described by the statistical models. Among the species (i.e., spruce, fir, and beech), slight increases in h_g were observed up to 100 years in stands where the p_{sp} showed decreasing values (Figure 2a). Thus, by age 70 years, spruce with a p_{sp} of 30% had a h_g of +0.9 m (+3.7%) greater than spruce, with a p_{sp} of 70%. Fir had a higher h_g, at +1.4 m (+6.2%), than beech, at +0.9 m (+3.9%). At 100 years, the differences were reduced to +0.6 m (+1.8%) for spruce, +1.1 m (+3.8%) for fir, and +0.8 m (+0.3%) for beech. At 140 years, for spruce and fir, the difference was +0.6 m, while for beech, the change in p_{sp} did not induce changes in h_g (Figure 2a).

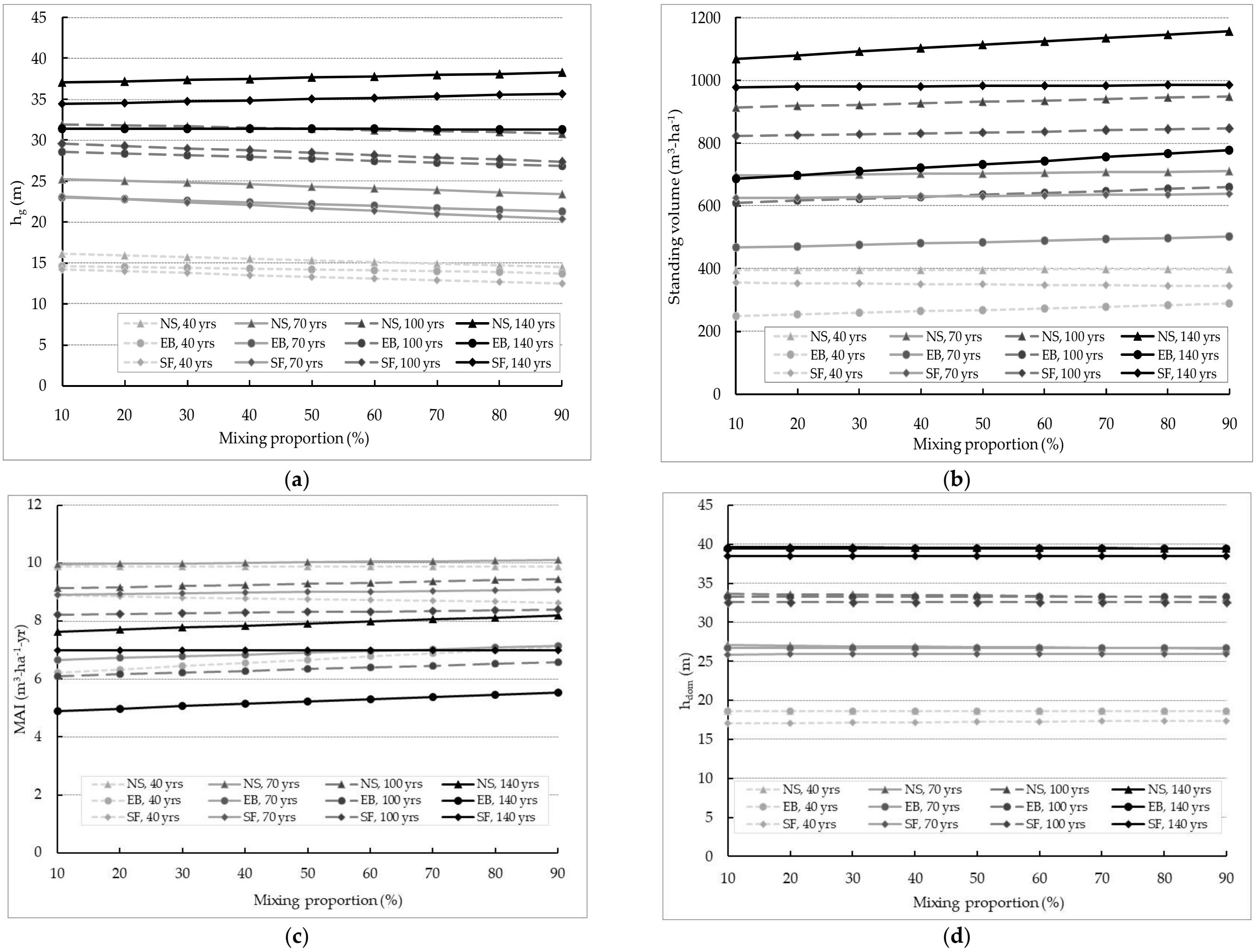


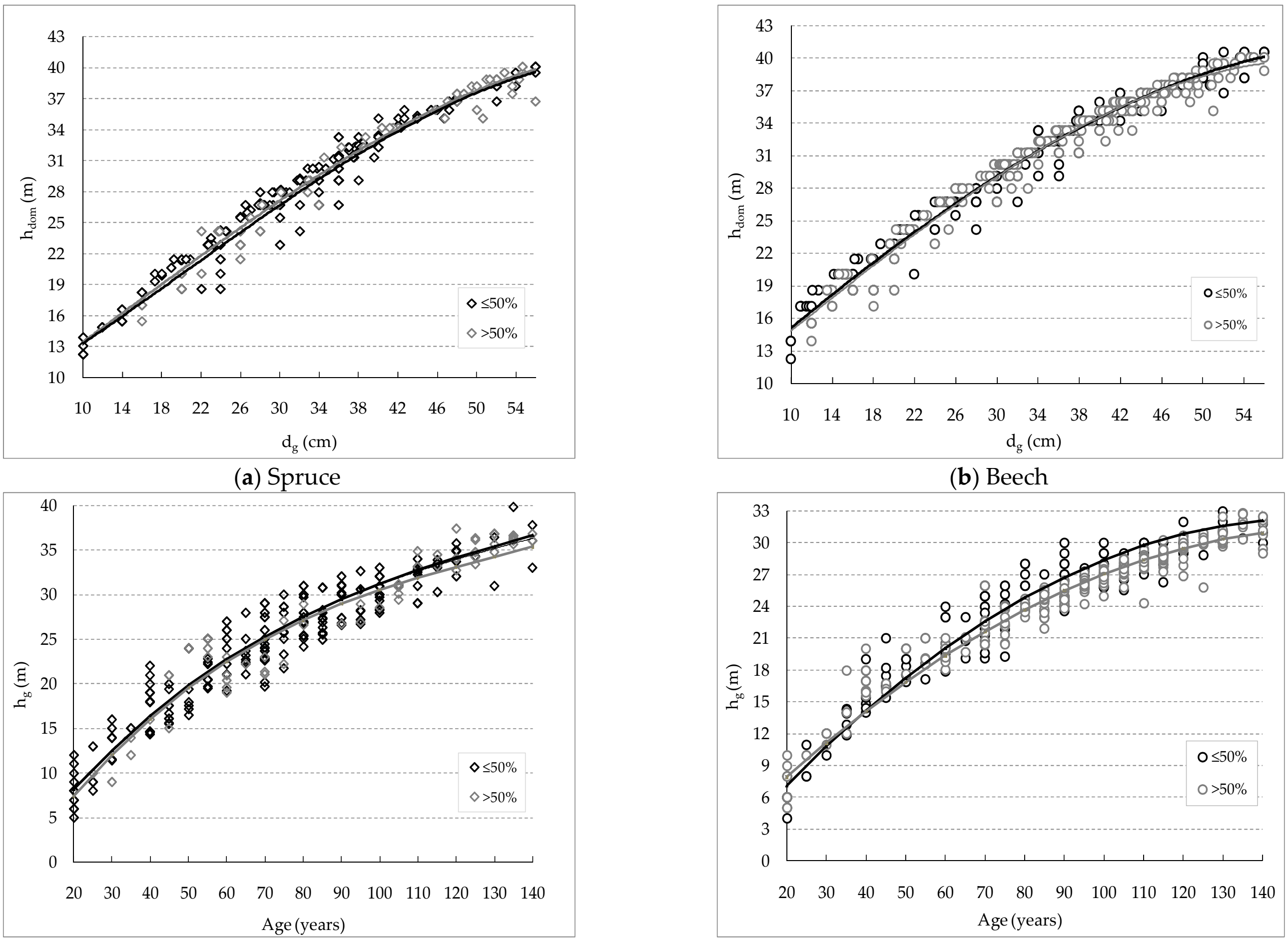
Figure 2. Spruce (NS), fir (SF), and beech (EB) in relation to their p_{sp} in mixed stands: (**a**) h_g variation; (**b**) V variation; (**c**) MAI variation; (**d**) h_{dom} variation.

