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# Exploring the influence of tree species richness on vertical structure variability in young plantations using terrestrial laser scanning

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#### ABSTRACT

Forest structure spatially varies at the landscape-scale (between-plot) but also local-scale (within-plot). Both scales of structural variability have significant impacts on forest ecosystem functioning and stability. However, we still have a limited understanding of how tree species richness affects the spatial structural variability. In this study, we disentangled within- and between-plot variability in stand structural variables depending on tree species richness level. Terrestrial laser scanning (TLS) technology, capable of developing forest vertical structure in 3D detail, was applied in the FORBIO tree diversity experiment at three sites in Belgium. One site was 9-year old (Hechtel-Eksel) and other two sites were 11-year old (Zedelgem and Gedinne). Each site included five different sets of one, two, three, and four tree species mixtures with one replica. At each plot, four single scan locations were used. Six stand structural variables were quantified based on TLS vertical plant profiles. We hypothesized that within-plot structural variability would increase with species richness, but that the betweenplot structural variability would decrease with species richness. Our study revealed notable differences in structural variability between monocultures and mixtures across all sites examined. However, the relationship between tree species richness and structural variability patterns is site-dependent. Specifically, at the Zedelgem site, we observed increased within-plot variability and decreased between-plot variability with species richness, supporting the hypothesis that species richness drives stand structural variability. However, the hypothesized pattern was not as strong at the Hechtel-Eksel and Gedinne sites. Moreover, the various structural variables displayed contrasting responses to changes in species richness. These findings indicated the potential influence of tree species richness on within- and between-plot structural variability in young plantations, particularly in favorable site conditions with well-adapted species pools. Hence, afforestation measures would benefit from planting multiple tree species to initiate structurally complex stands by considering species richness level.

#### 1. Introduction

Forest plantations are expanding rapidly around the world, fulfilling a crucial function of supplying wood products, indirectly contributing to protection of natural forests (Paquette and Messier, 2010; Verheyen et al., 2016). In practice, the majority of the forest plantations are established as monocultures, which are increasingly vulnerable to global-change related disturbances (Kelty, 2006; Liu et al., 2018; Messier et al., 2022). This has led to a rising focus on mixed-species plantations, which are argued to be more resilient and able to withstand abiotic and biotic disturbances (Verheyen et al., 2016; Messier et al., 2022).

Mixed-species plantations are expected to have a more diverse canopy structure compared to monocultures, because of stronger crown complementarity (Pretzsch, 2014; Perles-Garcia et al., 2021). Crown complementarity is a mechanism related to light interception and transmittance, which closely links to ecosystem productivity and canopy space-filling (Pretzsch, 2014; Williams et al., 2017; Schmid and Niklaus,

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2017). Even though trees can grow leaves in multiple canopy layers in monoculture stands, they may potentially suffer from competition as individuals of the same species occupy the same spatial niches. In contrast, in mixed-species stands, leaves from different tree species have the potential to occupy different canopy levels, thereby increasing the probability of forming a denser canopy than monocultures (Sercu et al., 2017). For example, shade-tolerant tree species can fill lower canopy layers, whereas some fast-growing tree species benefit most from strong light and populate the upper canopy layers (Schmid and Niklaus, 2017). Consequently, these differences in the light interception of different tree species enhance canopy space-use efficiency and, thus, a more complex stand structural diversity in mixed-species stands (Pretzsch, 2014; Riofrío et al., 2017).

Despite some research highlighting that species richness promotes stand structural diversity (Wacker et al., 2009; Perles-Garcia et al., 2021), little research has been conducted on how species richness affects the variability in structure within and between plantations. In general, the within-plot variability may refer to local-scale variability, while the between-plot variability may refer to landscape-scale variability (Zellweger et al., 2013). Here, we focus on the impact of tree species richness on stand structure variability and attempt to bridge the gap in how species diversity affects stand structure at both scales. Since tree species naturally differ in canopy structure and productivity, monocultures of different species are expected to exhibit larger between-plantation variability than mixed-species plantations. Within monoculture plantations, trees of the same species form similar canopies so that structure is expected to be homogeneous. In mixtures, tree species with different canopy structures co-occur, rather resulting in larger within-plot variability. With increasing species richness, the average stand structure becomes more similar across different species compositions. This should then result in smaller between-plot variability when compared to monocultures of different species. Both the within-plot and between-plot structural variability hold significant ecological and management implications. For example, higher within-plot structural variability is likely to offer a greater number of niches for local species. However, at the landscape level, forests with diverse structural types (exhibiting higher between-plot variability) are required to accommodate the entire range of species.

