Tree species identity and interaction determine vertical forest structure in young planted forests measured by terrestrial laser scanning

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ABSTRACT

Vertical forest structure is closely linked to multiple ecosystem characteristics, such as biodiversity, habitat, and productivity. Mixing tree species in planted forests has the potential to create diverse vertical forest structures due to the different physiological and morphological traits of the composing tree species. However, the relative importance of species richness, species identity and species interactions for the variation in vertical forest structure remains unclear, mainly because traditional forest inventories do not observe vertical stand structure in detail. Terrestrial laser scanning (TLS), however, allows to study vertical forest structure in an unprecedented way. Therefore, we used TLS single scan data from 126 plots across three experimental planted forests of a large-scale tree diversity experiment in Belgium to study the drivers of vertical forest structure. These plots were 9–11 years old young pure and mixed forests, characterized by four levels of tree species richness ranging from monocultures to four-species mixtures, across twenty composition levels. We generated vertical plant profiles from the TLS data and derived six stand structural variables. Linear mixed models were used to test the effect of species richness on structural variables. Employing a hierarchical diversity interaction modelling framework, we further assessed species identity effect and various species interaction effects on the six stand structural variables. Our results showed that species richness did not significantly influence most of the stand structure variables, except for canopy height and foliage height diversity. Species identity on the other hand exhibited a significant impact on vertical forest structure across all sites. Species interaction effects were observed to be site-dependent due to varying site conditions and species pools, and rapidly growing tree species tend to dominate these interactions. Overall, our results highlighted the importance of considering both species identity and interaction effects in choosing suitable species combinations for forest management practices aimed at enhancing vertical forest structure.

1. Introduction

Forests possess complex spatial structures, particularly through their strong vertical organization in vegetation layers (Zenner and Hibbs, 2000; Mura et al., 2015; Fotis et al., 2018). Forest structure directly influences its biodiversity and is believed to be closely linked to essential functional and ecological characteristics of the ecosystem (Lindenmayer et al., 1999; Gao et al., 2014; Ehrbrecht et al., 2017; Fotis et al., 2018; Walter et al., 2021). An intricate vertical organization can arise from densely packed canopies, resulting in enhanced forest productivity (Morin et al., 2011; Fotis et al., 2018). And a diversified vertical structure also offers a greater abundance of niche spaces, promoting the diversity of associated taxa within the ecosystem (Ampoorter et al., 2020).

In planted forests, mixed stands are presumed to provide a more diversified stand structure than monocultures (Pretzsch et al., 2017; Juchheim et al., 2020). One possible reason for higher structural diversity in mixed stands comes from crown complementarity, a concrete example of the fundamental niche complementarity mechanisms driving biodiversity–ecosystem functioning relationships (Juchheim et al., 2020; Ali, 2019). Species that differ in physiological and morphological traits
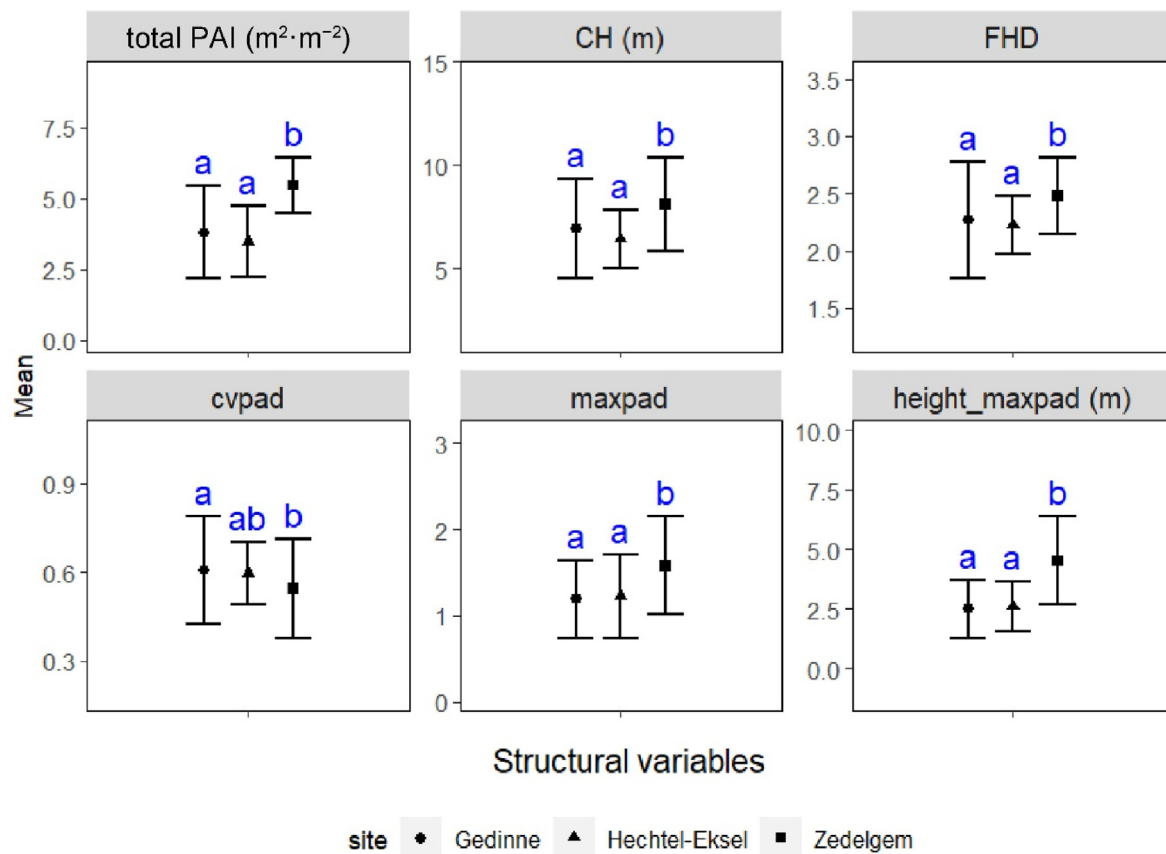
Fig. 1. Site-level mean for vertical forest structural variables. Including total PAI (total amount of plant material), CH (canopy height), FHD (foliage height diversity), cvpad (coefficient of variation for PAVD), maxpad (maximum density of PAVD profiles), and height_maxpad (height at the maximum density of PAVD profiles). Site-level mean values were derived by calculating plot-level mean values, which involved averaging each structural variable across four scan locations within each plot. Blue asterisks indicate the statistical significance level. The error bar represents the standard error of the mean for each structural variable. The blue letters 'a' and 'b' in Tukey's multiple comparison results represent statistically significant differences between sites. The results of the one-way ANOVA assessing stand structural differences among sites are summarized in Table S2.