d_g dimension was apparently positively influenced in stands where the species p_{sp} was increasing. However, it also had a positive effect on V. Thus, mixtures of 70-year-old trees in which a species had a p_{sp} of 70%, for example, had a positive effect on their production compared to mixtures in which the species had a p_{sp} of 30% (Figure 2b). Spruce showed an increase in production of +6.6 m^3 (0.9%), fir an increase of +7.1 m^3 (1.1%), and beech an increase of +17.9 m^3 (3.8%). At 100 years, the differences were +18.2 m^3 (2.0%) for spruce, +11.1 m^3 (1.3%) for fir, and +24.7 m^3 (4%) for beech. At 140 years, the differences were +43.3 m^3 (4.0%) for spruce, +3.4 m^3 (0.3%) for fir, and +46.2 m^3 (6.5%) for beech.

The MAI followed similar trends to V (Figure 2c), and h_{dom} had the same values across species, regardless of the species p_{sp} in the mixtures (Figure 2d).

The values of h_g, h_{dom}, V, and MAI were analyzed for each species (i.e., spruce, beech, and fir) at the level of two types of mixed stands, with p_{sp} ranging between 10 and 50% ($p_{sp} \leq 50$) and between 60 and 90% ($p_{sp} > 50$).

Dominant and mean height (Figure 3). In mixed stands, at 100 years, species with $p_{sp} \leq 50$ had higher h_g—by 0.7 m in spruce and 1.3 m in fir and beech. For spruce, the differences were slightly smaller, reaching +0.7 m (2.3%). In the case of h_{dom}, characteristic of species with $p_{sp} \leq 50$, the models predicted an increase of 0.1 m in spruce and 0.4 m in beech. Above the age of 100 years, these differences were maintained, tending towards 0.5 m, even in the conifers. The positive effect of p_{sp} on h_g decreased, which was explained by the way the trees were associated in the mixture. The h_{dom} of the fir was not influenced by the change in its p_{sp}.