The vertical distribution of plant material (e.g. leaves, twigs, branches etc.) is crucial for characterizing canopy structure and understanding its impact on habitat use, microclimate, and growth. Vertical plant profiles can be estimated by calculating the vertically resolved gap fraction and describing the vertical distribution of plant area volume diversity (PAVD) as a function of height (Calders et al., 2014). These plant profiles can be used to derive various forest structural metrics. Metrics such as total plant area index (total PAI) and canopy height (CH) facilitate the monitoring of aboveground biomass; whereas metrics like foliage height density (FHD) and height of maximum PAVD provide information on structural diversity and the vertical distribution of plant materials (Jupp et al., 2009; Calders et al., 2014; Calders et al., 2015; Meeussen et al., 2020). Terrestrial laser scanning (TLS) technology is a non-destructive and time-efficient technique to observe 3D structure of forest stands in detail at high spatial resolution, which offers the possibility to collect highly detailed measurements of the vertical distribution of plant area (Calders et al., 2014). Calders et al. (2014) developed a rapid and robust automated method for creating vertical profiles of vegetation using single scans from TLS, which offers an objective view of the entire stand and is less time-consuming than traditional measurements for monitoring forest structural diversity (Calders et al., 2014), such as basal area and tree size differentiation (Drössler et al., 2014; Keren et al., 2020). Satellite remote sensing, such as The Global Ecosystem Dynamics Investigation (GEDI), is capable of providing information of vertical forest profiles at a global scale (Schneider et al., 2020). However, it lacks the detailed consideration of 3D stand structures that can be achieved by TLS. TLS approach has the potential to significantly advance our understanding of forest structure and ecosystem functioning.

In this study, we used TLS to quantify the stand structural variation within and between the plots of a tree species diversity experiment in Belgium (FORBIO), established between 2009 and 2012 (Verheyen et al., 2013; treedivnet.ugent.be). Our primary objective was to investigate the effect of species richness on the within- and between-plot structural variability pattern. We anticipate to find within-plot variability to increase with tree species richness due to inherent variation in species-specific canopy form and crown plasticity resulting from interspecific interaction, i.e. leading to crown complementary. However, a high species richness is likely to share a similar mean in structural variables among species compositions, thereby a decrease in between-plot variability with tree species richness was expected.

# 2. Materials and methods

# 2.1. Study area

The study was conducted in a tree species diversity experiment in Belgium (FORBIO, FORest BIOdiversity and Ecosystem Functioning; Verheyen et al., 2013), which is part of the extensive network of biodiversity experiments worldwide, the TreeDivNet network (Verheyen et al., 2016). The FORBIO experiment is a multi-site experiment that replicates its design across three sites with contrasting site conditions. The general characteristics of the three FORBIO sites can be found in Table S1. The Zedelgem site can be considered to have the most favorable climatic and soil conditions, while the soil fertility and water availability are most limiting at Hechtel-Eksel, and the climatic conditions are less favorable at Gedinne. Gedinne consists of one block in Gribelle and one block in Gouverneurs.

The experimental design of the three sites is similar and follows a classical synthetic community approach (Nock et al., 2017). A pool of five site-adapted and functionally dissimilar tree species, as indicated in Table S1, was forested at each site, which was used to create a diversity gradient from monocultures up to four-species mixtures. A total of twenty treatments were established per site: all five monocultures, all five possible four-species mixtures, and a random selection of five twoand five three-species combinations with the condition that species were equally represented across all plots. Two replicates of each treatment were assigned to a different block with a slight difference in land-use history and soil type, which resulted in  $20 \times 2 = 40$  plots per site. An extra subtreatment was added at the Zedelgem and Gedinne sites, using one versus three provenances of oak (Zedelgem) and beech (Gedinne) in the first and second replicate of twenty plots, respectively. These extra plots were included in our analysis, with the different provenances considered as the same species. Therefore, two additional monocultures with the extra provenances were added in Zedelgem and four in Gedinne (two in Gribelle and two in Gouverneurs), resulting in 126 plots in total. Each plot is 42 by 42 m in size in Zedelgem, 36 by 36 m in Hechtel-Eksel, and 36 by 42 m in Gedinne, with all three sites planted on a 1.5 by 1.5 m grid (Table S1). Additional details can be found in Table S1 and Verheyen et al. (2013).

