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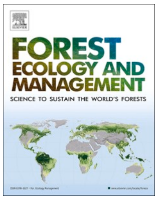

Explaining the relationship between structural diversity, tree and stand growth

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ABSTRACT

While homogeneity of forest stands was previously sought to simplify forest management planning, structurally rich stands are increasingly encouraged and implemented in contemporary forest management. One reason for this reversal is that structuring may promote forest stability and resilience as well as the provision of ecosystem services. However, the effect of structure on forest growth is not yet fully understood. In contrast, simple density-

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growth relationships are commonly used for modelling, forest planning, and as a background for forest management decisions without taking structure into account. Using the example of long-term Norway spruce (*Picea abies* (L.) H. Karst) stands covering a wide range of structures, densities, and site conditions, we investigated how stand structure modulates tree and forest stand growth and what mechanisms are behind this modulation. First, we show that under otherwise identical conditions, tree size variation increases the crown occupancy of the 3-dimensional space owing to the wider vertical distribution of tree crowns. We furthermore demonstrate that the occupancy of structurally diverse forests increases relative to the occupancy of homogenous forests with increasing stand density. Second, we found that, all other conditions being equal, stand growth increases asymptotically with increasing tree size variation; this applies to both managed and unmanaged forests although the level and rate of increase is higher in dense, un-thinned forests than in thinned forests. Third, we reveal the interdependency between size distribution and size-growth, demonstrating that structural diversity increases the growth efficiency of large trees in dense forests but increases the efficiency of smaller trees in sparsely stocked forests. Ensembles of trees with different sizes and efficiencies can make the best possible use of the growing space and resources and produce maximum stand growth. We discuss how previously contradictory views on the relationships between density and growth, density and symmetry of competition, and size and growth of trees become consistent when structural diversity is taken into account. Based on these findings, we also evaluate how growth responds to structurally oriented high thinning compared with homogenizing low thinning.

1. Introduction

There are currently many reasons to take a closer look at the effect of structure on forest stand growth. Structural diversity can effectively promote ecosystem functions and services such as biodiversity, stability, and aesthetics (Costanza et al., 2014; Biber et al., 2015; Brazaitytė et al. 2025; Brockerhoff et al., 2017; Achim et al., 2022), but does structuring come at the expense of productivity and carbon sequestration? Traditional low-thinning treatment programs were aimed at homogenizing stand structure, product quality, and mass yield (Larsen, 1995; Puettmann et al., 2012; Zeller et al., 2021). High thinning, such as future-crop-tree thinning, aims to improve a sub-population and neglects the overall mass yield of the stand (Klädtke et al., 2012). Mass yield is back in focus due to the scarcity of raw materials and the relevance of carbon sequestration (Gräfe and Köhl, 2020), but how do high-intensity thinning operations, which improve a selected sub-population, perform in terms of mass yield per hectare? Current studies of mixed stands show the key role of structural diversity in increasing crown density and growth (Ali et al., 2016; Dănescu et al., 2016; Pretzsch, 2021). The question addressed in this paper is to what extent size heterogeneity, the aspect of stand structure examined, can increase the growth of pure stands. The stand structure, indicated by the tree size distribution, is both a control variable for resource and growth partitioning (e.g. by letting radiation through or shading) and the basis for growth formation. Thus, the first important component in revealing the effect of stand structure on growth is the *relationship between structure and canopy space occupation* as an indicator of light absorption. Works by Ali et al. (2016), Dănescu et al. (2016), Pretzsch (2021) and Forrester et al. (2025) show how species mixing via structural diversity, complementary space occupation, and growth efficiency can ultimately result in higher growth rates in mixed compared to pure stands. Trees of equal size mean that their crowns are largely concentrated in one layer, whereas variation in size means greater vertical layering and deepening of the canopy space. Such effects of size variation on structure, space occupation, and stand growth, which Forrester (2019) also formulated conceptually, have hardly been studied for monospecific stand stands. But the investigation would be useful, because the crown structure controls light interception and growth. Case studies in mono-specific stands e.g. by Borggreve (1885), Vuokila (1977), (1980), Reininger (1987), and Sterba (1999), (2019) suggested that thinning from above increased structural heterogeneity and resulted in increased yields compared to unthinned stands and thinning from below which homogenized stands. Such findings are in line with eco-physiological experiments and model simulations. They show that structuring of the upper canopy reduces the reflection and loss of photosynthetic active radiation (Larcher, 2003; Ellenberg and Leuschner, 2010), allow higher proportions of light to penetrate into deeper stand layers (Naudts et al., 2015; Forrester et al., 2018), and can use photosynthetically active radiation more efficiently (Forrester et al., 2025). The relationship between size variation, vertical stratification and occupation of the canopy as hypothesized in Fig. 1a have not yet been systematically investigated for homo- and heterogenic forests.

How the structure, via resource and growth distribution/partitioning, affects the stand growth can be analyzed based on the *relationship between structural variables (e.g., coefficient of variation or Gini coefficient of tree sizes) and stand volume or biomass growth*. Studies on the relationship between structural diversity and growth have produced very divergent results. Positive effects of structural diversity on growth have been found by Lei et al. (2009), Glatthorn et al. (2018), and Torresan et al. (2020). In contrast, Soares et al. (2016), Zeller et al. (2021), and Zhai et al. (2024) report production losses due to structural diversity. According to these studies, production gains are explained by improved use of growing space and resources through niche complementarity. Production losses are explained by inefficient dominated trees, the removal of which was already recommended by Assmann (1961) to increase growth. In view of this inconsistent picture, Ali (2019) recommends further studies that take into account influencing factors in the relationship between structure and productivity that have not yet been considered. Forrester (2019) proposes a theoretical framework for systematically investigating stand growth based on structure, density, and the relationship between tree growth and tree size. Recent analysis of long-term Norway spruce experiments revealed a unimodal relationship between tree size variation and yield (Pretzsch et al., 2024), suggesting optimal productivity occurs at intermediate levels of structural diversity rather than at extremes. Simulation studies by Bohn and Huth (2017) suggest that contradictory findings may also arise because previous studies have mostly considered only limited excerpts from the broad spectrum of possible structures and production. Recent work by Deng et al. (2025) using aerial laser scanning demonstrated that tree diversity promotes aboveground biomass through complex canopy structures, with this relationship strengthening with stand age through enhanced species complementarity. There could be a stand structure that maximizes growth, i.e., an ensemble of trees of different sizes that make optimal use of the stand area and resources. More homogeneous would then result in suboptimal stand growth as hypothesized in Fig. 1b. The seemingly contradictory studies could thus prove to beexcerpts from a longer, nonlinear continuum.

For a better understanding and insight into the partitioning of growth between trees of different sizes, the relationship can also be traced down to the tree level. This is made possible by analyzing the *relationship between size distribution and the size-growth relationship.* The relationship between tree size and growth has often been used for diagnosing and quantifying natural resource limitations (Grams and Andersen, 2007; Condés and del Río, 2015; Forrester et al., 2022) or stress effects (Wichmann, 2001; Pretzsch et al., 2012; Alam et al., 2017; Kolisnyk et al., 2025) in forest stands.

The relationship between size and growth is often represented by a straight line. Such a representation implies that the behavior of individuals can be interrelated. For instance, the removal of large trees can feed back on the resource supply and the growth of the other remaining trees via changes in radiation conditions, while the removal of small trees can feed back via the water supply. This type of size-growth representation has several advantages in our context compared to the growth dominance coefficient by Binkley (2004), Binkley et al. (2006); West (2014) or the method by Metsaranta and Lieffers (2008). Compared with Binkley's approach it has reduced sample size requirements, compared with the method by Metsaranta and Lieffers it has relaxed assumption of linearity, and it can show which stand components increase or decrease in efficiency as a result of, for example, thinning, drought stress, or fertilization; that is, how the partitioning changes in detail.

Although the influence of structural diversification designed by silvicultural treatment is probable, this relationship between size and size increment has so far been studied mainly in fully stocked, untreated stands with self-thinning dynamics (Wichmann, 2001; Reynolds and Ford, 2005). West (2023) analyzed 121 unthinned and thinned blackbutt (*Eucalyptus pilularis* Smith) plots across a range of stand densities regarding effects on tree growth rates of symmetric and asymmetric inter-tree competition. However, he did not specifically consider obvious effects of strength and kind of thinning (structural diversity) on the size-symmetry or asymmetry of competition and growth. Bradford et al. (2010) found for red pine (*Pinus resinosa* Ait.) that growth dominance in unthinned stands was positive and increased with age. Growth dominance in stands thinned from above trended from negative at low stand densities to positive at high stand densities.

A clear understanding of the density–growth relationship is fundamental for interpreting stand-level productivity patterns (Pretzsch et al., 2024). In order to explain the density-growth relationship at the stand level and to control the growth of defined stand components in a targeted, knowledge-based manner, e.g., through low thinning or high thinning, it is essential to understand the effect of structure on the size-growth relationship as visualized in Fig. 1c.

To provide in-depth understanding of how structural diversity modulates tree and stand growth, we extended our previous analysis (Pretzsch et al., 2024) and examined data from forest experiments in monospecific Norway spruce (Picea abies (L.) H. Karst) stands across Europe. The dataset covered a wide spectrum of site quality, age, stand density (from maximum density to solitary growing trees), and management regimes (self-thinning, low thinning, and high thinning). Using this data, we addressed the following three questions illustrated in Fig. 1.