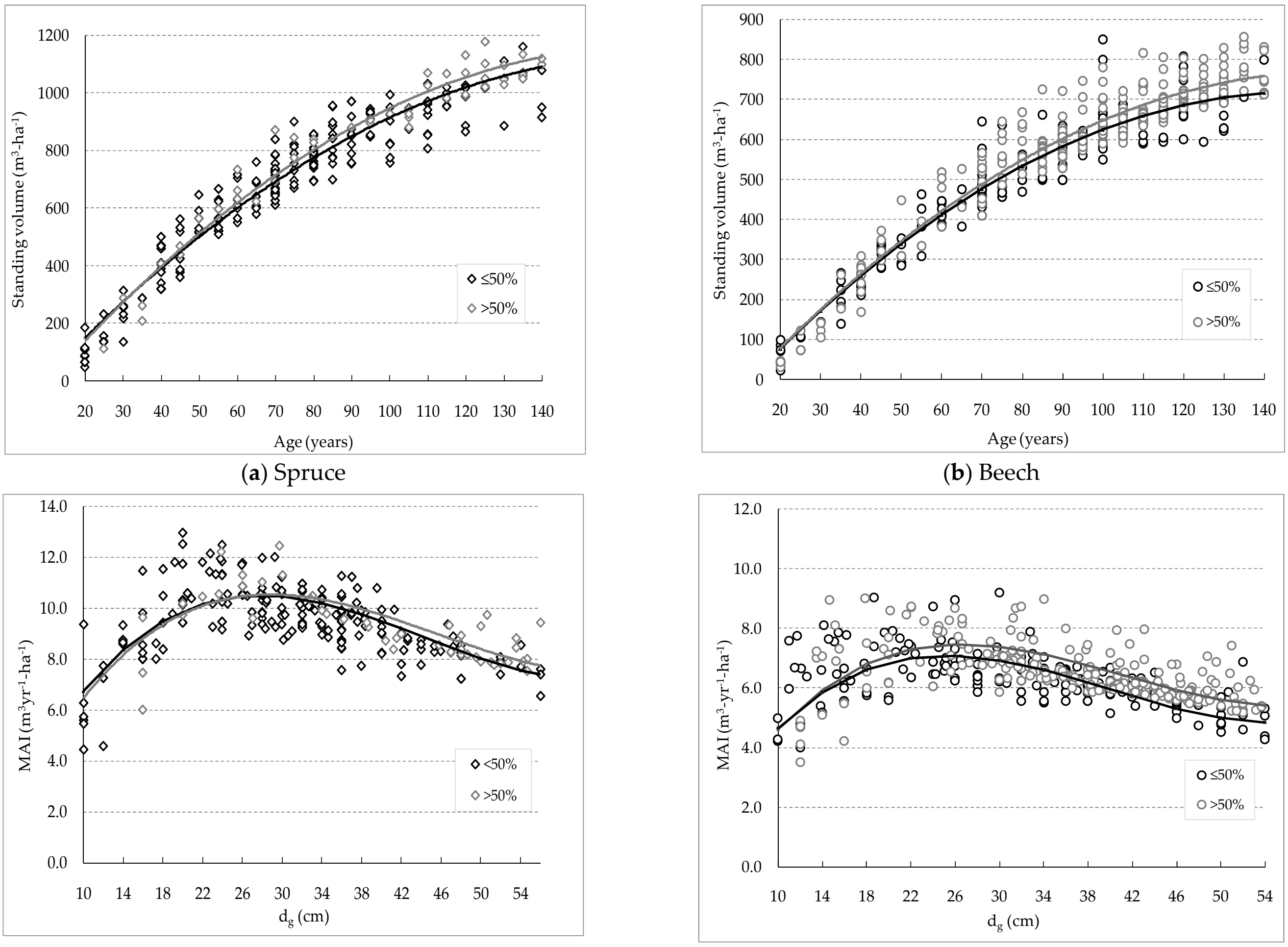
(**a**) Spruce (**b**) Beech (**c**) Spruce (**d**) Beech

Figure 3. Variation in h_{dom} in relation to diameter in: (**a**) spruce; and (**b**) beech; and h_g in relation to age in: (**c**) spruce; and (**d**) beech in mixed stands in which the species occurred in mixtures with a p_{sp} of between 10 and 90%.

Species proportions and their standing volumes. Increasing the p_{sp} (i.e., $p_{sp} > 50$) in mixed stands apparently had a positive effect on their standing volume yield per hectare. For species with $p_{sp} > 50$ in such compositions, the models predicted higher yields at age 100—for spruce, +35 m^3 ha^{-1} (+3.8%), for fir, +15 m^3 ha^{-1} (+1.7%), and for beech, +24 m^3 ha^{-1} (+3.8%) (Figure 4). At 140 years, the differences in yield tended towards 40–50 m^3 ha^{-1} (5–6%).

Species proportion and mean increment. The mean annual volume increment of spruce and fir also benefitted from their increased p_{sp} in the mixture. Differences in MAI generated by variations in the p_{sp} (i.e., $p_{sp} > 50$) were maintained at the same percentages as for the V. Thus, in those stands where species had $p_{sp} > 50$, there was also a volume increase (Figure 4).

When the maximum MAI was reached (i.e., at the age of 70), the differences were +0.7 m^3 yr^{-1} ha^{-1} (+2.8%) for spruce, +0.2 m^3 yr^{-1} ha^{-1} (+2.1%) for fir, and +0.3 m^3 yr^{-1} ha^{-1} (+5%) for beech (Table 6).



(**a**) Spruce (**b**) Beech

(**c**) Spruce (**d**) Beech

Figure 4. V in relation to age of: (**a**) spruce; and (**b**) beech; and MAI in relation to d_g of: (**c**) spruce; and (**d**) beech. Values expressed per hectare of forest, assuming 100% pure stands. The MAI was derived from the V. The basal areas of trees belonging to generations of trees within the species were included in the quadratic d_g calculation. Characteristic values for V and MAI for species in mixed stands were expanded a density of 1.0.

Table 6. Maximum MAIs.