#### 2.2. Terrestrial laser scanning

From June to August 2020, TLS data were acquired with a RIEGL VZ-400 instrument (RIEGL Laser Measurement Systems GmbH, Horn, Austria) to map the three-dimensional structure of each FORBIO plot. This time-of-flight scanner has a beam divergence of nominally 0.35 mrad and operates in the infrared (wavelength 1550 nm) with a range up to 350 m. The pulse repetition rate at each scan location was 300 kHz, the minimum range was 0.5 m and the angular sampling resolution was  $0.04^{\circ}$ . A single-scan position TLS method was carried out in this study. At each plot, four single scan locations were used. The scanner was mounted on a tripod (around 1 m above the ground) and six retroreflective targets were used to merge the upright and tilted (90 degrees) scan at each scan location (Calders et al., 2015).

To get a full hemispherical 3D dataset at each scan location, the upright and tilted scans at each location were co-registered by making use of the six reflectors and the calculated transformation matrices. Since most of the scanning positions were around 10 m away from the plot edge (Fig. 1), the point cloud data likely included some vegetation components outside the plot range, which do not represent the forest structure of the plot. Therefore, these lidar points from outside the plot of interest were clipped to keep only the azimuth range pointing to the interior of the stand (Fig. 1), and this azimuth range was recognized and recorded by plotting the clipped point cloud.

Following the method described by Calders et al. (2014), a local plane fit was performed to correct for topographic effects and the azimuth range (Fig. 1) was used to limit minimum and maximum azimuth. Vertical plant profiles quantify the vertical structure of vegetation material from the forest floor to the top of the canopy and are often used to illustrate the horizontally averaged plant structure (Calders et al., 2014). Vertical profiles of plant area per volume density  $(m^2 m^{-3})$  (PAVD) as a function of canopy height were created for each scan position from the topographic corrected point cloud and a limited azimuth range. Profiles were calculated from the average percentage of gap fraction across the zenith angle  $5-70^{\circ}$  in  $5^{\circ}$  zenith bins, with  $35-70^{\circ}$  from upright scans and a supplementary  $5-35^{\circ}$  from tilted scans. Zenith bin  $0-5^{\circ}$  was not included in creating the profiles because there is high variance with large gaps near the zero zenith angle (Jupp et al., 2009). A fully described calculation of the vertical plant profiles is explained in Calders et al. (2014) and vertical plant profiles were calculated in Python using the Pylidar library (http://www.pylidar.org/).

# 2.3. Stand structural variables

Based on the vertical plant profiles outputs from Pylidar, six forest structural variables (Table 1) were summarized using the R version 4.2.2 (R Core Team, 2022). Firstly, two structural variables that could serve as proxies for aboveground biomass were extracted (biomass variables). Total plant area index (total PAI), which is defined as the total area of woody (e.g. branches and stems) and non-woody plant elements (i.e. leaves) per unit of surface area, was extracted for each location as the integral of the PAVD over the canopy height. The total PAI reflects the average aboveground biomass of a stand, an open forest or a recently

Tab	le 1	

List	of	all	stand	struct	tural	varia	oles

Group	Symbol	Description	Unit
Biomass variables	total PAI	Total plant area index reflects the average aboveground biomass of a stand	${m^2 \over m^{-2}}$
	CH	Canopy height of a stand	m
Vertical distribution	maxpad	The maximum density of PAVD profiles	$\mathrm{m}^{-1}$
variables	height_maxpad	The height at the maximum density of PAVD profiles, which represents the height at which plant material is most densely aggregated	m
	cvpad	coefficient of variation for PAVD represents vertical variation in plant materials	
	FHD	foliage height diversity represents vertical structural diversity of plant material	