Q1: How does the variation in tree size affect the vertical structure of the stand and crown space occupancy?

Q2: How does tree size variation, in addition to stand density, modulate stand growth?

Q3: How are the size-growth relationship and growth efficiency of trees controlled by structural diversity?

We discuss the consequences for population biology, production ecology, and silvicultural prescriptions.

2. Material and Methods

2.1. Material

Questions 1–3 were answered using the example of even-aged, monospecific stands of Norway spruce as a particularly broad data set could be compiled for this tree species. By including fully stocked, unthinned, low- and high-thinned, and solitary stands, a broad spectrum of tree size variation could be covered. Since the stands also cover a broad spectrum of site indices, stand density, and age phases, these characteristics can be taken into account as covariates.

Our study included space and thinning experiments (N = 11), plots of age series (N = 18), and triplet plots (N = 20) (Table 1). Experiments of the first data set are long term research plots. Plots which belong to age series experiments specifically cover a range of stand age with identical growing conditions. They cover mixed and monospecific stand parts, we used the parts

with monospecific Norway spruce. The data from Triplets cover a set of three plots with two different tree species, each of them in monospecific stands and one plot in mixture of both (Bravo-Oviedo et al., 2018; Ruiz-Peinado et al., 2021). The experiments are located in Denmark, Norway, Sweden, Lithuania, Estonia, Latvia, Poland,

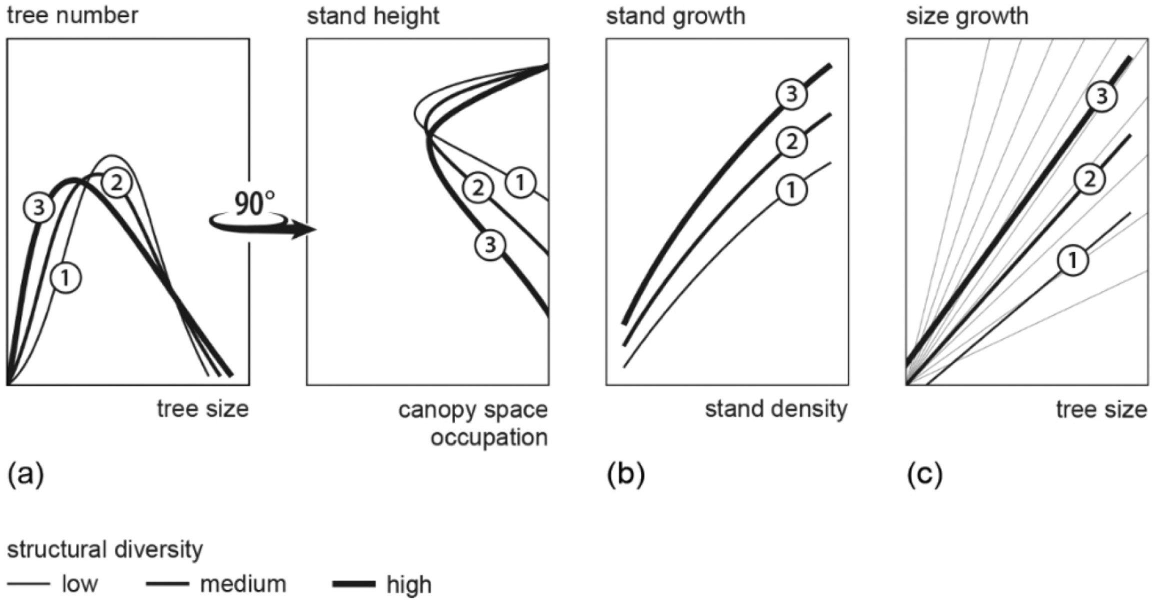

Fig. 1. Visualization of the basic questions Q1-Q3 of this study. (a) How does the tree size variation modify the vertical stand structure?, (b) How is the stand density-stand growth relationship modulated by tree size variation?, (c) how is the tree size-growth relationship shaped by structural diversity? The lines marked with 1, 2, and 3 indicate low, medium, and high structural diversity.

Table 1
Overview of the plot design and characteristics separated by the data sources long-term thinning experiments, age series components, and triplet components. From the latter data source we included the unthinned Norway spruce reference plots. A-, B-, C-, D-, E-grade thinning according to definition provided in Section 2.2.

Type	Thinning experiments	age series components	Triplet components
Experiments (number)	11	3	20
Plots (number)	3–24	5–8	1
Surveys (number)	6–18	2–5	1
Plot size	0.09–0.25 ha	0.07–0.3 ha	0.025–0.32
First survey	1882–1993	1991–1997	2017
Last survey	1990–2022	2008–2012	2017
Age last survey	44–143	36–168	45–93
Thinning	A-, B-, C-, D-, E-grade	A-grade	A-grade

Germany, and Slovakia at latitudes between 47.8° and 60.88° north and longitudes between 10.5° and 27.3°, with the majority being located in southern Germany (Supplementary Figure 1). The elevations range from 35 to 790 m above sea level, the average annual temperature is between 3.0 and 8.9°C, and the average annual precipitation ranges between 614 and 1200 mm. The soil substrate varies between sand and silt loam, and the soil type between nutrient-poor podzols and nutrient-rich brown soils. The range of the site index is correspondingly broad, ranging from 20.5 to 47.8 m mean tree height at age 100 (Table 2). For more detailed information about the site characteristics see Supplementary Table 1, a-c (Table 3).

The experimental plot data included in the study have already been published in detail (Pretzsch and Hilmers, 2024). An overview of the growth series data can be found in Pretzsch and Schütze (2021), and an overview of the triplet data in Ruiz-Peinado et al. (2021). Therefore, only a brief overview of the stand and tree data is provided here.

2.2. Methods

Quantifying structural diversity: For characterizing the structural diversity we used the coefficient of variation of the stem diameter (CV_{dbh}=standard deviation of stem diameters/mean diameter). It is frequently used, easy to derive, and correlates very closely with other measures of size heterogeneity such as the Gini coefficient.

Quantifying stand density: For quantifying the stand density we used Reineke's stand density index ($SDI = N \times (25/D_q)^a$) with a being the species-specific allometric scaling coefficient (Pretzsch and Biber, 2005) for Norway spruce ($a = -1.664$). We used the SDI because it is a widely applied stand density measure (Sterba, 1987) and only the most readily available variables, tree number and mean diameter, are required for its calculation (Reineke, 1933). To quantify the density on the thinned plots, their SDI ($SDI_{thinned}$) was divided by the SDI of the untreated plots ($SDI_{reference}$) in the same experiment at the same time of recording ($rel_{SDI}=SDI_{thinned}/SDI_{reference}$).

Table 2
Overview of the stand level data of the altogether 34 experiments, 125 plots, and 610 surveys. H_q refers to the height of the tree with the quadratic mean diameter.

Variable	explanation	unit	mean	minimum	maximum
A	stand age	years	43	11	143
SI	site index	H_q at age 100	36.9	20.5	47.8
N	tree number	ha^{-1}	2347	150	9941
D_q	quadratic mean diameter	cm	24.7	2.5	59.0
H_q	quadratic mean height	m	17.8	2.6	43.6
V	standing volume	$m^3\ ha^{-1}$	413.2	5.0	1637.0
I_V	stand volume growth	$m^3\ ha^{-1}\ yr^{-1}$	22.3	1.0	41.50
SDI	stand density index	ha^{-1}	902.1	75.7	1613.1
relSDI	relative stand density	./.	0.77	0.15	1.00
CV_{dbh}	var. coeff. of stem diameter	./.	0.26	0.07	0.56

Table 3
Overview of the size and growth of the n = 67.298 individual trees underlying this evaluation. Volume and volume growth refer to merchantable volume as volume with diameter > 7 cm at the smaller end.

Variable	explanation	unit	mean	minimum	maximum
d	stem diameter	cm	17.9	0.40	87.2
h	tree height	m	16.3	0.90	46.9
v	stem volume > 7 cm	m^3	0.41	0.02	10.26
i_{dbh}	diameter increment	cm yr^{-1}	0.41	0.01	1.78
i_v	volume increment > 7 cm	m^3 yr^{-1}	0.018	0.0001	0.202

Thinning grades: The experiments included unthinned plots as reference and plots subjected to various thinning grades as defined by Wiedemann (1935) and elaborated in detail by Kramer (1988, pp. 179–183). The thinning grades are categorized as A-, B-, and C-grade, representing slight, moderate, and heavy thinning from below. On A-grade plots, only dead or dying trees were removed. B- and C-grade plots involved the removal of mainly small trees, with B-grade leaving only pre-dominant, dominant, and co-dominant trees and C-grade retaining only the pre-dominant and dominant trees. D- and E-grade thinning denote moderate and heavy thinning from above, removing mainly pre-dominant and dominant trees to promote the growth of the remaining trees. The key distinction between D- and E-grade lies in the horizontal distribution of the interventions (D-grade being uniformly distributed, E-grade concentrated around future crop trees) rather than the extent of density reduction (Wiedemann, 1935). In Section 3.1, we will give an overview of the ranges of the coefficients of variation of stem diameters, the relative SDI, and the height to crown base specified for the different thinning grades. We combined the D- and E-grade plots into one group for two reasons. On the one hand, D- and E-grades differ mainly in terms of the horizontal distribution of trees; however, our evaluation could only take vertical structuring into account because stem maps were only available for a few plots. On the other hand, the number of E-grades was too small for a separate evaluation. For a more comprehensive explanation of the internationally defined thinning grades, see Assmann (1970) and Verein Deutscher Forstlicher Versuchsanstalten (1902), (1873).