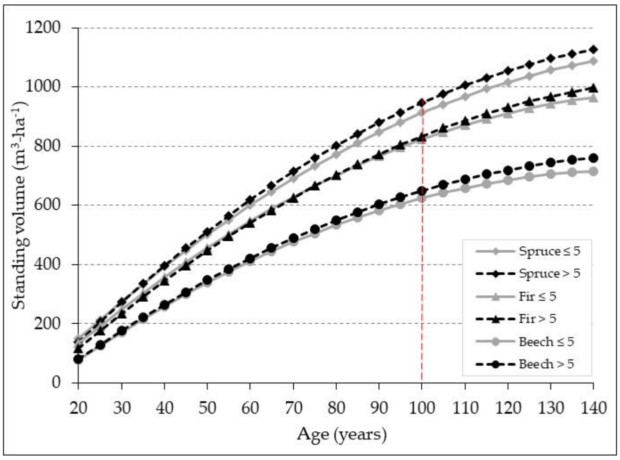
Parameter		Species					
		Spruce		Fir		Beech	
		Age (Years)	Index (m^3 ha^{-1} yr^{-1})	Age (Years)	Index (m^3 ha^{-1} yr^{-1})	Age (Years)	Index (m^3 ha^{-1} yr^{-1})
p_{sp}	≤50%	70	10.7	70	9.2	70	7.2
	>50%	70	11.0	70	9.4	70	7.5

The effect of species mixing at the reference age of 100 years is shown in the values of the h_g, h_{dom}, V, and MAI indicators in Table 7. Spruce, in the mixtures surveyed, remained the most productive species (Table 7 and Figure 5) and, together with fir, increased the production of mixed beech–coniferous stands.

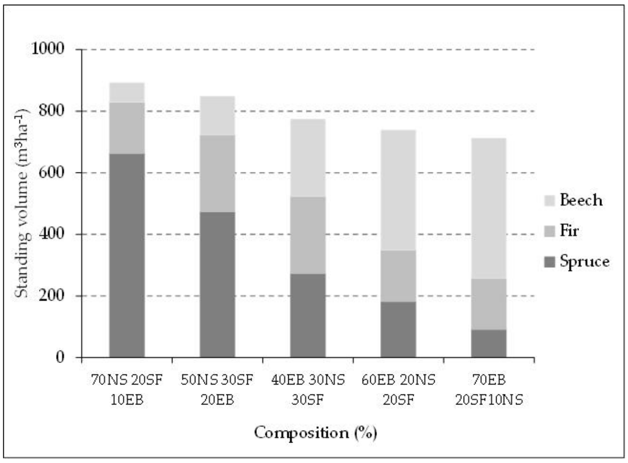
Table 7. Yield indicators of mixed stands at 100 years.

Species	Species p_{sp}	Indicator			
		h_g (m)	h_{dom} (m)	V (m^3)	MAI (m^3 ha^{-1} yr^{-1})
Spruce	$p_{sp} \leq 50\%$	31.2	33.4	912	9.1
	$p_{sp} > 50\%$	30.5	33.3	947	9.5
Fir	$p_{sp} \leq 50\%$	30.4	32.7	833	8.3
	$p_{sp} > 50\%$	29.1	32.7	848	8.5
Beech	$p_{sp} \leq 50\%$	28.4	30.5	625	6.3
	$p_{sp} > 50\%$	27.1	30.1	649	6.5

Note. A favorable influence of an increase in psp was noted in the case of the V and MAI. Contrastingly, hg slightly increased in stands where the psp showed decreasing values, while hdom had the same value, regardless of the psp of the species in the mixtures. Characteristic values for V and MAI for species in mixed stands were expanded to a density of 1.0.



(**a**)



(**b**)

Figure 5. (**a**) Model-predicted standing volume yield at age 100 (models in Table 8) for spruce, fir, and beech in mixed stands; and (**b**) standing volume yield from five mixture types at age 100. The models simulated the V for cases where the p_{sp} was between 10 and 50% ($p_{sp} \leq 5$) and between 60 and 90% ($p_{sp} > 5$). The values predicted by the models were extended to a density of 1.0. When they were used for stands with other densities, the values indicated by the models had to be adjusted to the actual density of each species. In addition, to express increases in the V and MAI in the mixtures, the projected model values had to be reduced by the p_{sp}.