Fig. 1. TLS plot setups used in FORBIO's experimental forest plantations, featuring four levels of species richness ranging from monocultures to four-species mixtures. The small grids within the plot represent individual trees, with varying filled-in colors representing different tree species. The scans were performed at the center of four representative subplots (depicted by the white stars in the square subplots). In the top left and bottom right panel, the angle between two black solid lines indicates the selected azimuth range.

thinned forest will receive a relatively lower total PAI while it will increase with increasing plant material of the forest. Canopy top height (CH) was generated based on the 99% PAVD-percentile to remove a limited number of returns from the atmosphere (Meeussen et al., 2020). The amount of plant material and aboveground biomass are positively related to the canopy height (Fotis et al., 2018). Secondly, a group of structural variables was extracted to represent the vertical distribution of aboveground biomass (vertical distribution variables). The maximum density of PAVD profiles (maxpad) and its height (height\_maxpad) were derived from the profiles, which indicate the specific location where the plant material is concentrated and the amount of plant material in this location (Meeussen et al., 2020). Then, foliage height diversity (*FHD*) was quantified to represent vertical structural diversity in plant material along the profile, it was calculated as the Shannon-Wiener index for diversity (Meeussen et al., 2020):

$$FHD = -\sum_{i,s}^{i} p_i \times \log p_i \tag{1}$$

With *pi* 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. Note that *FHD* is sensitive to the way in which height classes are defined. It might not be a suitable metric to define vertical heterogeneity, but rather vertical structural diversity (McElhinny et al., 2005).

A normalized measure of vertical dispersion of foliage density through the canopy is given by the coefficient of variation for *weight-edPAVD* (*cvpad*), it was calculated with *weightedPAVD* values between 1.5 m height and the canopy top height:

$$cvpad = \frac{\sigma_{weightedPAVD}}{\mu_{weightedPAVD}}$$
(2)

*cvpad* was used to quantify the vertical variation in plant materials; monocultures with some simple layers at the canopy lead to a larger *cvpad* value, representing more concentrated plant materials at a certain vertical layer (Cosenza et al., 2022).

#### 2.4. Statistical analysis

The stand structural variables were related to tree species richness (SR) making use of multilevel distributional models (Bürkner, 2018). In these models, we regressed both the mean (location effect) and variance (scale effect) of the structure variables against the tree species richness and account for the between plot (through a group-level 'random' effect) as well as (residual) within plot variance, the analyses of Dhiedt et al. (2022) who looked at species richness effects on within versus between-plot variation in chemical soil variables. The models allowed the between-plot standard deviation ( $\sigma_{between}$ ) and the within-plot standard deviation ( $\sigma_{within}$ ) to differ among SR levels. We thus got estimates for the variation within and between monoculture plots, within and between two-species mixtures, three-species mixtures and four-species mixtures. Note that  $\sigma_{within}$  refers to the residual variation of the model and corresponds to the variation between the four scan locations within a plot. We also included the two blocks as a random effect because the difference in land-use history and soil type between the two blocks has the potential to affect stand structural diversity. The intraclass correlation (ICC) was then calculated by dividing the between-plot variance  $(\sigma^2_{between})$  by the sum of the between-plot and within-plot variance  $(\sigma_{between}^2 + \sigma_{within}^2)$ . The ICC provides an insight into the relative importance of the between-plot variation compared to the within-plot variation. With a higher ICC value, a higher variance will be received between plots. When the ICC value is less than 0.5, the within-plot variance is greater than the between-plot variance. All models were fitted through the brms package with R version 4.2.2, with the probabilistic programming language Stan behind the scenes (Bürkner, 2018; R Core Team, 2020). We used the default priors for these multilevel models and ran three chains of 6000 iterations each with a warm-up of 3000 iterations included.