Forest stand data: In this study, the characteristics at the stand level were derived from successive surveys, which included tree diameters, tree heights, and records of the felled and dead trees. In the case of plots from triplets, increment cores were used to estimate growth (see details in Ruiz-Peinado et al., 2021). We used standard evaluation methods in accordance with the DESER-norm, which is recommended by the German Association of Forest Research Institutes (in German "Deutscher Verband Forstlicher Forschungsanstalten") (Biber, 2013, Johann, 1993). The calculation of stem volume was conducted using regional-specific stem form equations and coefficients according to Franz et al. (1973) (see Supplementary Explanation 1). The results of the standard evaluation included the quadratic mean tree diameter, stand volume, and volume growth. To determine an integrated measure for site quality, we assessed the site index plot- and survey-wise, utilizing the yield tables for Norway spruce by Wiedemann (1936). It is important to note that the site indexes reported in this text are always interpreted as the expected stand heights at an age of 100 years.

Canopy space occupation: In addition to the vertical profiles shown in Fig. 2 the analysis of crown space occupancy provided measures of how much crown space is occupied (ocs), at what height the crown space is most densely occupied (hcmax), and how deep the canopy space

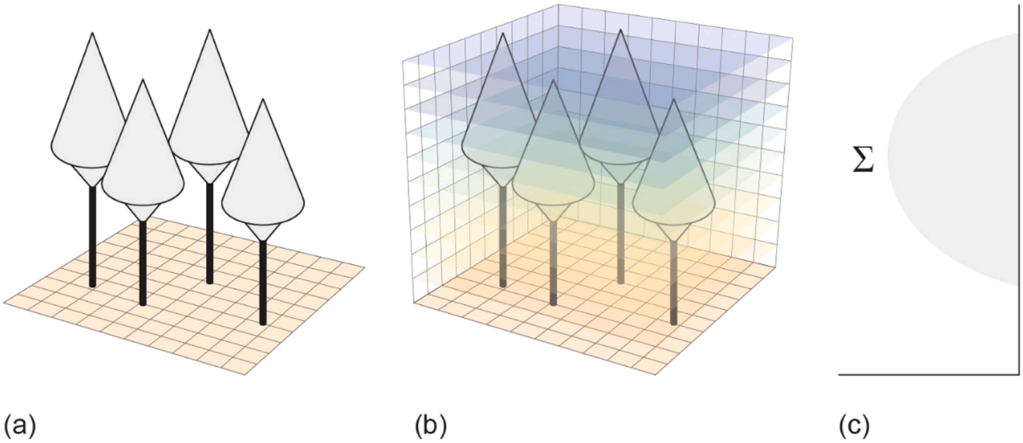

Fig. 2. Vertical profile of canopy space occupation derived by voxelization of all individual crowns. (a) Three-dimensional modeling of the crown extension based on measured tree height, height to the crown base, crown diameter, and species-specific crown models. (b) Identification of the tree crowns' presence in different absolute or relative height layers by dot-count principle. (c) Profiles of canopy space occupation.

occupancy extends towards the forest floor (hcb).

To derive the crown structure of the individual trees and species-specific canopy space occupation, idealized crown shapes for each individual tree can be modeled based on field measurements of total tree height, crown base height, and crown diameter. Crown shapes were assigned according to a set of parametric models (Pretzsch et al., 2002; Pretzsch, 2021; Tockner et al., 2022), which define crown geometry by three species-specific parameters: the relative height of the crown's maximum width and two curvature parameters that determine the taper of the crown above and below that point (Fig. 2a). For details about the crown shape models, which were derived for the five most important tree species in South Germany by extensive crown measurements on long-term experiments see Pretzsch (1992, p. 111–114). Based on these crown shapes, the crown volume of each tree can be estimated in total but also in defined fine horizontal segments (Fig. 2b). For each site, plot, and inventory year, we determined the maximum tree height and divided the vertical space from the forest floor to this maximum height into regular layers representing 0.5% increments of that height. This resulted in a normalized, vertically resolved representation of crown space occupation within a stand (Fig. 2c).

For cross-stand analyses (e.g., comparisons between stands with different thinning or mixture), the profiles can be standardized in terms of both their height and lateral extent. This is achieved by rescaling of the stand height and crown volume density values for each stand to a range between 0 and 1. This yields standardized values for the height of the maximum crown cover or the depth range of the crowns.

The method for analyzing canopy space occupation is explained briefly here, but in more detail in Supplementary Explanation 2.

Size-growth relationship and efficiency of growth investment: As a preparatory step for modeling the size-growth relationship as function of stand characteristics (structural diversity, stand density, site index, stand development phase), we quantified the size–growth relationship for each of the $n = 454$ empirical datasets by fitting a second-degree polynomial to tree size and increment (e.g., $i_{dbh} = a + b \times dbh + c \times dbh^2$, analogously for basal area and volume). Although the size–growth relationship is often assumed to be linear (Prodan, 1965; Forrester, 2019), such a simplification may obscure characteristic patterns of growth partitioning within the stand.

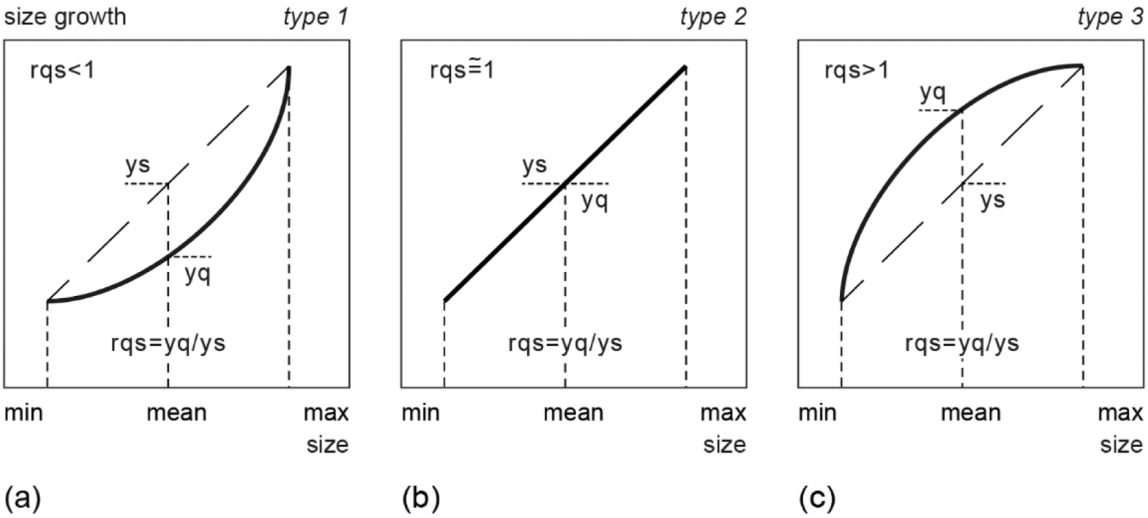

Fig. 3. Assignment of size-growth relationships ($i_{dbh} - dbh$, $i_{ba} - ba$, $i_v - v$) to three types with convex, linear, and concave curves (viewed from below). The classification into types 1–3 (a-c) was based on the ratio rqs=yq/ys. Each size-growth relationship was fitted using a quadratic polynomial function. For the tree with mean size in the respective value range, yq was taken from the quadratic function, while ys was obtained from the linear interpolation between the smallest and the largest observed tree sizes (dashed line). A ratio $rqs < 1$ indicates a convex curve, $rqs \approx 1$ a linear curve, and $rqs > 1$ a concave curve (types 1–3). We defined $0.95 \leq rqs \leq 1.05$ as the range for type 2. min, mean, max: minimum, mean, and maximum size of the included trees; ys, yq: predicted growth at mean size from the linear and quadratic relationships, respectively.

To classify each relationship, we followed the scheme illustrated in Fig. 3. For every fitted polynomial, we first determined yq, which is the predicted growth of a tree of mean size, i.e. the function value obtained from the polynomial at the mean dbh (or ba or volume). Next, we determined ys, the value at the same mean size under a linear approximation, derived by using a linear formula connecting the smallest and largest observed size values with a straight line (the dashed line in Fig. 3).

According to Fig. 3, curves with rqs < 1 were classified as convex (type 1), curves with rqs ≈ 1 ($0.95 \leq$ rqs ≤ 1.05) as linear (type 2), and curves with rqs > 1 as concave (type 3). Supplementary Explanation 3 shows that all three patterns occurred across the dataset, with a predominance of concave type-3 curves.