The model predictions of the values of the dendrometric parameters were similar to their experimental values. Models 17–32 (Table 8) and their parameters were significant ($p < 0.05$). Despite the lower values for R^2 (0.79–0.89), the models were nevertheless selected on the basis of the other statistical indicators. However, the MAI model expressed the trend in MAI of the stands as an expression of the values obtained by relating the V to stand age. This was a major factor that led to the choice of the current annual volume increment models with the lower R^2 values, while for V, the models developed explained 94%–97% of its variance.

Table 8. Statistical parameters of the models used in the relationship between species proportion and stand productivity.

Species	Variable y	Variable x	Equation Number	p_{sp}	a	b	c	d	R^2	RMSE	MAE	MAPE (Relative)
Spruce	h_{dom} (m)	diameter (cm)	(17)	<50	7.346	0.574	0.0051	-0.9×10^{-5}	0.986	1.353	1.046	0.043
			(18)	>50	7.264	0.551	0.006	-0.1×10^{-4}	0.983	1.240	1.023	0.036
Beech			(19)	<50	7.130	0.824	-1×10^{-3}	-5.6×10^{-5}	0.945	1.220	0.910	0.035
			(20)	>50	7.216	0.761	1×10^{3}	-7.5×10^{-5}	0.871	3.041	2.667	0.084
Spruce	h_g (m)	Age (years)	(21)	<50	−2.292	0.589	33.4×10^{-5}	0.8×10^{-6}	0.961	2.242	1.870	0.080
			(22)	>50	−3.980	0.645	−0.004	0.1×10^{-5}	0.961	2.198	1.838	0.076
Beech			(23)	<50	0.764	0.381	-11.8×10^{-4}	–	0.962	1.908	1.517	0.084
			(24)	>50	−1.073	0.440	-14.5×10^{-4}	–	0.963	1.766	1.467	0.065
Spruce	MAI (m^3 yr^{-1} ha^{-1})	diameter (cm)	(25)	<50	−0.06	0.897	−0.0235	1.76×10^{-5}	0.899	0.966	0.748	0.083
			(26)	>50	−0.429	0.899	−0.0225	1.62×10^{-5}	0.842	0.825	0.645	0.073
Beech			(27)	<50	−0.675	0.726	−0.021	1.75×10^{-5}	0.834	0.736	0.559	0.089
			(28)	>50	−1.003	0.757	−0.021	1.7×10^{-5}	0.794	0.716	0.558	0.086
Spruce	V (m^3 ha^{-1})	Age (years)	(29)	<50	−159.0	15.76	−0.047	–	0.973	72.19	58.50	0.148
			(30)	>50	−127.0	14.69	−0.043	–	0.967	60.42	45.63	0.080
Beech			(31)	<50	−136.4	11.41	−0.038	–	0.952	47.29	38.30	0.093
			(32)	>50	−135.1	11.44	−0.036	–	0.947	47.48	38.31	0.083

Note. R^2 has high values, while the MAI values are lower. The greater variation in the MAI values can be explained by the variation in stand density due to the applied interventions. The reduction in stand density stimulated the increase in volume. This was more due to the increase in diameter compared to denser stands. Thus, the different percentages in tree diameter increment were also transmitted to the volume increment. Between the RMSE and MAE values, the differences were small in all variables, indicating low variance in individual errors in the sample and, at the same time, low variance in the frequency of large errors. The low MAPE values also indicate a high accuracy of the values predicted by the models.

4. Discussion

4.1. Soil Trophicity and Stand Productivity

In the case of the mixed stands, the species in the stands enhanced the site potential and responded differently as a consequence of the site and stand structure conditions. The applied statistical tests (F and χ^2), at $p < 0.05\%$, did not indicate significant differences between the two trophicity levels (i.e., 80–100 and 101–120), although small differences in indicator values did occur. A study based on 62 long-term experimental plots, carried out in mixtures of Norway spruce and European beech, with a site gradient with an SI ranging between 20 and 40, did not reveal a significant interaction between site conditions and the mixing effect on h_g at age 100 [48].