may co-exist within different forest layers composed of multiple species, leading to higher structural diversity and efficient resources use (Kelty, 1992; Laurans et al., 2014). For example, tree species differ in the quantity and heterogeneity of light transmittance both during and after leaf expansion, leading to vertical stratification and more efficient utilization of above-ground space (Morin et al., 2011; Sercu et al., 2017; Juchheim et al., 2020; Hui et al., 2019). Consequently, there has been an increasing focus on harnessing niche complementarity effects within tree mixtures to promote the development of more diverse forest stand structures (Ali, 2019; Huuskonen et al., 2021). Moreover, the interspecific interactions, denoted as "species interaction effect", may exhibit variability across diverse species compositions, presenting as either positive, negative or neutral effects. Accurate quantification of the direction and magnitude of these interspecific interactions is important for selecting species that contribute to the most complex vertical structure, especially when both positive and negative interactions occur (Kirwan et al., 2009; Baeten et al., 2019).

The measurement of stand structural variables has been widely acknowledged as a major challenge (Ehbrecht et al., 2017; Storch et al., 2018). Traditional stand structural variables, such as basal area, stand density, and tree size differentiation are easily measured by traditional forest inventories but only provide a crude estimate of structure, and are generally very time-consuming to measure (Drössler et al., 2014; Keren et al., 2020). Satellite remote sensing provides accurate stand structural measurements at a global scale, such as global mapping of forest canopy cover and canopy height, but it does not consider the three-dimensional (3D) stand structures in detail (Tang et al., 2019; Potapov et al., 2021;

Skidmore et al., 2021). Measurements of forest stand structure at a local scale (e.g., 0.1 ha forest inventory plots) are the basis for global mapping of forest resources, and have the potential to comprehensively represent the structural complexity within the forest canopy (Newnham et al., 2015; Perles-Garcia et al., 2021).

Terrestrial laser scanning (TLS) is a powerful technology for detailed plot-scale forest monitoring (Newnham et al., 2015). With the benefit that TLS could overcome the limitations of both traditional forest inventories and satellite remote sensing, the use of TLS for plot-scale measurements started approximately two decades ago (Newnham et al., 2015). TLS has been shown to accurately derive vertical plant profiles, providing a comprehensive exploration of the three-dimensional structure of forest stands by capturing the vertical distribution of plant material in the canopy space (Calders et al., 2014; Skidmore et al., 2021). At the plot-scale, vertical plant profiles derived from TLS data have been proven to be useful for mapping forest stand structure and tracking its temporal changes (Calders et al., 2015; Yépez-Rincón et al., 2021; Nguyen et al., 2022). Furthermore, vertical plant profiles offer intuitive insights into forest structure, including the height of plant material concentration and the quantity of material at that height, serving as valuable forest structure variables. Structural variables that represent vertical heterogeneity, such as the coefficient of variation for plant materials along canopy height, can also be calculated from the profiles. Consequently, highly detailed TLS data has a broad application prospect in plot-scale structural diversity monitoring and forest structure management (Pereira et al., 2013).