To express the efficiency of growth formation, we divided the polynomial by the size variable, for example i_{dbh}/dbh, i_{ba}/ba, i_v/v. This provides increment per unit size and therefore a measure of how efficiently trees of different sizes convert their structural capital into growth.

2.3. Statistical models

We used linear mixed-effects models to investigate how stand structure and density, size variation and site conditions influenced (i) vertical stand structure (Q1), (ii) stand volume and stand volume growth (Q2), and (iii) the shape of the size–growth relationship (Q3). All analyses were implemented within a common modelling framework to ensure full comparability across response variables.

All models followed the general formulation

$$y_{ijkn} = f(X_{ijkn}) + b_i + b_{ij} + b_{ijk} + \varepsilon_{ijkn},$$

in which the fixed-effects term $f(X)$ contained the candidate explanatory variables and their interactions, while b_i, b_{ij}, and b_{ijk} were random intercepts for experiment, plot and survey year, and ε_{ijkn} denotes the residual error. The residuals were assumed to be independent across observations, normally distributed with mean zero and constant but unknown variance σ^2. Random effects were assumed independent across grouping levels. Residuals were assumed independent across observations, and random effects were assumed independent across grouping levels following the standard assumptions for mixed-effects models (Mehtätalo and Lappi, 2020).

Across all analyses we used a common set of stand-structural and site-related predictors, as these represent the key factors expected to influence crown structure and stand- and tree-level growth. The predictors included quadratic mean diameter (D_q) as an indicator of stand development stage, the coefficient of variation of stem diameter (CV_{dbh}) as an indicator of stand structure, relative stand density (relSDI), and site index (SI) as an indicator of site productivity. For the size–growth analyses (Q3), the appropriate size variable (diameter, basal area, or stem volume) was included to define the size axis of the relationship.

To capture complex structural responses, we evaluated main effects and second-order interactions in all analyses and selected third-order interactions particularly for Q3. These higher-order terms enabled the models to represent shifts between size-asymmetric and size-symmetric growth distribution and to account for changes in the curvature of the size–growth relationship.

All strictly positive response variables were log-transformed to stabilize variances and improve linearity. Explanatory variables were tested both in their original form and log-transformed, because different transformations emphasized different biological mechanisms. In some models, both transformed and untransformed versions of a variable were retained when they captured distinct aspects of the response. For Q3, the dependent variable (i_V) remained on its natural scale, because the polynomial representation of the size–growth curve requires tree size to remain in its original units to preserve interpretable convex, linear and concave curve forms.

For Q1, we modelled crown-base height (hcb), the height of maximum crown expansion (hcmax), and canopy space occupation (ocs) using the full candidate set of structural and site variables. For Q2, we analyzed stand volume growth (I_V), standing volume (V), and the proportion of standing volume contributed by trees above the mean stem size (relVa). In the case of stand volume growth, we first fitted a model for unthinned stands to have the growth behavior in untreated stands as a reference, and secondly, we fitted a model for thinned and unthinned stands to understand growth patterns in all stands. For Q3, we modelled the magnitude and shape of the size–growth relationship by expressing the linear and quadratic size terms as functions of stand structure and site conditions. This allowed the model to represent size-asymmetric and size-symmetric relationships, and to shift between convex, linear and concave forms of the size–growth curve depending on stand characteristics.

Model selection for all questions was based on AIC, BIC and −2 log-likelihood. Competing models differed in their predictor sets, transformations, and interaction terms. The final models for Q1–Q3 (Models 1–8) and full model specifications, parameter estimates, and diagnostic figures are provided in the Supplementary Material. For dealing with collinearity in model formulation, see Supplementary Model Specifications.

All models were evaluated using standard diagnostic procedures, including Q–Q plots and residual-versus-fitted plots, to verify variance homogeneity and normality assumptions. Slightly fan-shaped residuals, i.e., slight heteroscedasticity, were accepted in order to avoid making the models even more complex by adding further variables or transformations. This means that those models are less accurate when extrapolated. Since the models were primarily derived to improve biological understanding and less for estimation and forecasting, slight heteroscedasticity seemed acceptable to us. All analyses were conducted in R 4.1.0 (R Core Team., 2024) using the packages nlme (Pinheiro et al., 2021) and lme4 (Bates et al., 2015).

3. Results

3.1. Tree size variation and canopy space occupation

Tree size variation had strong and systematic effects on vertical stand structure. Fig. 4 illustrates the influence of thinning grade on three structural attributes. Size variation was highest in unthinned A-grade stands and in stands thinned from above (D/E grades; $CV_{dbh} = 0.26$–0.27), and lowest in stands thinned from below (B/C grades; $CV_{dbh} = 0.20$–0.21; Fig. 4a). Relative stand density showed the opposite pattern, declining progressively from relSDI ≈ 1.0 in A-grade stands to ≈ 0.65 in D/E-grade stands (Fig. 4b). The bold appearance of the box and whisker plot in the case of the A-grade plots in Fig. 4b is due to the high concentration of the measured values around the median. These structural differences were reflected in the relative height at which crown space was most densely populated, with hc_{max} being highest in stands thinned from below (≈ 0.64–0.67) and lowest in stands thinned from above (≈ 0.51; Fig. 4c).

The coefficient of ln CV_{dbh} (-0.45, $p = 0.052$) implies that a 1% increase in CV_{dbh} resulted in a 0.45% downward shift of the crown base, while crown base height increased with stand development (1.36, $p < 0.001$). These effects were consistent across development phases (supported by Model 1; Supplementary Model Specifications and Supplementary Table 2).

Higher tree size variation was associated with a lower crown base height (Fig. 5a).

The height of maximum crown occupancy responded in a similar way. Increasing size variation reduced hc_{max} (-0.14, $p = 0.002$), and stand development had a modest positive effect (0.11, $p < 0.001$). The negative interaction between $\ln(D_q)$ and $\ln(CV_{dbh})$ (-0.06, $p = 0.011$) indicated that the downward shift became stronger in older stands (supported by Model 2; Supplementary Model Specifications and Supplementary Table 2; Fig. 5b).

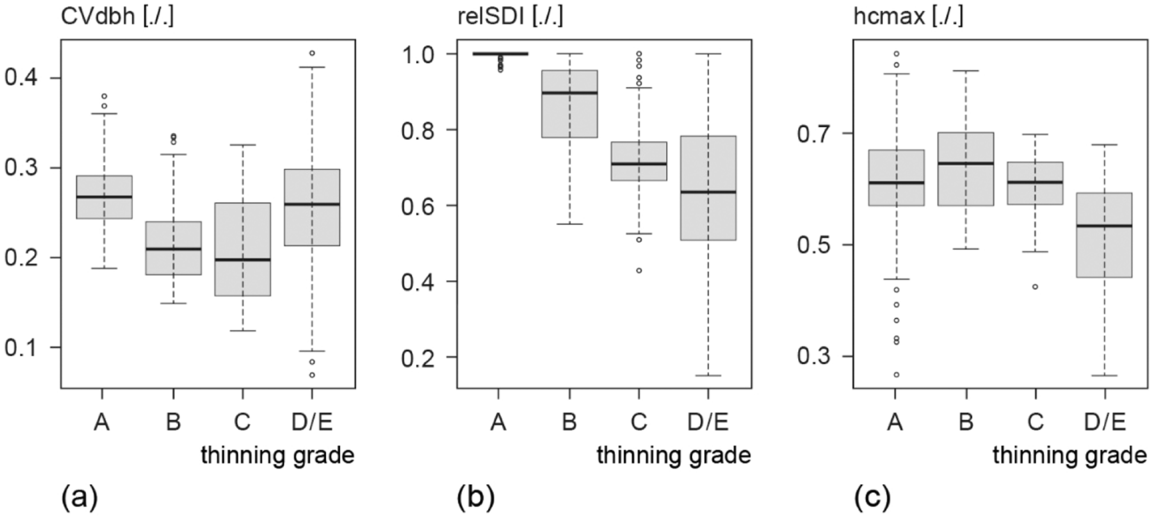

Fig. 4. Effect of thinning grade on (a) the coefficient of variation of stem diameter (CV_{dbh}), (b) relative stand density (relSDI), and (c) the relative height of maximum crown occupancy (hc_{max}). Boxes show the interquartile range with the median; whiskers represent 1.5 × IQR and therefore do not indicate confidence intervals or significance. A-grade: unthinned; B- and C-grade: moderate and strong thinning from below; D- and E-grade: moderate and strong thinning from above.