In the same soil trophicity conditions, differences in productivity can be explained by variations in stand structure conditions and in the local climate. With respect to stand structure, the increase in stand productivity could be due to the effect of density modification. It is common knowledge that the density effect may be site-invariant, depending mainly on the structural complementarity of the species [8,48]. Therefore, the growth rate of spruce has been found to be 14% in spruce–beech mixed stands [48]. Particularly in top sites, a reduction of up to 50% in maximum density can cause losses of up to 26% in total stand yield by age 100 [49]. Further, in better sites, beech in mixtures with spruce tends to expand its roots and thus compete for water and nutrients in the soil, which can have negative effects on spruce growth, just as the position of spruce in the upper cenotic classes may have negative effects on beech growth through the preemption of light [16]. On the other hand, in mixtures with spruce, beech has favorable effects on the temperature and soil, which can facilitate spruce growing conditions [16]. In an interspecific environment, under drought conditions, spruce growth was 25%–50% less affected, and beech growth was 23% more affected. While beech acclimated faster in all the growing conditions, spruce recovered faster only in the beech environment [18]. Simulations under the climate conditions of the

Dinaric Mountains [20] showed a tendency of reduction in the proportion of fir, from 53% in 2010 to 14%–37% in 2110, while the proportion of spruce can remain relatively constant (13% in 2010 and 9%–13% in 2110).

Research in uneven-aged forests has shown change in species composition and growth as a result of climate change, with shade-tolerant species such as fir and beech having a greater advantage over light-demanding species such as pine and spruce. Accordingly, the optimal balance of non-uniform forests may fluctuate over time as a consequence of changing environmental conditions, with implications for the adaptation of the management of these forests [21]. In the case of the stand structure of a single-tree selection and the intimate spruce-fir-beech mixture, studies of tree basal area growth patterns indicate significant variation in inter- and intraspecific competition depending on neighborhood density and tree dominance [12]. In our study, only HC and V_B were included in the calculation of the TI level, with the implication that their values include the influence of climatic conditions (for each 100 m increase in altitude, HC and V_B decrease by 16%). At 100 years and older, the percentage of basal area increment was much higher than the percentage of height increment [50], so the volume growth increased in relation to the basal area increment. This study shows that fir and beech experienced greater height growth at altitudes above 1000 m, where the climatic conditions were also more favorable.

4.2. Species Proportion and Their Productivity

The effect of p_{sp} was assessed through the values of productivity indicators (i.e., h_g, h_{dom}, V, and MAI). The calculations were carried out in bulk, at the level of the whole management unit. The values of the applied statistical tests (F and χ^2) indicated that the experimental distributions, structured relative to p_{sp}, were estimates of the same general distribution. Essentially, the tests revealed the homogeneity of the dendrometric parameters when they came from mixed stands with different p_{sp}. Thus, for mixtures composed of species that occurred in the composition in different proportions, the differences in productivity indicator values, as a measure of the variation in p_{sp}, were insignificant. While the statistical tests applied did not indicate significant differences between the experimental values of the analyzed productivity indicators at the level of the two p_{sp} categories, the models still predicted differences in h_g in all species, albeit with small values. Other research conducted in spruce–beech stands [48] has highlighted the positive influence of the mixture on the diameter increment in beech which has strongly benefitted from the mixture.

Studies on the current growth in tree basal area over the last 100 years in the Slovakian part of the Carpathian Mountains reveal a steady decline of spruce. Fir has recovered in the last 40 years and beech has had a slow but steady growth. However, there were no differences in growth between trees growing in different levels of mixture [19]. Although biogeoclimate influences tree radial growth, along an altitudinal gradient in fir and beech there were no significant correlations between tree radial growth and the Martonne aridity index [17]. However, in other climatic conditions specific to the hilly region, the climatic factors had the greatest effect on radial growth, with spruce being the most sensitive species [51].