To test if there is an increase in within-plot spatial variability and a decrease in between-plot variability with species richness, we sampled 1000 times out of the 3000 times posterior distributions of  $\sigma_{between}$ ,  $\sigma_{within}$ , and the ICC of the different SR levels. To evaluate our hypothesis, we consecutively calculated the difference of  $\sigma_{between}$ ,  $\sigma_{within}$ , and the ICC for each pair of the two SR levels (between SR level 1 and 2, 1 and 3, 1 and 4, 2 and 3, as well as 2 and 4 and 3 and 4). Based on the proportion of differences that is smaller or larger (depending on our hypothesis) than zero, we evaluated to what degree this difference differs from zero. The closer this proportion of difference is to 0, the less statistically supportive our findings are of our hypothesis. The proportion of differences in the  $\sigma_{within}$ , for each SR pairs that is smaller than zero, and the proportion of differences in the  $\sigma_{\textit{between}}$  and the ICC for each SR pair that is larger than zero was calculated depending on our hypothesis. In order to show the results more intuitively, we subtracted all the differences from 1, therefore the closer the 1 - differences is to 0, the more reasonable our hypothesis is (Dhiedt et al., 2022).

# 3. Results

As an illustration, we first compare the profiles of a birch monoculture (the leftmost panel), oak monoculture (the middle panel), and birch-oak mixture (the rightmost panel) (Fig. 2). The two monocultures exhibited comparatively lower total PAI but higher maxpad. The canopy height and height\_maxpad in the birch-oak mixture were lower than birch monoculture but higher than oak monoculture. The foliage height diversity was higher in the mixture, indicating greater vertical structural diversity, whereas the monocultures had a higher *cvpad* due to the clustering of plant material.

Our findings in Zedelgem supported that the within-plot structural variability increases with species richness, whereas the between-plot variability decreases with species richness (Figs. 3–4). For vertical distribution variables, *cvpad* completely supported our hypothesis; maxpad, height\_maxpad, and *FHD* supported our hypothesis for species richness levels 1, 3 and 4, whereas two-species mixtures showed similar patterns as the monocultures. For aboveground biomass variables, CH displayed similar results as vertical distribution variables, while the patterns of variability for total PAI were not clearly related to species richness levels. Notably, in both Hechtel-Eksel and Gedinne, we did not observe patterns for any of the structural variables that completely aligned with our hypothesis.

The between-plot standard deviation for the majority of structural variables was comparatively greater in monocultures than in mixtures across all three sites(Figs. 3–4). However, a completely opposing trend was observed for *cvpad* in Hechtel-Eksel, where monocultures showed lower between-plot standard deviation than two-species, three-species and four-species mixtures.

Monocultures demonstrated lower within-plot standard deviation than mixtures for structural variables across all sites (Figs. 3–4). For example, height\_maxpad consistently showed smallest within-plot variability in all three sites. Most structural variables displayed smaller within-plot variability in monocultures compared to three- and four-species mixtures in Zedelgem and Hechtel-Eksel. However, twospecies mixtures exhibited smaller within-plot standard deviation than monocultures for specific structural variables. In Zedelgem, CH, maxpad, and *FHD* exhibited smaller within-plot standard deviation in twospecies mixtures than monocultures. Similarly, in Hechtel-Eksel, all structural variables except height\_maxpad exhibited smaller within-plot standard deviation in two-species mixtures than monocultures. Additionally, the same patterns were observed in Gedinne for maxpad, *cvpad*, and *FHD*, with maxpad demonstrated a completely divergent within-plot variability pattern.

Our results revealed that the differences between each SR pair were relatively minor when comparing two consecutive levels of species richness (Table S2). For instance, the differences observed between



**Fig. 2.** Three sets of PAVD profiles and their corresponding site photos. From left to right, the sequence represents birch monoculture, oak monoculture, and birchoak mixture. (top) Vertical profiles of plant area per volume density (PAVD) as a function of the canopy height were shown for four scan positions (represented by different colors) in each plot. (bottom) The site photos were taken on the day of TLS data acquisition.

monocultures and two-species mixtures were significant only for height\_maxpad in within-plot standard deviation across all three sites. Moreover, when comparing three-species mixtures and four-species mixtures, we found that only total PAI in Hechtel-Eksel and Gedinne, maxpad in Zedelgem showed significant differences in between-plot standard deviation. Some similar outcomes were obtained regarding ICC differences.