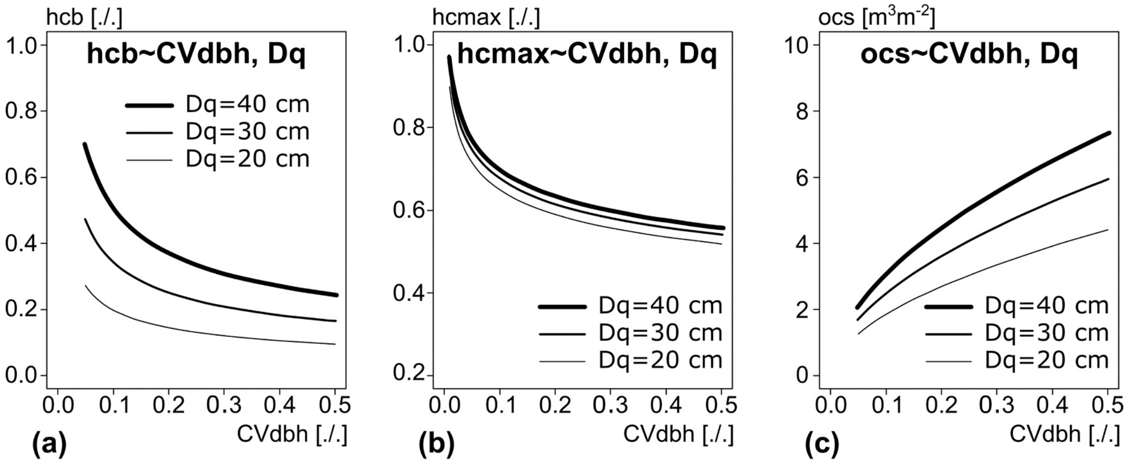

Fig. 5. Modeled effect of tree size variation (CV_{dbh}) on vertical stand structure and canopy space occupation. Shown are the relationships between CV_{dbh} and (a) crown base height (hcb), (b) the height of maximum crown occupancy (hc_{max}), and (c) canopy space occupation (ocs). Curves are displayed for three stand development stages represented by quadratic mean diameter ($D_q = 20$, 30, and 40 cm). All other explanatory variables were held at their mean values for visualization. Statistical details of the selected models (Models 1–3; Supplementary Model Specifications) are provided in Supplementary Table 2 and Supplementary Figures 2–4.

Canopy space occupation increased markedly with structural diversity (Fig. 5c). Size variation showed a strong positive effect (0.92, $p < 0.001$), stand density further enhanced canopy space occupation (2.60, $p < 0.001$), and the interaction between $\ln(CV_{dbh})$ and ln(relSDI) (1.31, $p < 0.001$) indicated that structurally diverse and dense stands were particularly efficient in filling the vertical canopy space (supported by Model 3; Supplementary Model Specifications and Supplementary Table 2).

The combined structural adjustments are summarized in Fig. 6. Stands with medium and high size variation showed a consistent downward shift of both crown base height and the height of maximum crown occupancy, leading to a more compact and vertically condensed canopy architecture. These structural changes form the basis for the stand- and tree-level growth responses examined in the subsequent sections.

3.2. The effect of structural diversity and density on stand growth

Stand-level volume growth was analyzed in two complementary steps to evaluate how structural diversity influences productivity in both unthinned and thinned stands. First, unthinned, fully stocked stands were examined to determine how structural diversity affects the intrinsic growth potential of unmanaged stands, using the selected stand-growth model for A-grade plots (Model 4). Second, structural effects were analyzed across the full gradient of thinning intensities and stand densities to quantify how structure and density jointly determine stand growth, based on the stand-growth model for mixed stocking conditions (Model 5). Standing volume and the proportion of large trees were evaluated with the corresponding models for stock attributes (Models 6 and 7). The full model equations, parameter estimates, and diagnostic plots are provided in Supplementary Model Specifications, Supplementary Tables 3–4 and Supplementary Figures 5–8.

In fully stocked stands, structural diversity had a clear and nonlinear effect on stand growth (Model 4; Supplementary Table 3). Volume

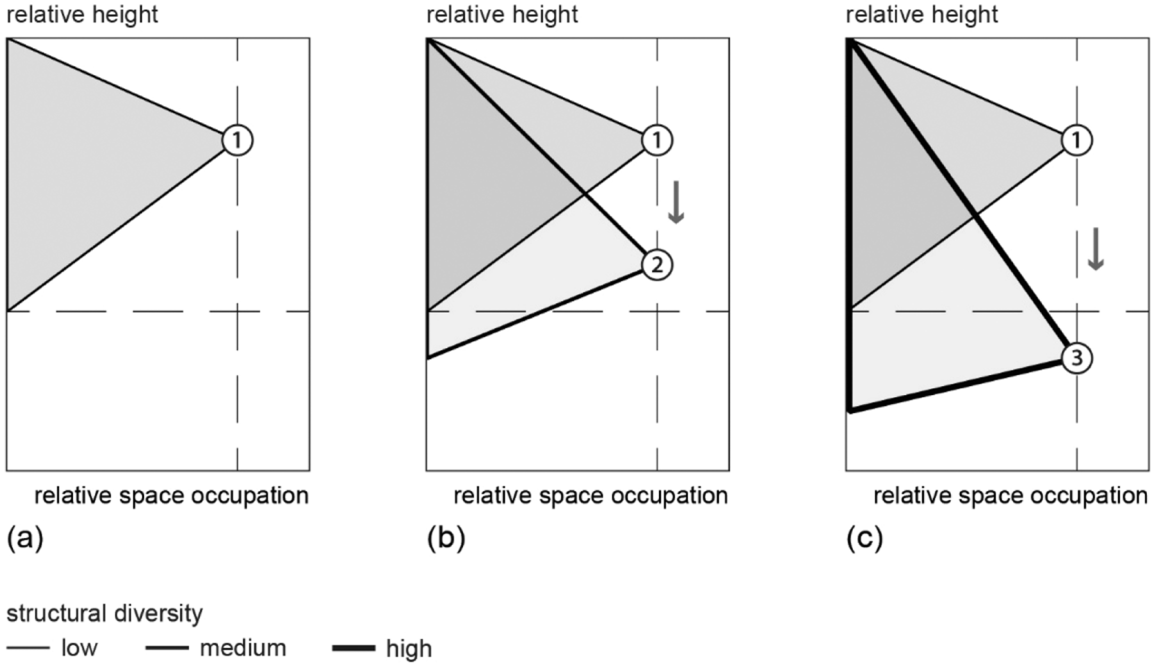

Fig. 6. Schematic visualization of the effect of low, medium and high structural diversity (a-c) on the canopy space occupation in terms of height to the crown base, height of the canopy layer with maximum canopy space occupation, and canopy space occupation in total. The lines marked with ①, ②, and ③ indicate the canopy space occupation under low, medium, and high structural diversity. The broken horizontal and vertical lines serve as a reference. They indicate the crown base height and maximum canopy space occupation in stands with low structural diversity.

growth (I_V) increased with CV_{dbh} up to an optimum of approximately $CV_{dbh} \approx 0.50$ and declined beyond this point (Fig. 7, a and b). This unimodal relationship indicates that moderate size variation enhanced stand growth, whereas very high variation was associated with slightly lower growth. Growth decreased with increasing stand development (D_q) and increased with site productivity (SI) (Fig. 7, c and d). The magnitude of this structural effect was substantial within the empirical range: about 95% of CV_{dbh} values ranged between 0.25 and 0.35 (mean $\approx$ 0.30), and the associated IV predictions were 6.5, 8.1, and 9.9 $m^3\ ha^{-1}\ yr^{-1}$, corresponding to -20% and $+21\%$ relative to the growth at $CV_{dbh}=0.30$. Because only A-grade plots were included, relative stand density did not add explanatory power, indicating that SI already captured the site-specific stand density in these unthinned stands.

Across thinned and unthinned stands, stand growth increased with structural diversity, but the strength and even the direction of this effect depended strongly on stand density (Model 5; Supplementary Table 3). At high relative stand density (relSDI), IV increased steeply with CV_{dbh}, approaching an asymptote (Fig. 8a). With decreasing stand density (relSDI = 1.00, 0.75, 0.50…), the positive effect of CV_{dbh} weakened progressively. From a stand density of relSDI $\approx$ 0.50, structural diversity reduced stand growth, reflecting the negative $CV_{dbh} \times$ relSDI interaction in the selected model (Fig. 8a, bottom curve). Fig. 8b show this effect for different level of CV_{dbh} ($CV_{dbh}=$ 0.50, 0.35, 0.20). These density-dependent relationships between structure and stand growth were consistent across different levels of site quality (SI) and stand development phases (Dq) (Fig. 8b–f). Although absolute growth levels increased with higher site productivity and declined with greater D_q, the qualitative response to structural diversity remained stable.

Structural diversity also influenced standing volume and the distribution of volume among tree sizes (Models 6 and 7; Supplementary Table 4). Standing volume (V) increased with CV_{dbh} at high relSDI (Fig. 9a). For example, increasing CV_{dbh} from 0.20 to 0.30 raised predicted standing volume from 463 to 497 $m^3\ ha^{-1}$, an increase of roughly 7% under otherwise mean conditions. This effect diminished at lower stand densities. The relative volume share of trees exceeding the mean stem volume (relVa) increased even more consistently. Across the observed CV_{dbh} range, relVa increased by about 11% (Fig. 9b), and this pattern was stable across all levels of relSDI, SI, and D_q. Thus, structurally more diverse stands consistently contained a greater proportion of large trees, independent of site productivity or stand development stage.

3.3. *The size-growth relationship as modified by structural diversity and stand density*

The empirical size–growth relationships in our dataset showed considerable heterogeneity. Based on the second-degree polynomial fits (see Supplementary Explanation 3), 454 curves were assigned to three structural types: convex, linear, and concave. Most relationships (64%) were concave, indicating that growth often increases less than proportionally with tree size. A smaller fraction of stands showed linear or convex patterns (Supplementary Explanation 5, Fig. 1).