However, mixed stands can have higher maximum densities due to species niche complementarity, with 2%–28% higher maximum densities compared to pure stands. Knowledge of these values is possible through the density change coefficients of mixed stands [22]. It follows that species mixing can change the productivity of individual trees in mixed stands compared to trees of the same species in pure stands [13]. The groups of trees that contribute most to stand growth can be identified by applying the concept of stand growth dominance together with the growth rates of trees [52]. Total biomass or biomass growth would be the best alternative to compare the production of mixed stands versus pure stands [39]. In spruce-beech stands with different compositions (under the influence of climatic factors such as temperature or precipitation and atmospheric pollution), studies on growth core have determined that mixed forests have on average 7.7% higher timber production compared to spruce monocultures and 47.3% higher compared to beech monocultures [10]. In other mixtures such as Douglas-fir and European beech, beech tended to lose growth compared to pure stands, so it produced 8% less volume, meaning 1.25 $m^3yr^{-1}ha^{-1}$, while Douglas-fir produced 20% more volume than in pure stands [53].

From our study, it appears that the stem volume of species in mixtures is positively influenced by the increase in species proportion (Figure 4b). This can also be explained by the beneficial effect of increasing p_{sp} on d_g after age 70. At the age of 70 years, V differences range from 0.9% (spruce) to 3.8% (beech), and increase with age, reaching 5–6% at 140 years. Increasing V is more significant after 100 years because, as is well-known, after this age, the annual percentage current annual increment of the tree basal area contributes a relatively high share (>80%) to the percentage current annual volume increment, compared to the percentage current annual form-height increment [50]. In terms of MAI, the differences between species become more pronounced after its maximum (i.e., after 65–70 years), so that at 140 years for conifers, they reach +4% and +12% for beech. According to the results of other research in mountain mixtures, spruce should be maintained in the large diameter categories and beech in the small and medium categories, thus increasing stand productivity [15]. Norway spruce grows similarly or even better in mixed stands compared to monospecific stands, so that in the long term, mixed stands of Norway spruce and European beech spruce may production more than monospecific stands [14]. Our research indicates that h_g values are higher at a species proportion of 30% compared to a species proportion of 70%. The percentages decrease up to 100 years, in spruce to +1.8% and in beech to +0.3. In mixtures (e.g., spruce-beech mixture) a significantly positive effect of inter-specific neighborhood on growth was observed along a site gradient (SI = 20–40 m) [48].

5. Conclusions

The mountainous region of Romania offers suitable conditions for the growth and development of beech–coniferous mixed stands. The results obtained from this study show that, in the higher-productivity sites of the investigated mixed stands, there were no site-specific differences that significantly influenced the values of the productivity indicators (i.e., h_g, h_{dom}, V, and MAI) at the species level. Consequently, the differences in these indicators are likely due to the stand structure, and mainly to the species mixture. In order to capture stand development under varying structural conditions, the study was extended to stands of different ages and p_{sp}. Insufficient data for certain proportions led to a clustering of the mixtures into two categories in relation to the p_{sp}—-mixtures in which p_{sp} = 10%–50% ($p_{sp} \leq 50$) and those in which p_{sp} = 60%–90% ($p_{sp} > 50$). From the derived models, it appears that, in general, low p_{sp} had a positive influence on species h_g. The differences decreased as the stands became older. For h_{dom}, the different p_{sp} in the mix had a limited influence, the predicted values of the models leading to differences of up to 1% at age 100 years. In terms of V and MAI, a positive effect of increased p_{sp} was determined. The same trend was observed for the MAI. Differences in the values of the indicators at different soil TI levels and for different p_{sp} in mixtures may also be influenced by the management measures applied. Silvicultural interventions can contribute to a change in p_{sp} by modifying the structural conditions towards achieving management targets, and these are reflected in the amounts of stand yield and growth.

Supplementary Materials: The following supporting information can be downloaded at: https://www.mdpi.com/article/10.3390/f13101651/s1, Table S1: Statistical parameters of the models used in the relationship between soil trophicity and stand productivity; Figure S1: Variation of species production in relation to fir diameter (a) and in relation to beech age (b); variation of average MAI growth in relation to fir diameter (c) and beech age (d). Mixed stands located in high quality sites with a soil trophicity level (T (i.e., TI)) between 81–100 and 101–120 were considered. The variation curves indicate values of V and the increase of MAI per hectare under the assumption of 100% density; Figure S2: Variation of mean height (hg) in relation to mixed stands age: fir (a) and beech (b); variation of dominant height (hdom) in relation to diameter: fir (c) and beech (d). Values of the stand's height located on soils with a high trophicity level (81–100 and 101–120).

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