## 4. Discussion

We examined the structural diversity of young biodiversity experimental plantations through six structural variables derived by terrestrial laser scanning. Our results indicated the structural variability patterns depended on species richness levels and varied by site. Specifically, our findings at the Zedelgem site revealed that within-plot variability increases with species richness, while between-plot variability decreases, thus supporting the hypothesis that species richness is a crucial factor in driving within- and between-plot structural variability patterns. However, not all structural variables at each site demonstrated this pattern, and a strong pattern was not shown in the Hechtel-Eksel and Gedinne sites. Nonetheless, differences in structural variability between monocultures and mixtures were observed at all sites.

The present study found that within- and between-plot structural variability patterns differed considerably depending on the experimental site. The variability in site conditions might be an important factor contributing to the observed differences in within- and betweenplot structural variability patterns. Whereas the site with the most

favorable climatic and soil conditions (Zedelgem) exhibited strong spatial patterns for most of the structural variables, the site with limited soil fertility and water availability (Hechtel-Eksel) and harsher climatic conditions (Gedinne) did not exhibit such strong patterns. Figs. S1-S3 provided evidence that most species exhibited greater aboveground biomass and vertical diversity in Zedelgem. For example, the monocultures of birch, oak, and pine exhibited greater aboveground biomass in Zedelgem compared to Hechtel-Eksel. Similarly, Zedelgem oak monocultures had greater biomass and structural diversity (FHD) than in Gedinne. On the other hand, beech monocultures in Gedinne displayed better biomass outcomes than those in Zedelgem, possibly due to the complete disturbance of one beech plot in Zedelgem. The occurrence of wet conditions during the time of planting in the affected beech plot led to the plantation failure in the initial years after establishment. The better tree growth of monocultures in Zedelgem for most species could be attributed to ample resource availability and favorable growing conditions. This superior tree growth has subsequently resulted in more pronounced patterns of variation within and between plots. In such sites, fast-growing species like birch exhibited stronger vertical development compared to slow-growing trees, thereby contributing strongly to variation in between-plot crown formation. Additionally, even less locally adapted trees might still survive intense competition for growing space in such site (Magalhães et al., 2021), enabling to form a more complex canopy structure within mixtures. In contrast, in sites with limited soil fertility and water availability and harsher climatic conditions, the differences in vertical growth among tree species were not as strong. This led to more subtle between-plot variation of monocultures.



**Fig. 3.** The hypothesized within- and between-plot variability pattern and the within- and between- plot variability and the posterior distribution of the intraclass correlation (ICC) of each species richness level for two biomass variables in three sites of the FORBIO experiment. On the far top are the hypothesized pattern and legend panel, followed with three rows displaying total PAI and canopy height at three sites separately. For each variable, (left) the median of the posterior distribution of the between-plot standard deviation (sd) is plotted along the x-axis and the median of the posterior distribution of the within-plot standard deviation is plotted along the y-axis for the four species-richness (SR) levels, the first and third quantile on these standard deviations is indicated by error bar, (right) the posterior distribution of the intraclass correlation (ICC) for the four SR levels, the median is represented by a vertical line in the respective colors.

Furthermore, the most vigorous trees were considered to have competitive advantages over neighboring trees in mixtures in such sites, potentially weakening the crown complementarity effect and resulting insignificant pattern of within-plot variability (Magalhães et al., 2021).

Environmental conditions were not the only contributing factor to the observed differences among sites, differences in species pools across sites might also be a contributing factor. As shown in Figs S1-S3, the structural variables of monocultures of each tree species varied across different sites. It is worth noting that the most successful tree species at each site were not entirely consistent due to differences in species pool. Birch dominated in Zedelgem and Hechtel-Eksel, whereas larch and douglas grown better in Gedinne. These inherent were likely to affect the interactions and competition among tree species in mixtures, thus influencing the within- and between-plot structural variability patterns. In conclusion, similar patterns of hypothesized stand structural variability were observed in five structural variables (excluding total plant area index) at Zedelgem, which might due to the rapid changes in stand structure over time in a young plantation at a favorable site with a more site-adapted species pool. During the initial stage of a plantation, when the branches of trees have not yet intertwined, the juvenile tree growth is primarily influenced by the tree species and the environmental conditions, such as sunlight, soil nutrients, and climate. As the stand age increases, the variability pattern in the stand structure becomes more complex due to tree interactions, competition, and space and resource availability, and the degree of this complexity would vary with species pool. This structural variability changes throughout the entire growth period, making it possible for the hypothesized structural variability pattern to occur in young plantations.