To quantify how structural diversity and stand density systematically modify these patterns, we used Model 8 (Supplementary Model Specifications), which predicts volume growth (i_v) as a function of tree size (v), structural diversity (CV_{dbh}), relative stand density (relSDI), site productivity (SI), and stand development (D_q). Fig. 10 illustrates representative i_v–v curves (panels a–c) and the corresponding growth efficiencies i_v/v (panels d–f) for combinations of structural diversity and stand density that span the range observed in our data.

In dense stands (relSDI = 1.0), structural diversity increased the relative contribution of large trees to stand growth (Fig. 10a). The i_v–v curves became more convex with increasing CV_{dbh}, meaning that large trees captured a greater share of the available growth. At intermediate densities (relSDI = 0.75), diversity had only minor influence on the distribution of growth across size classes (Fig. 10b). At low densities (relSDI = 0.50), the effect reversed: structural diversity reduced the growth allocated to larger trees, and smaller trees captured relatively more of the available growth (Fig. 10c).

The corresponding growth-efficiency patterns (panels d–f) show the same shifts. In dense stands, structurally diverse stands exhibited both

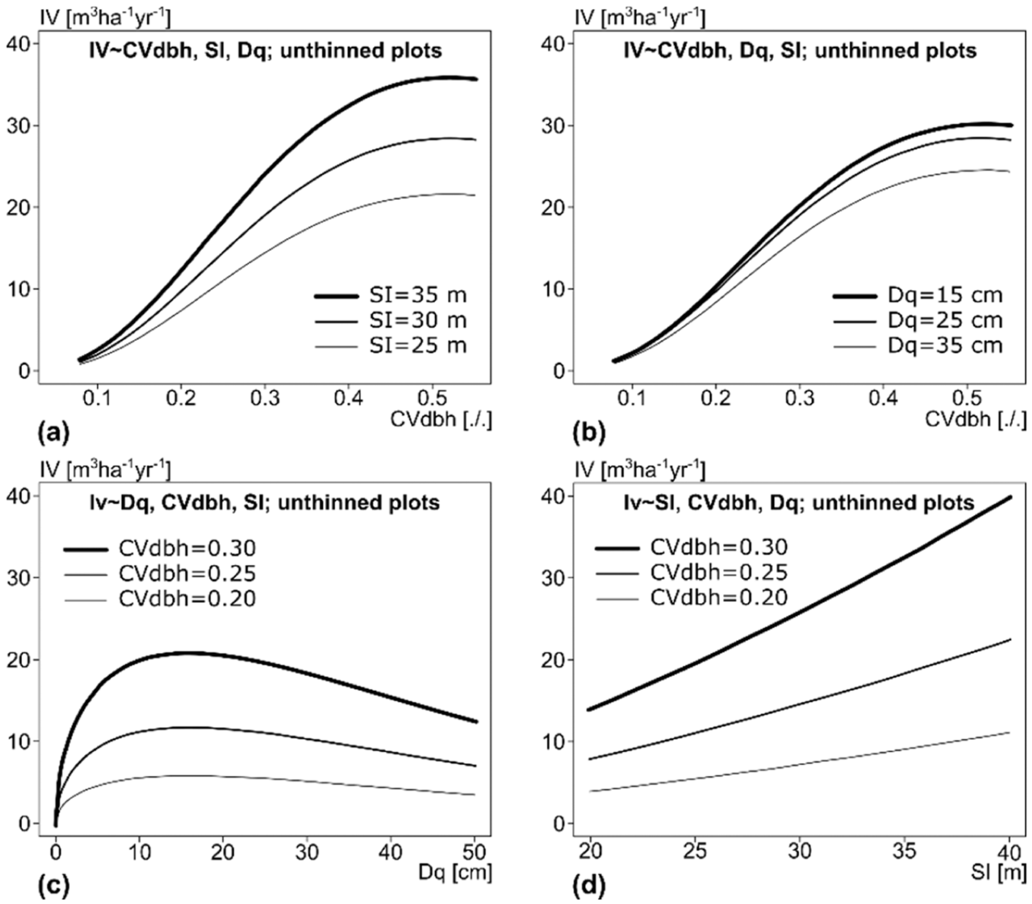

Fig. 7. Dependence of stand volume growth (IV) in fully stocked, unthinned stands on structural diversity (CV_{dbh}). The effect of CV_{dbh} on I_V is shown for (a) different site indices (SI), (b) stand development phases represented by quadratic mean diameter (D_q), (c) the D_q development trajectory, and (d) gradients of site productivity. Curves represent predictions from the selected model for unthinned stands (Model 4), with full model specification and statistical details provided in Supplementary Model Specifications, Supplementary Table 3, and Supplementary Figure 5.

higher overall efficiency and a strong efficiency concentration on larger trees (Fig. 10d). At medium densities (Fig. 10e), efficiency patterns were flatter, and differences between structural diversity levels diminished. At low density (Fig. 10f), the highest efficiency gains occurred in small and medium-sized trees, whereas large trees benefited only weakly. Thus, the efficiency ranking between homogeneous and heterogeneous stands depends strongly on stand density.

These interactions between size distribution, efficiency, and density are the mechanistic basis for the stand-level growth responses shown in Sections 3.1 and 3.2 (see Figs. 8 and 9). Supplementary Explanation 4 provides a worked example of how the size–growth relationships integrate to the density-dependent stand-growth patterns.

4. Discussion

4.1. Tracing the effect of structure on growth from the stand to the tree level

Our analysis showed a positive effect of structural diversity on crown space occupancy and stand growth at the stand level. Structural diversity was created in the underlying stands through high thinning; however, natural disturbances in the upper canopy, uneven-aged stands, or species mixtures can also produce similar structural diversity (Alonso Ponce et al., 2017; Pretzsch et al., 2016). The positive effect of structure on stand growth was particularly pronounced in dense stands and weakened as stand density decreased. This is in line with the findings in other studies (Leuchner et al., 2007; Larcher, 2003; Dirmhirn, 1964) that the light reflection due to the closed upper canopy and the low light penetration to deeper crown layers can cause a suboptimal resource supply and stand growth (Forrester et al., 2018). Our canopy space analyses (Figs. 4–7) suggest that in structurally diversified stands, the light reaches deeper into the canopy space, the overall growth is more efficient, and that stand growth can be increased compared with homogeneously structured stands.

To better understand this stand-level effect, we traced the influence of structural diversity from the canopy profile down to the distribution of individual trees. Structural diversity affected both the distribution of tree sizes and the functional relationship between size and growth (Fig. 10; Model 8). Together, these two components determine how the available growing space is partitioned among trees of different sizes and which combinations of size classes can realize high stand-level growth.

Our analysis in Section 3.3 showed that ensembles of trees with different sizes and efficiencies can make the best possible use of the growing space and resources and produce maximum stand growth. Heterogeneous ensembles created by light to moderate thinning from above can cause overyielding by 10–20% compared with homogeneous ensembles in stands that are unthinned or thinned from below. The numerous studies aimed at identifying particularly growth-efficient individual trees, sub-collectives, or layers (Mayer., 1958, Maguire et al., 1998, Reid et al., 2004) are not sufficient to find out the best possible growth at the stand level. For example, dominant trees can be particularly efficient, but their presence can reduce the growth of many medium-sized and small trees, resulting in suboptimal stand growth.

Clarifying how the increase in stand growth came about at the next higher level of resolution provides access to the following new insights, among others: It shows which size ensemble yields maximum stand