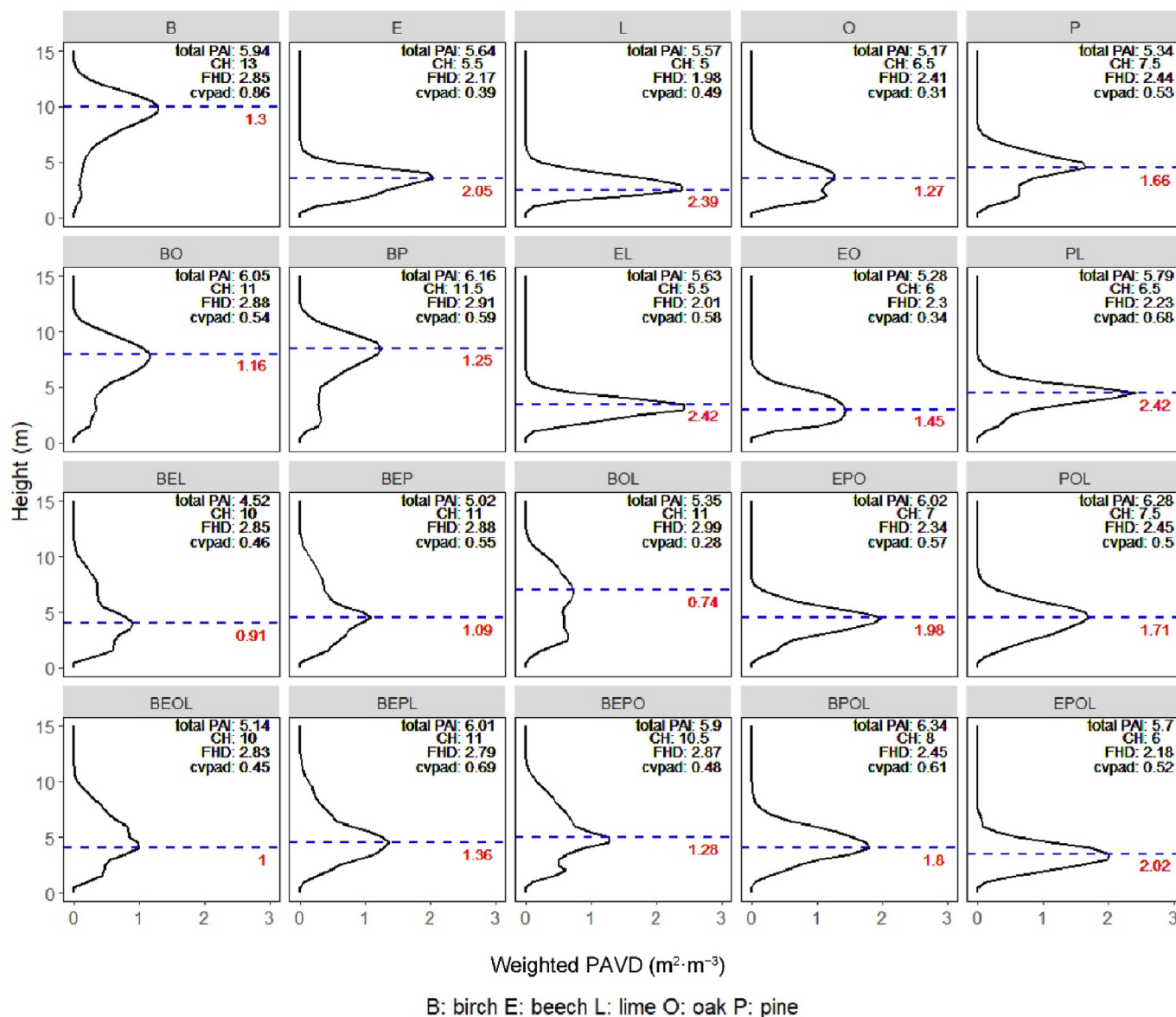We applied TLS in a tree diversity experiment to understand the

Fig. 2. Layout of the experimental sites in different locations in Belgium, showing the variation in plot-level mean total plant area index. The mean total PAI is calculated by averaging the total PAI values across four scan locations within each plot. The intensity of the green color represents the PAI level, with darker shades indicating higher PAI values. Plot number and tree species compositions are indicated in white, and the species index is available in the legend (A for larch, B for birch, D for douglas, E for beech, L for lime, M for maple, O for oak, and P for pine). The Gedinne site consist of two subsites, Gribelle and Gouverneurs, highlighted by a dashed rectangle.

influence of species richness, species identity, and species interactions on the vertical forest structure. Through TLS profiles, we acquired a comprehensive visualization of vertical plant materials across various tree species compositions. Due to variations in the physiological and morphological traits of composing tree species, along with potential interspecific interaction effects on vertical development, we hypothesize that species identity and interaction have a greater influence on vertical forest structure than species richness alone. We used linear mixed models to access the impact of species richness on vertical forest structure. Subsequently, we applied a hierarchical diversity interaction modelling framework to evaluate the role of species identity versus species interaction effects in shaping vertical structure. Our study intended to investigate the determinants of vertical forest structure while identifying structurally diverse and heterogeneous species combinations. Through this, we aimed to offer valuable insights into forest management strategies prioritizing the maintenance of stand structural diversity.

2. Material and methods

2.1. Experimental sites

Our study was conducted at three sites of the Belgian FORBIO tree diversity experiment, part of TreeDivNet (www.treedivnet.ugent.be). The study sites in Zedelgem and Gedinne were planted in spring 2010 and the experiment in Hechtel-Eksel was planted two years later. The Gedinne site consist of two subsites, Gribelle and Gouverneurs. The three sites differ in soil type, climate, and former land use, but all have the same experimental design (see Verheyen et al., 2013). The site-level design of the forests follows a classical synthetic community approach,

using a fixed species pool of five site-adapted tree species (Table S1) to create a diversity gradient from monocultures over two, three to four tree species mixtures (Fig. S1). Twenty different species compositions were established per site: all five monocultures, all five possible four-species mixtures, and a random selection of five two- and five three-species combinations. Each site consists of 40 plots as a result of replicating all combinations twice. An additional subtreatment was introduced at the Zedelgem and Gedinne sites, where one versus three provenances of oak (Zedelgem) and beech (Gedinne) were used, respectively. As a result, two new monocultures were added with the extra provenances in Zedelgem and four in Gedinne (two in Gribelle and two in Gouverneurs). In total, there are 126 plots. In Zedelgem, each plot measures 42 m × 42 m, while in Hechtel-Eksel, the plots are 36 m × 36 m. In Gedinne, the majority of plots are sized 42 m × 42 m, with a subset having dimensions of 42 m × 37.5 m. All three sites were planted on a 1.5 m by 1.5 m grid. In mixed plots, trees are planted in small monospecific patches of 3 × 3 trees. Patches were arranged in a checkerboard pattern in the two-species mixtures and randomly mixed in the three- and four-species mixtures. Additional details illustrating the layout of study sites and experimental plots can be found in Figs. S1 and S2.