It should be noted, however, that not all structural variables demonstrated a strong variability pattern in Zedelgem, as total PAI (Fig. 3) did not demonstrate the hypothesized pattern. We found a

significant difference between monoculture and tree mixtures, but the differences among two-species mixtures, three-species mixtures, and four-species mixtures were minor according to the ICC value of total PAI (Table S2). Plant area index is an essential structural variable that can represent total plant biomass and forest productivity (Zhang et al., 2014). Although previous research has found a positive relationship between aboveground biomass and tree species richness (Morin et al., 2011; Zhang et al., 2017; Van de Peer et al., 2018; Feng et al., 2022), within-plot structural diversity is not a direct indicator of plant area index or aboveground biomass. For example, in a pine mixed forest, within-plot structural diversity may be higher than that of a pine monoculture due to tree species interaction and light use efficiency, but the plant area index or aboveground biomass is not necessarily higher than that of a monoculture. Multiple species in a plot may facilitate complementary resource use across vertical layers, but this may not necessarily translate into an increase in total plant biomass. Instead, in young plantations, plant area index may be more influenced by the unique characteristics of each species and the competitive balance between them (Yachi and Loreau, 2007; Wacker et al., 2009). Moreover, a mere examination of plant area index is insufficient to study structural diversity. It is necessary to analyse multiple structural variables to investigate the proposed pattern, since even weak patterns observed in plant area index may cover important patterns in more detailed structural variables (Figs. 3-4). For example, the integrated average of PAVD (total PAI) in the birch and oak mixture (5.96) surpassed that of birch (5.70) or oak (5.45) monocultures (Fig. 2). However, the clustering of plant material in the upper canopy of the birch monoculture resulted in a higher coefficient of variation in plant area volume density, indicating that a higher total plant area index may exhibit lower values in other structural variables.

We also found that there were differences in structural variability



**Fig. 4.** The within- and between- plot variability and the posterior distribution of the intraclass correlation (ICC) of each species richness level for four vertical distribution variables in three sites of the FORBIO experiment (with three panels displaying four structural variables at three sites separately). For each variable, (left) the median of the posterior distribution of the between-plot standard deviation (sd) is plotted along the x-axis and the median of the posterior distribution of the within-plot standard deviation is plotted along the y-axis for the four species-richness (SR) levels, the first and third quantile on these standard deviations is indicated by error bar, (right) the posterior distribution of the intraclass correlation (ICC) for the four SR levels, the median is represented by a vertical line in the respective colors.

between monoculture and mixtures even if there were varied species pools and environmental conditions. Monocultures mainly exhibited intraspecific resource competition, while interspecific competition was expected in mixtures. Mixed-species plantations have been found to be successful in combining fast-growing species with slow-growing ones, as well as light-demanding species with shade-tolerant ones (Liu et al., 2018). However, the relationship between species richness and stand structure was complex. When comparing mixtures with different species richness, it was found in Figs. 3-4 and Table S2 that a lower species richness level was occasionally associated with a tree composition exhibiting greater structural diversity, whereas it was not consistently observed that higher species richness levels resulted in superior stand structure when certain tree combinations were used. This implied that simply counting the number of species is inadequate for comprehending the stand structure, species identity and their interactions may play a critical role in determining the stand structural diversity. Moreover, two consecutive levels of species richness (i.e. species richness levels 1 and 2, 2 and 3, as well as 3 and 4) exhibited less difference in both within- and between-plot variability, possibly because of the shared species pool, leading to the presence of certain identical species pairs within these mixtures. This might weaken the hypothesized pattern.