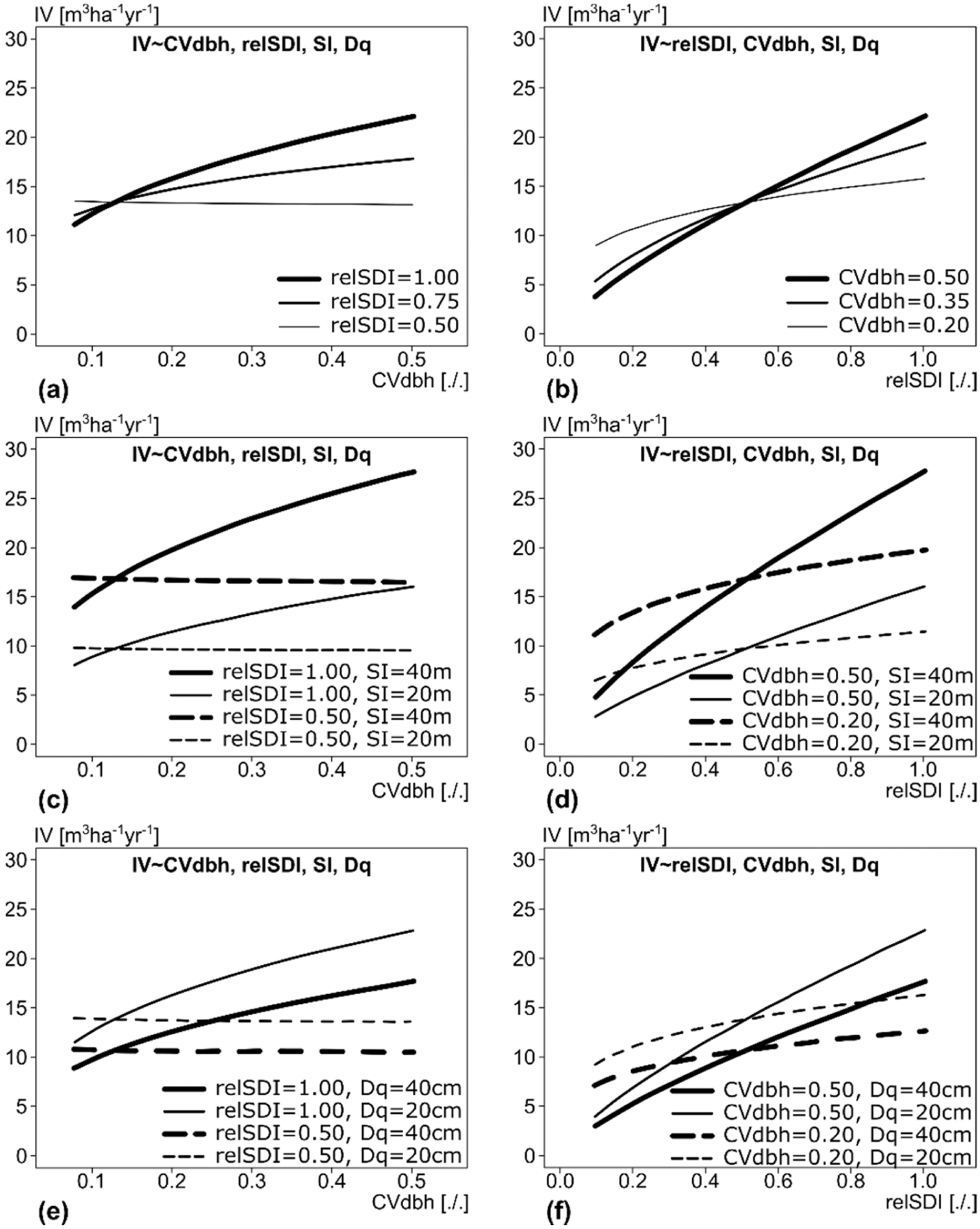

Fig. 8. Dependence of stand volume growth (I_V) in thinned and unthinned stands on structural diversity (CV_{dbh}), stand density (relSDI), site quality (SI), and stand development phase (Dq). Panels show how I_V is influenced by (a) different relative stand densities (relSDI), (b) different levels of structural diversity (CV_{dbh}), (c and d) site quality (SI), and (e and f) stand development phase (Dq). Curves represent predictions from the selected stand-growth model for thinned and unthinned conditions (Model 5); the full model specification and diagnostics are provided in Supplementary Model Specifications, Supplementary Table 3, and Supplementary Figure 6.

growth and how latter can be increased through structural diversification as addressed by science (Ali, 2019, Forrester, 2019) and practice (Reininger., 1987, Sterba, 2019). It further reveals how stand growth is distributed across tree size classes depending on structural diversity, and which tree sizes will be particularly promoted or reduced in terms of growth, e.g., in thinning from above compared to from below.

When using the relationship between growth and size to diagnose and quantify natural resource limitations (Grams and Andersen, 2007; Condés and del Río, 2015; Forrester et al., 2022) or stress effects (Wichmann., 2001; Pretzsch et al., 2012; Alam et al., 2017) in forest stands, it should be taken into account that this relationship can be modified by silvicultural stand management in terms of density and size distribution. The revealed non-linear size-growth relationship and its dependency on structure may avoid premature attribution of size-symmetric or asymmetric size growth correlations to light or nutrient limitation (Schwinning and Weiner, 1998) as it has been shown that stand density and tree size variation are essential covariates for the form of this relationship. Structural complexity in unthinned stands might even mediate the site quality.

4.2. *Rethinking and further development of previously assumed relationships*

Stand density-stand growth relationship: Our results suggest an extension of Assmann's. (1961) stand density-growth relationship by including the stand structure. We found that structural diversity in fully

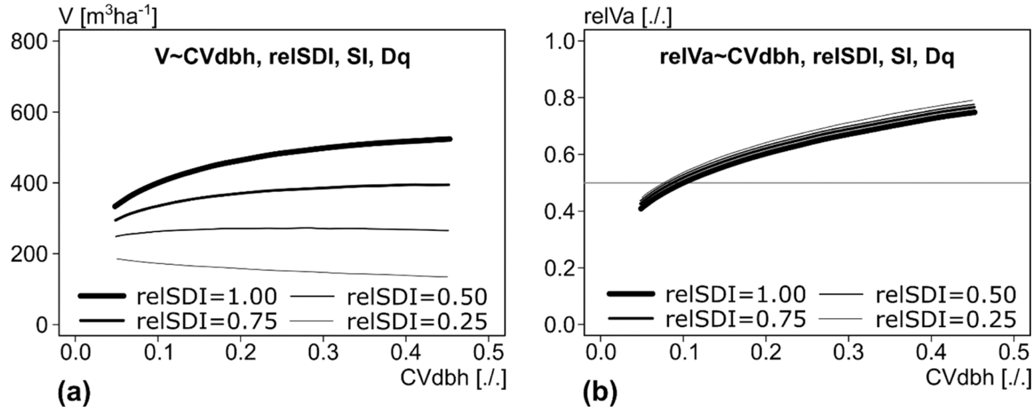

Fig. 9. Effect of structural diversity (CV_{dbh}) on (a) standing volume (V) and (b) the relative proportion of stand volume contributed by trees above mean stem volume (relVa). Curves show predictions from the selected structural-diversification models for standing stock and size-class distribution (Models 6 and 7). All other stand variables not shown in the respective panels were held at their mean values. Full model specifications and diagnostic statistics are provided in Supplementary Model Specifications, Supplementary Table 4, and Supplementary Figures 7–8.

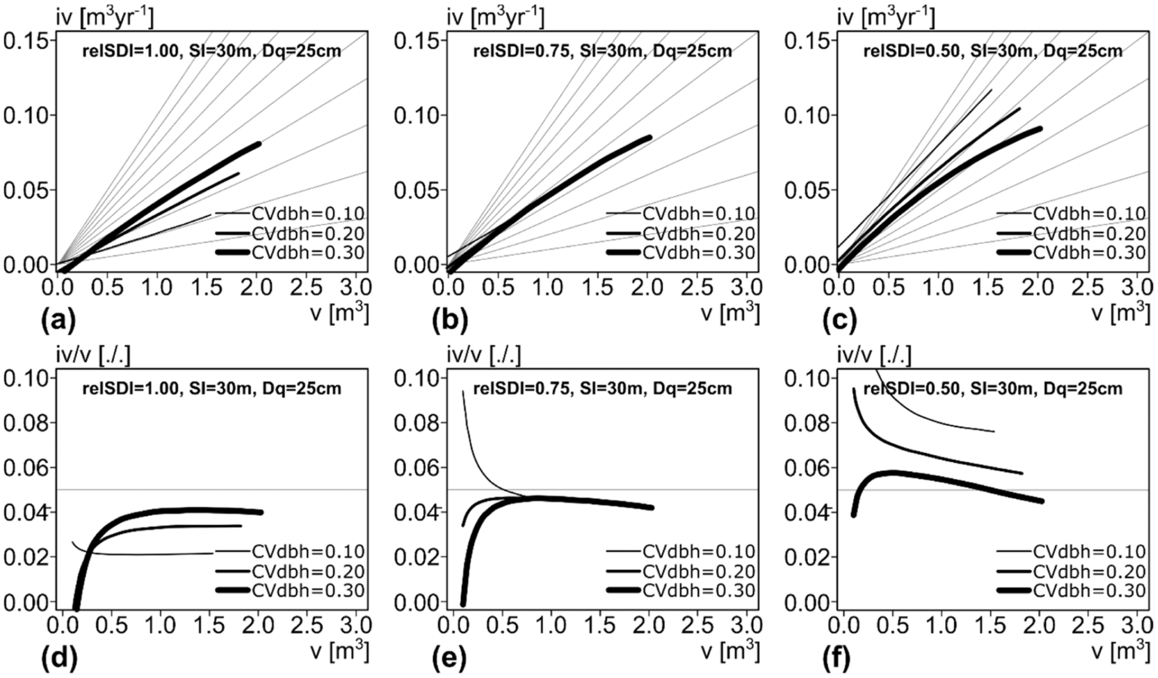

Fig. 10. Volume-volume growth relationships (a-c) and the respective volume-volume growth efficiencies (d-f) for different levels of structural diversity ($CV_{dbh=}$0.10–0.30) and stand density (relSDI = 1.00, 0.75, 0.50). Panels (a–c) show model-predicted relationships iv = f(v, relSDI, CV_{dbh}, SI, D_q). Panels (d–f) show the corresponding efficiencies iv/v derived from the same model. SI and D_q were held at mean values. Model structure and diagnostics are provided in Supplementary Model Specifications, Supplementary Table 5, and Supplementary Figures 8–9.

stocked stands has a positive influence on growth, and that this positive influence decreases with density reduction and can even become negative (Figs. 8 and 9). Our findings align with recent research demonstrating structural diversity's role in forest productivity. The mechanisms we identified (improved crown space occupancy and differential growth efficiency) parallel the species complementarity effects observed by Deng et al. (2025) in mixed forests, where structural complexity becomes increasingly important with stand age. In addition to the influence of stand age on species mixture effects, density tends to strengthen positive species mixture effects as reviewed in Bauhus et al. (2017).