2.2. TLS sampling and post-processing

In the summer of 2020, TLS single scan data were acquired at four representative locations in each plot to obtain a locally comprehensive stand structure. These locations were chosen to ensure that all species within the plot were included, while also maintaining a similar distance from the scanning centre for each species near the scanner (Fig. S2). These measurements were conducted using a RIEGL VZ-400 3D

Fig. 3. PAVD profiles for 20 tree species compositions (plots 1–20) at Zedelgem site. The panels are organized from top to bottom to represent monocultures (B for birch, E for beech, L for lime, O for oak, and P for pine), two-species mixtures, three-species mixtures, and four-species mixtures. Each panel shows the mean vertical PAVD profiles as a function of canopy height, combining TLS data from four scan locations in each plot. Stand structural variables, including total PAI, CH, FHD, and cvpad, are displayed in the top right of each panel. The maxpad value is highlighted in red, aligned with the blue dashed line indicating height_maxpad.

Table 1

Summary of stand structural variables with explanations of their significance.

Symbol	Description	Unit
total PAI	Total plant area index represents total amount of plant materials, reflecting the stand productivity.	$m^2 \cdot m^{-2}$
CH	Canopy height of a stand reflects vertical development of species under various tree compositions.	m
maxpad	The maximum density of PAVD profiles indicates the amount of plant materials at leaf aggregation area.	m^{-1}
height_maxpad	The height at the maximum density of PAVD profiles, which represents the height at which plant material is most densely aggregated (leaf aggregation area).	m
cvpad	Coefficient of variation for PAVD represents vertical distribution of plant materials. Smaller cvpad stands for a more uniform vertical distribution.	
FHD	Foliage height diversity represents vertical structural diversity of plant material. A vertically simple profile will receive a low FHD value.	

Table 2

The linear regression coefficient of species richness models in three sites. Significant levels are shown with *, ** and *** indicating a significance of <0.05, <0.01 and <0.001 respectively.

	Zedelgem	Hechtel-Eksel	Gedinne
total PAI ($m^2 \cdot m^{-2}$)	0.17	−0.11	0.34
CH (m)	0.77*	0.41*	1.00***
FHD	0.14**	0.07*	0.20**
cvpad	−0.01	0.0009	0.04
maxpad (m^{-1})	−0.11	−0.10	−0.03
height_maxpad (m)	−0.07	−0.04	−0.13

terrestrial scanner (RIEGL Laser Measurement Systems GmbH, Horn, Austria) with the same scanner settings. The scanner has a beam divergence of 0.35 mrad and operates in the infrared (wavelength 1,550 nm) with a scanning range up to 350 m. The pulse repetition rate at each scan location was 300 kHz, with a minimum range of 0.5 m and an angular

sampling resolution of 0.04°. The scanner was mounted on a tripod at a height of approximately 1 m above the ground. Six retro-reflective targets were used to co-register the upright and tilted (90°) scans, capturing full zenith range point cloud data at each scan location (Calders et al., 2015). For each location, with the scan location as the center, point clouds that point out of the plot are not included for post-processing. Further details on TLS setup and post-processing can be found in Fig. S2 and Wang et al. (2024).

Following the method described by Calders et al. (2014), the topographic effect was corrected using a local plane fit method. Vertical profiles of plant area per volume density (m$^2 \cdot$m^{-3}) (PAVD) as a function of canopy height (0.5 m height bin) were created for each scan position from the topographic corrected point cloud and an azimuth range that point to interior of each plot. The zenith angle 5°–70° in 5° zenith bins was used to avoid high variance zenith range 0°–5° in creating vertical profiles for each scan position within a plot (Jupp et al., 2009). Subsequently, the average of these four individual profiles was employed to represent the stand profile. PAVD profiles were processed in Python using the Pylidar library (https://github.com/armstonj/pylidar-tls-canopy) and further details regarding the algorithm can be found in Calders et al. (2015).

In this study, we are mainly interested in vertical forest structure measured by TLS, this is a structural aspect that is hardly covered in studies that use traditional inventories. The TLS derived vertical profiles of plant materials (PAVD) is a key parameter to describe vertical forest structure, six vertical forest structural variables were extracted in R software (R Core Team, 2022) based on PAVD profiles. One variable, plant area index (total PAI) represents the one-sided area of the woody (e.g. branches and stems) and non-woody plant elements (i.e. leaves) per unit of surface area, defining the total amount of plant material of a stand. Five additional variables were calculated as proxies for vertical distribution of plant materials. The canopy height (CH) was defined as the height at which 99% PAVD were cumulated, the 1% PAVD was ignored to remove atmospheric noise (Meeussen et al., 2020). The maximum density of PAVD profiles (maxpad) and its height (height_maxpad) were derived, indicating the specific location where the plant material is concentrated and the amount of plant material in this location (Meeussen et al., 2020). Additionally, foliage height diversity (FHD) and the coefficient of variation for PAVD (cvpad) were calculated to quantify the vertical heterogeneity in plant material along the profile, using PAVD values between 1.5 m height and the canopy top height. FHD was calculated as the Shannon-Wiener index for diversity:

$$\text{FHD} = -\sum\nolimits_{1.5}^{i} p_i \times \log p_i \tag{1}$$

with p_i representing the proportion of plant material in the i_{th} 0.5 m vertical layer. A vertically higher diverse canopy will receive higher FHD value.

cvpad were used to indicate the measure of vertical dispersion of the density of plant materials through the canopy, it was calculated as the coefficient of variation for PAVD values between 1.5 m height and the canopy top height:

$$\text{cvpad} = \frac{\sigma_{\text{PAVD}}}{\mu_{\text{PAVD}}} \tag{2}$$

A lower cvpad value indicates a more even distribution of plant material along the height profile, while a higher cvpad value signifies the concentration of plant material within a specific height layer. The PAVD profiles in Fig. 3, Figs. S1 and S2 provided a comprehensive overview of how these six structural variables perform across diverse tree species compositions at each site.