This study revealed contrasting responses of the various structural variables to changes in species richness. Most structural variables in monocultures across the three sites exhibited highest between-plot variability (except for coefficient of variation in plant area volume density in Hechtel-Eksel). The normal growth of monocultures in Hechtel-Eksel under local environmental conditions, without any plots exhibiting particularly poor growth or animal damage, resulted in the concentration of plant material in a certain layer due to competition for the same niches. This similarity led to lower between-plot variability in vertical variation in plant material. On the other hand, the outcome of within-plot variability for each variable was more complex. Canopy height, height maxpad, and foliage height diversity, which positively associated with vertical structural diversity, consistently exhibited relatively smaller within-plot variability in monocultures. However, the other variables demonstrated varying outcomes. For example, in Gedinne, maxpad, cvpad, and total PAI exhibited larger within-plot variability in monocultures. One possible explanation is that the Maple monocultures did not thrive well and were poorly growing, with only a few scattered trees presented in the plots. This could cause significant variations in the structural variables across the four locations. Similarly, total PAI in Zedelgem demonstrated a similar result due to one of the beech plots being damaged, resulting in only several small beech trees were growing in the plot. Therefore, for certain structural variables, a pool of well-growing tree species in the local environment may serve as the basis for the hypothesized pattern to occur.

The implementation of TLS technology in our study overcame limitations of traditional forest inventories and satellite remote sensing for measuring stand structure. Traditional structural metrics from field data are very time-intensive and lower dimensionality (Drössler et al., 2014; Keren et al., 2020). While satellite remote sensing is a promising technique in globally detecting forest structure, it provides less detailed information scale (Schneider et al., 2020). TLS allows for automated and 3D measurements of canopy structure, offering novel insights into local-scale forest ecology and dynamics studies. Moreover, plot-level TLS data can be integrated with spaceborne data, enabling the monitoring of ecosystem structure at landscape and global scales (Calders et al., 2020). Quantitively measuring forest structure at local and larger scales is crucial for understanding forest ecosystem processes like productivity, biodiversity, and resilience (Beland et al., 2019).

# 4.1. Management implications and conclusions

This study used TLS to assess structural variables in young plantations. We have demonstrated that the pattern of within- and betweenplot structural variability in young plantations with a well-adapted species pool and favorable site conditions is strongly influenced by tree species richness. Our results demonstrated that adjusting species richness levels can regulate and improve stand structure diversity in young plantations, thus providing valuable insights for silviculture. Both high within-stand structural variability (local-scale) and a high structural variability between stands (landscape-scale) were potential important drivers of ecosystem stability and multifunctionality (Mori et al., 2013; Ali et al., 2016; van der Plas et al., 2016; Ratcliffe et al., 2017; Perles-Garcia et al., 2021; LaRue et al., 2019; LaRue et al., 2023). Higher within-stand structural diversity benefits local biodiversity by providing varied niches for forest organisms. A diverse landscape structure, including both high and lower local structural diversity, is crucial for maintaining forest sustainability and protecting biodiversity more broadly. Certain animals may prefer more diverse forest areas, while these areas can be disadvantageous for other species (Walz, 2011). Hence, maintaining stand structural diversity at both scales is being widely advocated in silviculture to improve the resilience and adaptability of managed forests (Mizunaga et al., 2010; Puettmann and Tappeiner, 2014). However, we must note that the within- and between-plot stand structural variability pattern can vary considerably depending on the site conditions and species pools, highlighting the necessity of adopting site-specific approaches to forest management and conservation.

# Author statement

KV, QP, and BM contributed as site managers of the FORBIO sites; MW and KC and their colleagues collected the data; JA worked on developing the Pylidar package; MW processed the data, performed the analyses, and drafted the paper; LB supported with the statistical analysis; the original idea for the study emerged from discussions between MW, LB, KC, HV, FVC; and all the authors contributed substantially to the submitted version.

#### CRediT authorship contribution statement

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

#### **Declaration of Competing Interest**

The authors declare the following financial interests/personal relationships which may be considered as potential competing interests: Mengxi Wang reports financial support was provided by China Scholarship Council. If there are other authors, they declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

# Data availability

Data will be made available on request.

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#### Data accessibility

Data will be made available on request.

# Appendix A. Supporting information

Supplementary data associated with this article can be found in the online version at doi:10.1016/j.foreco.2023.121662.

## Appendix B. Supporting information

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