The unimodal relationship we documented supports our previous findings (Pretzsch et al., 2024), suggesting forest management should aim for specific structural configurations that optimize resource utilization rather than simply maximizing diversity. If stands that are kept relatively dense and structurally diverse, maximum growth can be achieved with them. If their density is reduced the structuring becomes a disadvantage. This interaction between density and structure effects on stand growth remains consistent across the spectrum of stand development phases and site productivity.

Differences in structural diversity, which may be due to differences in stand establishment (e.g., planting, sowing, natural regeneration) or thinning (homogeneity by thinning from below, heterogeneity by thinning from above), could therefore explain the different patterns of density-growth relationships reported by Kramer and Akça (1995) and Zeide (2001), among others. Interesting and new was that highest possible growth rates are likely to be achieved by silvicultural treatments that structure stands in a highly diverse manner like moderate thinning from above or selection thinning without reducing density too much.

We used SDI as a measure of stand density. It is based on the number of trees and the mean quadratic diameter, and has proven particularly useful for homogeneous pure stands (Zeide, 2005). As stand structure increases, the variation and right skewness of the stem diameter distribution increases, and consequently the representativeness of the mean diameter decreases. In studies of even more structured stands (e.g., selection forests, old-growth forests), other density measures should therefore be used.

Assmann's yield level: The finding that structural diversity can significantly increase the growth of untreated, fully stocked stands under otherwise identical conditions answers some open questions regarding stand dynamics. Under otherwise identical average conditions, stand growth in more homogeneous stands was 20% below and in more heterogeneous stands 21% above the growth of stands with average structuring. This range in I_V values corresponded remarkably closely to the I_V and total yield range between the upper and lower yield levels according to mean values ± 20% (Assmann 1960, p. 166). This correspondence is notable because Assmann and Franz (1965) acknowledged different yield levels but did not systematically examine stand structural characteristics as a potential cause. Our results suggest structural diversity may explain this variation: greater structural diversity enables improved vertical stratification and differential growth efficiency, leading to more complete growing space utilization and higher yield levels. Conversely, homogeneous stands may underutilize available resources despite identical site conditions. The magnitude of our structural effect (±20%) matching Assmann's yield level range, combined with the mechanistic basis we identified, supports this interpretation. While alternative explanations such as unmeasured site factors or genetic differences cannot be ruled out, we hypothesize that differences in stand structure, which Assmann and Franz (1965) did not examine in detail, contribute substantially to the as yet unexplained yield level.

A-grade plots as reference: When analyzing the stand density-stand growth relationship, A-grade plots and untreated stands are used as reference. The growth response to density reductions on treatment plots is commonly set in relation to the growth on the control plots. Using this approach, Assmann (1961) arrived at unimodal density-growth relationship, while Curtis et al. (1997) and others assumed an asymptotic density-growth relationship. This contradiction (Zeide, 2001) could be resolved if structural diversity were taken into account. This is because if the stands selected as reference stands are structurally rich per se, their growth level is higher from the outset and thinning is more likely to reduce growth. If, on the other hand, the reference areas are more homogeneous, interventions diversifying structure (acceleration of the growth of large trees, preservation of small trees by opening up the canopy) are more likely to come off superior. In the first case, one may assume an asymptotic density-growth relationship, and in the second case, a unimodal one.

Overyielding by structuring and species mixing: The fact that even in untreated pure stands, an increase from medium to strong structural diversity can trigger a 20% increase in growth reveals the growth promoting effect of structural diversity. This suggests that the overyielding of mixed stands, which are mostly more structured compared to pure stands, is also triggered, at least in part, by structural diversity (Ali et al., 2016; Dănescu et al., 2016; Pretzsch, 2021). Interestingly the overyielding in mixed stands is usually around 20% (Piotto, 2008, Pretzsch and Schütze, 2018, Jactel et al., 2018), which is similar to the increase gained by structuring monospecific stands found in this study.

Nonlinear size-growth relationship: Usually, this relationship is assumed to be linear (Prodan, 1965; Forrester, 2019), but this might obscure the actual partitioning patterns and oversimplify them. The revealed polymorphic size-growth relationship underscores that assuming a linear relationship (Prodan, 1965; Kramer and Akça, 1995; Forrester, 2019) is an oversimplification that can lead to significant errors when extrapolating from the tree to the stand level. The fact that we found mainly concave relationships means a misjudgment of the growth, especially for small and large trees.

4.3. *Consequences for silvicultural stand management*

Our results show that silvicultural interventions or natural disturbances that create a vertically differentiated canopy can increase stand growth beyond the levels observed in uniform stands that were thinned from below. This is consistent with findings by Sterba (1999), (2019), Vuokila (1977), (1980) and Reininger (1987), but our analysis provides a more mechanistic explanation by linking structural diversity directly to changes in growth allocation along the tree size distribution.

A central insight is that structure interacts strongly with stand density, and this interaction determines which tree sizes benefit most from the available resources. In dense canopies, a clear vertical stratification leads to a larger share of growth being allocated to the upper crown layers and thus to larger trees. With moderate density reduction, the contrast between size classes becomes weaker and growth is partitioned more evenly. Under very light stocking, the competitive advantage of large trees declines. Smaller trees respond with the largest relative efficiency gains because they can exploit the increased growing space more effectively. In other words, heavy thinning reverses the usual size hierarchy of growth benefits.

These patterns have important consequences for thinning strategies. In dense, uniform stands, large trees do not dominate growth as strongly as often assumed. Medium sized and small trees maintain a considerable share of total production. This helps explain why uniform thinning from below can reduce stand growth. Many smaller trees benefit, but the collective response is not optimal for total yield. In contrast, dense and structurally diverse stands such as those created by thinning from above direct more growth into the dominant cohort and can therefore exceed the production of monolayered stands.

With stronger thinning, however, the situation changes fundamentally. The relative advantage of smaller and medium sized trees becomes greater than that of the dominant trees. This creates a silvicultural dilemma. Heavy thinning increases the growth of the desired larger crop trees, but it increases the growth of their competitors even more. Stand level productivity therefore remains high even at low density, but the dominance of large trees is weakened. This can be advantageous if the goal is to maintain small trees for long rotation periods or for transforming stands towards uneven aged structures, but it is disadvantageous if the objective is to maximize the growth of the dominant cohort. In addition, the relative reduction in large tree growth vs. the promotion of small tree growth through heavy thinning makes it harder to identify and continuously promote crop trees (Schröpfer et al., 2009).

Understanding how the size distribution interacts with the size growth relationship provides a more precise basis for silvicultural decision making. It clarifies which combinations of tree sizes maximize stand growth under different structural conditions and how interventions shift the balance between promoting future crop trees and stimulating subordinate trees. This is highly relevant for management systems that aim at structural diversification, regeneration under shelter or transitions towards uneven aged structures (Schütz, 2001; Sterba, 2004).

The reaction patterns shown here, using Norway spruce as an example, are likely to differ in tree species that are less shade-tolerant and have less crown plasticity. In order to unleash the potential for diversification of structure and species composition, the relationships between genetic and structural variation and the growth behavior of stands should be investigated across species (Bravo et al., 2024).

5. Conclusion

For Norway spruce stands, the effect of structural diversity on crown space occupancy, increment distribution among trees, stand growth, and light use efficiency was quantified. For example, structuring with moderate density reduction (moderate high-thinning) deepens light penetration, increases crown space occupancy, increases the proportion and growth efficiency of large trees, and raises stand growth above the level of less structurally diverse stands. Homogenizing interventions (low-thinning) reduce penetration depth and space occupancy. They result in a more size-symmetric and less efficient size-growth pattern and reduce stand growth.

On the one hand, these insights are useful for resource-efficient, knowledge-based forest management, since structure is relatively inexpensive to obtain compared to measures such as pruning, fertilization, or mixing. In existing stands structural diversity may be created by thinning from above, selection thinning, or underplanting. When establishing a stand, structural diversity can be achieved, among other measures, through genetic diversity of plants, natural regeneration, age unevenness, or variation of spacing patterns.

On the other hand, structure is identified as an essential covariate for understanding stand dynamics. In this study, structural diversity was quantified solely on the basis of tree diameter variation. If height measurements and trunk base coordinates had been available for all trees, the height structure could have been included in the analysis more accurately, as could the horizontal tree distribution pattern. The high explanatory power of diameter distribution alone suggests that future studies should also include height and tree distribution information.

Regularities such as the relationships between density and stand growth, tree size and growth, density and growth allocation, among others, become more consistent by incorporating the structural component. The positive growth responses observed to the structuring of pure stands could also explain overyielding in mixed stands, since these are usually more structurally rich than similar comparison stands.

Given the demonstrated effect of structural diversity on increment, the known relevance of structure for many ecosystem services, and the increasing accessibility of information on stand structure, the revealed principles should also be analyzed for tree species and tree species combinations with other functional traits.

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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. Supporting information

Supplementary data associated with this article can be found in the online version at doi:10.1016/j.foreco.2026.123699.

Data availability

Data will be made available on request.

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