2.3. Statistical analysis

The one-way ANOVA analysis was employed to demonstrate the statistical differences among sites. To investigate the impact of species richness on vertical forest structure, a linear mixed models was performed, incorporating the block as a random effect for the intercept (similarly for subsequent models).

$$Y = \alpha \text{SR} + b_k + \varepsilon \tag{3}$$

The response variable Y represents a structural variable, the coefficient α is the species richness effect. b_k is the random intercept term for each block, with $k = 1, 2$, indicating the index for the block, ε is the error term.

We then used the diversity interaction modelling framework (Kirwan et al., 2009) to investigate species identity and species interaction effects contributing to forest structural variables across the mixtures. For each structural variable, we compared models based on the different ecological assumptions to better understand what diversity effect drives variation in forest structural variables in the mixtures (Kirwan et al., 2009).

The null model is the simplest model. It assumes all species identity effects are equal and no interspecific interactions occur. Considering that the initial overall abundance of our plots is equal within each site, b_k in this context represents the overall performance of a structural variable for each block.

$$Y = b_k + \varepsilon \tag{4}$$

The identity model describes species identity effect alone without species interaction:

$$Y = \sum_{i=1}^{5} \beta_i \text{SI}_i + b_k + \varepsilon \tag{5}$$

SI$_i$ is species' relative abundances, namely the initial proportion of species i in the stand. For example, for a monoculture of species i, SI$_i = 1$. In mixed stands, this performance was weighted by initial proportions of each species. In our case, the proportion of each tree species is the same, thus in a two-species mixture, the initial proportion of both species is 50%, SI$_i = 0.5$. The coefficient β_i is the identity effect, i.e. expressing the performance of species i in monoculture

The evenness model describes an average interspecific interaction for all pairwise species combinations:

$$Y = \sum_{i=1}^{5} \beta_i \text{SI}_i + \delta_{\text{AV}} \sum_{i,j=1;\ i<j}^{5} \text{SI}_i \text{SI}_j + b_k + \varepsilon \tag{6}$$

δ_{AV} is the single interaction coefficient that represents equal interspecific interaction for all pairwise species. The SI$_i$ and SI$_j$ are the relative abundances of the two species as explained above.

The additive model describes the case where a species makes an equal contribution to stand structure when it interacts with any other species:

$$Y = \sum_{i=1}^{5} \beta_i \text{SI}_i + \sum_{i,j=1;\ i<j}^{5} (\gamma_i + \gamma_j) \text{SI}_i \text{SI}_j + b_k + \varepsilon \tag{7}$$

The coefficient γ_i or γ_j is the contribution that species i or j makes when interacting with any other species.

The pairwise model describes interspecific interactions between pairs of species:

$$Y = \sum_{i=1}^{5} \beta_i \text{SI}_i + \sum_{i,j=1;\ i<j}^{5} \delta_{ij} \text{SI}_i \text{SI}_j + b_k + \varepsilon \tag{8}$$

The coefficient δ_{ij} measures the strength of interspecific interaction between species i and j, and the sign of δ_{ij} indicates whether the relationship is positive, negative, or zero, the contribution of the interaction between species i and j to the stand structure is $\delta_{ij}\text{SI}_i\text{SI}_j$ (Kirwan et al., 2009). More details about diversity interaction modelling can be found in Kirwan et al. (2009).

Table 3

Coefficients of optimal fit models for six structural variables at three sites. Significant or semi-significant parameter estimates are shown with +, *, ** and ***, indicating a significance of <0.1, <0.05, <0.01 and <0.001 respectively. The species identity effect was always significant and was included in the table to allow interpreting of the contribution magnitude and sign of different species identity effects. E represents the evenness effect, "species_add" denotes the additive effect of specific species, the term "species × species" refers to the interaction effect between pairs of species. The term "SD (Intercept Block_ID)" represents the standard deviation of the random effect. The significant or semi-significant species interaction effects were highlighted in bold.

Sites	Zedelgem						Hechtel−Eksel
Structural variables	total PAI	CH	FHD	cvpad	maxpad	height_maxpad	total PAI
Optimal models	identity	additive	pairwise	additive	additive	identity	pairwise
Birch	5.894***	11.520***	2.674***	0.905***	1.542***	8.967***	5.491***
Beech	3.672***	4.074***	1.832***	0.448***	1.106***	2.112***	
Pine	6.078***	7.449***	2.450***	0.533***	1.831***	4.821***	5.419***
Oak	5.919***	6.857***	2.343***	0.509***	1.701***	4.260***	0.780*
Lime	5.704***	4.644***	1.890***	0.506***	2.828***	2.523***	
Douglas							3.933***
Larch							1.998***
Maple							
E							
Birch_add		**7.858***		−0.831***	−2.948***		
Beech_add		**3.397+		0.222	1.038		
Pine_add		−1.253		0.272	0.659		
Oak_add		0.650		−0.269	0.103		
Lime_add		2.142		0.075	**−1.269+		
Douglas_add							
Larch_add							
Maple_add							
Birch × Beech			**3.102***				
Birch × Pine			**1.014*				0.621
Birch × Oak			**1.515***				1.308
Birch × Lime			**2.529**				
Beech × Pine			0.519				
Beech × Oak			**0.918*				
Beech × Lime			0.095				
Pine × Oak			−0.675				**5.089**
Pine × Lime			0.185				
Oak × Lime			1.242				
Birch × Douglas							**−10.37**
Birch × Larch							0.276
Douglas × Pine							0.833
Douglas × Oak							−1.354
Douglas × Larch							**3.423+
Pine × Larch							−1.677
Oak × Larch							−3.437
Beech × Douglas							
Beech × Maple							
Beech × Larch							
Douglas × Maple							
Maple × Oak							
Maple × Larch							
SD (Intercept Block_ID)	0.190	0.472	0.084	0.000	0.000	0.388	0.000

+$p < 0.1$, *$p < 0.05$, **$p < 0.01$, ***$p < 0.001$.

We followed the hierarchy of diversity interaction models described above to test biological hypotheses about how species identity and interaction effects affect stand structural variables. The Akaike information criterion (AIC) was employed to assess the goodness of fit of all models. A superior model is characterized by a lower AIC value. Note that for the difference in AIC < 2 units, we choose the simpler model. That means there's not a strong discrimination between certain models. We ran models separately for data from the three sites, due to the difference in species pools and abiotic conditions. Our statistical analysis of species richness models and hierarchical diversity interaction models was performed using linear regression models from the "lme4" package, all statistical analyses were conducted in R version 4.2.2 (Bates et al., 2015).

3. Results

3.1. General results gained from TLS vertical profiles

Mean values of all studied structural variables at each of the experimental sites can be found in Fig. 1.

Notably, all six structural variables exhibited statistically significant differences among sites (Fig. 1, Table S2). The total PAI was significantly higher in average in Zedelgem than the other two sites (56.7% higher than Hechtel-Eksel and 43.3% higher than Gedinne), the difference in mean total PAI among sites can be found in the overview map (Fig. 2). The variation in mean total PAI can also be found within site, with Zedelgem site has a range of 0.13–6.38 $m^2 \cdot m^{-2}$, Hechtel-Eksel site has a range of 0.51–5.73 $m^2 \cdot m^{-2}$, and Gedinne site has a range of 0–6.35 $m^2 \cdot m^{-2}$. Structural variables showing vertical distribution of plant materials were also found higher in Zedelgem, despite a slightly lower value for cvpad was found in Zedelgem which also showed higher vertical heterogeneity.

The PAVD profiles revealed distinct vertical plant material distributions among all distinct monocultures at the Zedelgem site (Fig. 3). Birch stood out with a notable concentration of plant material around 10 m, whereas other tree species concentrated their plant materials within the 2.5–5 m height range. Despite birch having a relatively lower maxpad compared to most other shorter tree species, its total PAI remained slightly higher due to the wider distribution of its plant material. Birch

Hechtel−Eksel					Gedinne					
CH additive	FHD pairwise	cvpad pairwise	maxpad additive	height_maxpad identity	total PAI evenness	CH additive	FHD additive	cvpad identity	maxpad identity	height_maxpad pairwise
8.784***	2.519***	0.673***	1.550***	5.417***						
					2.852**	4.142***	1.766***	0.610***	1.508***	1.912***
5.360***	2.010***	0.541***	2.412***	2.769***						
3.353***	1.557***	0.695***	0.560**	1.341***	3.803***	5.639***	2.146***	0.613***	1.403***	2.540***
5.328***	2.054***	0.554***	1.733***	1.788***	3.376**	6.732***	2.210***	0.906***	1.317***	1.799**
5.300***	2.027***	0.732***	0.983***	1.684***	6.394***	9.814***	2.745***	0.501***	1.125***	6.336***
					1.106	2.562**	1.066***	0.388***	0.438	1.244*
3.253**			−1.922***		0.685+					
						1.011	0.212			
0.251			−0.032							
3.825**			0.443			−0.659	−0.162			
0.839			−0.862*			−0.549	−0.134			
0.308			0.069			8.517***	1.400**			
						6.635***	2.076***			
	1.219*	−0.766								
	2.055***	−0.900**								
										−0.831
	1.381***	−0.090								
	0.593	0.144								
	1.092***	−0.808**								
	0.125	0.097								
	0.129	0.955								0.030
	1.000**	−0.414								0.817
	−0.854	0.434								
	0.671	−0.037								−2.562
										−3.327
										4.349*
										−7.253+
										3.838*
										1.000
										−8.695*
0.272	0.056	0.000	0.063	0.000	1.209	0.470	0.144	0.073	0.280	0.550

was primarily distributed in the 5–15 m range, while beech and larch occupied the 0–5 m range, and oak and pine spanned the 0–7 m range.

Tree species richness and composition have generally altered the vertical forest structure (Fig. 3). In two-species mixtures, when shorter tree species were paired, the plant material still concentrated within the 2.5–5 m height range. However, when birch was combined with shorter tree species, the peak of plant material shifted to around 7.5 m, approximately equal to the average height_maxpad of the two tree species in their monocultures. Moreover, the maxpad value was lower than that of any tree species in their monocultures. Nevertheless, due to the expanded vegetation distribution range of 0–15 m, their total plant area index increased rather than decreased. Three-species and four-species mixtures exhibited more complex variations, intuitively characterized by some plant profiles displaying two or more peaks. It is worth noting that plots with the lowest three maxpad values all occurred in mixtures without pine (BOL, BEL, and BEOL), and these three stands demonstrated a relatively uniform vertical vegetation distribution. This was reflected in their smaller cvpad values compared to other three-species and four-species mixtures.

Similar figures for Hechtel-Eksel and Gedinne sites can be found in Figs. S3 and S4. In Hechtel-Eksel, despite birch, douglas and pine had a relatively higher total PAI, larch and oak both had very low total PAI. The highest total PAI occurred in birch and pine monocultures, as opposed to two, three, or four-species mixtures (Fig. S3). Birch showed lower canopy height and vegetation concentration height than that observed in Zedelgem. Furthermore, the height_maxpad for all mixtures at this site was notably lower than in Zedelgem, with most of them concentrated on around 2.5 m (Fig. 3 and Fig. S3). In Gedinne, larch demonstrated superior performance in terms of total PAI (6.35 $m^2 \cdot m^{-2}$) and canopy height (10 m). In contrast, pure maple failed to thrive in Gribelle, as evidenced by having no plant material (Fig. S4). The maple monoculture in Gouverneur, however, displayed greater success, featuring a 5 m canopy height and a total PAI value of 2.5 $m^2 \cdot m^{-2}$. Two-species mixtures involving larch planted in the plot exhibited approximately twice the canopy height and total PAI than other two-species mixtures. Three and four-species mixtures in Gedinne had their plant material concentrated on around 2.5 m, which was consistent with the observations at the Hechtel-Eksel site (Figs. S3 and S4) (see Table 1).

3.2. The influence of species richness and species composition on vertical forest structure

While at the three sites, we observed significant variations in CH and FHD with species richness, species richness did not significantly impact the other structural variables (Table 2). Attributing the effects of tree species identity and interaction on vertical forest structural variables also showed differences among metrics (Table 3). Specifically, total PAI and height_maxpad in Zedelgem, height_maxpad in Hechtel-Eksel, and cvpad and maxpad in Gedinne were only influenced by species identity, i.e., the values found in mixtures could be predicted from the component species' monocultures in the absence of an interaction effect. The other structural variables in these three sites were influenced by various interaction effects (evenness, additive, or pairwise effects), in addition to species identity. A more comprehensive result of species identity and interaction effect in each site can be found in Table 3 and Table S3.

The contribution of species identity was strongly significant for almost all structural variables in all three sites, with the exception of maple's presence having no strong impact on total PAI and maxpad in Gedinne (Table 3).

The effects of species interactions on vertical forest structure were found to depend both on site and species pools, the direction and magnitude of interaction effects were specified in Table 3. For example, for the total amount of stand plant material (total PAI), a positive evenness interaction effect was found across all pairwise species combinations in Gedinne. In Hechtel-Eksel, a negative pairwise interaction was observed between birch and douglas, while a positive interaction was found between pine and oak. More details concerning diverse interaction effects on variables related to vertical distribution can be found in Table 3.

4. Discussion

Various species compositions have the potential to shape different vertical forest structure via interspecific interactions. Vertical plant profiles derived from TLS scans provided an intuitive presentation of the difference in vertical forest structure across species and the species combinations where are planted. Diversity interaction modelling further explained the relative importance of species identity and interaction in shaping vertical forest structure. Our findings indicated that species interaction effects influenced vertical forest structure and that the vertical structure is more dependent on the particular species planted in the mixtures than the tree species richness. This is based on the finding that (1) species richness had minimal explanatory power for the variation observed in forest structure; (2) species identity exerted a statistically clear influence on forest structure at the three sites; and (3) species interaction effects on forest structure were observed and shown as pairwise interaction effect, or simplified evenness, additive interaction effects. Notably, some instances of such interactions demonstrated synergistic effects, in which species interactions led to values in forest structural variables that were higher than one would expect based on the monoculture performance of the component species, while others exhibited antagonistic effects, resulting in lower-than-expected values in structural variables.

Silviculture plans are increasingly tasked with prioritizing a diverse and heterogeneous forest structure, to achieve long-term environmental resilience and forest productivity. Several studies have demonstrated that higher species richness levels lead to multilayered forest, which further exhibits greater environmental resilience compared to monocultures (Con et al., 2013; Perles-Garcia et al., 2021). For instance, Perles-Garcia et al. (2021) demonstrated that tree species richness facilitates an early increase in stand structural diversity in an experimental plantation (BEF-China) with a broad gradient of tree species richness (1–24 species) (Bruelheide et al., 2014). In our study, we observed a significant difference in vertical structural diversity (canopy height and foliage height diversity) with species richness across three sites. However, we also

observed conflicting results regarding foliage height diversity for specific tree compositions. Specifically, in Zedelgem, a four-species mixture comprising beech, pine, oak, and lime (i.e., EPOL) did not show greater vertical diversity, in terms of foliage height diversity, compared to certain monocultures, two- or three-species mixtures (e.g., P; PL; POL). Furthermore, no significant difference was observed for the other four structural variables, as illustrated in Table 2. These results provided evidence that species richness alone is not enough to explain and steer variation in multiple aspects of vertical forest structure (Lelli et al., 2019). For example, the total PAI in birch monoculture in Zedelgem exhibited a higher value than some three and four species mixtures (e.g., BEL, BEOL). Conversely, at the BEF-China site, Huang et al. (2018) highlighted the positive relationship between species richness and forest productivity. These inconsistencies in both vertical structural diversity and forest productivity with earlier literature could be because our experiment only considers a tree species diversity gradient of 1–4 tree species, thus the potential impact of tree species richness on stand structure may not be well represented. Additionally, our studied forest is still in an immature state and it can be anticipated that species-specific differences in growth rates will increasingly cause vertical stratification in mixtures when it develops further. Another possible explanation could be, functional diversity, i.e., a larger range of functional trait expressions, may play a more important role than species richness in shaping the vertical structure of the forest (Lelli et al., 2019; Lian et al., 2022).

In majority of cases, interspecific interactions were detected among functional groups in mixtures, mostly dominated by pioneer species with higher growth rates. In Zedelgem, the interaction of birch with shorter species was found to promote a more diversified vertical forest structure, as indicated by a positive interaction on canopy height and foliage height diversity, but a negative effect on cvpad. Birch trees, characterized by their rapid growth and a canopy height exceeding twice that of the other four tree species (Fig. 3), exhibited a complementary relationship with the leaf aggregation areas of the other species, leading to a more uniform vertical distribution of plant material (smaller cvpad) and a higher canopy with efficiently used vertical space. In Hechtel-Eksel, birch also dominated interaction effects on vertical structure, while a significant negative interaction was found between birch and douglas affecting total PAI. This is attributed to birch being a light-demanding tree species, and the strong shade casting ability of douglas potentially reducing the growth of birch. Considering to reach higher stand productivity, it is not recommended to plant these two species together in a single plot under similar site conditions. Instead, another pioneer tree species pine interacts positively with oak in terms of stand productivity at this site (Table 3). Despite pine having less space below the plant concentration height (lower height_maxpad) than a birch stand (Fig. S3), the relatively higher shade tolerance of oak enables successful growth when mixed with pine. Pioneer larch trees did not thrive in Hechtel-Eksel site but exhibited great performance in Gedinne, where they dominated the interaction effects on vertical structure. This is evidenced by positive interaction effects with all other shorter species on both stand productivity and vertical plant material distribution (Table 3). Overall, mixing pioneer fast-growing species with higher shade tolerance species could contribute to the overall stand productivity and the vertical forest structure via interspecific interactions (Bravo-Oviedo et al., 2018; Pretzsch et al., 2019).

Site differences also need to be taken into consideration when explaining the variations in species interaction effects (Forrester et al., 2013; Mina et al., 2018). Overall, these variations in species interactions across sites can be attributed to differences in the species pools used for plantation. While there was some overlap in the selected tree species across the three sites, they were not identical. In the meanwhile, the sites are not the same age, Hechtel-Eksel is about two years younger, which will have an influence on how strong vertical structure could already develop in this site. For example, at the Zedelgem site, the presence of birch species played a dominant role, leading to various interaction effects including pairwise, additive, and evenness effects. In the

Hechtel-Eksel sites, although birch also interacts with other species, it did not exhibit clear dominance. Instead, the interaction effects were more evenly distributed among all tree species. This result with birch was primarily due to its higher growth at Zedelgem site relative to Hechtel-Eksel, potentially linked to differences in stand age between the two sites. Moreover, certain species may not have acclimated well to different sites due to varying environmental conditions. For example, the interactions between pine and oak significantly improved total plant materials in Hechtel-Eksel but not in Zedelgem, possibly due to the specific soil conditions (the dry sandy soil with a gravel substrate) in Hechtel-Eksel favoring pine growth and its interaction with other species (Kuznetsova et al., 2010). In Gedinne, despite the very limited growth of maple monoculture in one of the two blocks (Gribelle), it had mostly synergistic interactions with other species. For example, maple was paired with any other species would get a higher canopy, and a more heterogeneous vertical structure (Fig. S4, Table 3). This suggests that even if a tree species does not perform well in monoculture settings, it has the chance to enhance the vertical forest structure through interactions with other species in mixtures, and such interactions do not always lead to antagonistic effects. Overall, the divergent performance of tree species under different site conditions contributes to variations in complementarity effects, which are influenced by composition of the species pools, stand age, as well as the environmental conditions (Tilman et al., 1997; Ouyang et al., 2019).

Our study conducted a quantitative analysis of the effects of species identity and interaction on TLS derived vertical forest structure in young planted forests for the first time. Vertical profiles and structural variables obtained from TLS data provided new insights for forest management on how to mix tree species to achieve strong productivity (total PAI) and more complex vertical structure. For instance, in the case of Zedelgem, the mixing of birch, oak, pine, and lime resulted in a notably higher total PAI, as depicted in Fig. 2. This suggests that for afforestation plans in Zedelgem aiming to maximize the total plant material, these four species may be suitable candidates for planting together. And the combination of birch, oak, and lime has the potential to yield a more intricate vertical structure at this site. To achieve a balance between robust productivity (total PAI) and vertical structure development in Zedelgem, the combination of birch and pine stood out as a favorable choice (Fig. 2). In Hechtel-Eksel, pine had the highest total amount plant material. Considering both aspects, total amount of plant material and vertical structure development, the mixing of birch, pine, and maple was a good consideration (Fig. S3). Although birch and pine combination was not incorporated into the experiment design at this site, we assume that their coexistence has a great chance to form a diverse vertical structure and stronger productivity, given their notable individual performance in monocultures. In Gedinne, larch exhibited the highest total amount of plant material. Considering both aspects, the combination of larch, beech, and douglas represents a promising option (Fig. S4).

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Data availability

The data that support the findings of this study will be openly available in figshare

CRediT authorship contribution statement

Mengxi Wang: Writing – review & editing, Writing – original draft, Investigation, Funding acquisition, Data curation. **Lander Baeten:** Writing – review & editing, Resources, Methodology, Formal analysis, Conceptualization. **Frieke Van Coillie:** Writing – review & editing, Supervision, Formal analysis. **Kim Calders:** Writing – review & editing, Supervision, Methodology, Formal analysis. **Kris Verheyen:** Writing – review & editing, Data curation. **Quentin Ponette:** Writing – review & editing, Data curation. **Haben Blondeel:** Writing – review & editing, Data curation. **Bart Muys:** Writing – review & editing, Data curation. **John Armston:** Software. **Hans Verbeeck:** Writing – review & editing, Supervision, Conceptualization.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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Appendix A. Supplementary data

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