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The effect of structural diversity on the self-thinning line, yield level, and density-growth relationship in even-aged stands of Norway spruce

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ABSTRACT

Diversity of tree species and structure have the potential to increase various forest ecosystem services such as stress resistance, biodiversity, and productivity. Recent studies indicate the relevance and potential of both diversity of tree species and diversity of stand structure. Here, we analyze the effect of stand structure on the stand-level behavior of even-aged stands of Norway spruce (*Picea abies* (L.) H. Karst.). Drawing from 11 long-term thinning experiments encompassing 77 plots and 425 surveys, we analyzed the effect of tree size and growth frequency distributions on (i) the self-thinning line, (ii) the Eichhorn rule and yield level, and (iii) the stand density-growth relationship. We revealed an optimum relationship between the inequality of tree size and growth within forest stands and the maximum stand density, standing volume, total yield, and stand density-growth relationship. Highest stand density, standing volume, total volume yield, and stand volume growth occurred at moderate structural diversity, in terms of the inequality of tree size and growth. All else being equal, strongly homogeneous, or very heterogeneous stand structures were found to be suboptimal in terms of growth and yield. Our findings emphasize that incorporating information about tree size frequency distributions can greatly improve upon classical models of stand dynamics, even for even-aged spruce monocultures. The profound influence of stand structure on stand growth and yield, even when the classical stand attributes are analogous, warrants further scientific attention; e.g., neglecting differences in stand structure can lead to skewed interpretations of growth reactions to density regulation or species mixing. From a forest management perspective, our results unveil the untapped potential of structural diversification, even for mono-specific and even-aged stands. We elucidate the growth trade-offs when structural diversity is either neglected or overly emphasized.

1. Introduction

The prevailing ethos within human society and its corresponding demands on the forest stands determine the desired forest structure and diversity. While forest management might target even-aged mono-specific stands for utmost homogeneity (Bauhus et al., 2010; Gadow et al., 2001), it might also generate heterogeneous stands by selecting and strongly releasing a chosen number of crop trees and sidelining the remainder (Kerr and Haufe, 2011; Boncina et al., 2007). Alternatively, it might maintain both structural and functional diversity by combining a defined portion of trees of different sizes, ages, and species (Pommerening and Murphy, 2004; Gadow et al., 2002). Analogous societal trends towards more diversity of individuals for the sake of flexibility, resistance, and adaptation can be observed in human organizations, e.g., in universities, companies, schools, the army, and society as a whole.

The historical focus on wood production in forest management frequently led to even-aged and monospecific stands that were thinned from below, homogenized in structure, and standardized regarding assortment yield (Messier et al., 2015; Pretzsch et al., 2008). The current shift towards heterogeneously structured stands stems from the

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expectation that they more effectively deliver ecosystem functions and services, including stress resistance, carbon sequestration, and aesthetic and recreational benefits, compared to their homogeneous counterparts (e.g., Mo et al., 2023, Dronova, 2017, Sutherland et al., 2016, Biber et al., 2015). Finally, diversification can strongly improve the disturbance recovery (Turner and Seidl, 2023).

Consequently, numerous studies have explored mixed-species stands (del Río et al., 2022; Jactel et al., 2018; Liang et al., 2016) and the transformation of regular to more irregular forest stands (e.g., Hilmers et al., 2020, Pretzsch, 2019, Schütz, 2001). Particular emphasis has been placed on the effect of tree species diversity on the productivity (Toïgo et al., 2015), density (Pretzsch and Biber, 2016), and mortality (Pretzsch et al., 2023) of forest stands. Recent studies indicate that the benefits derived from tree species mixing are contingent not only on the species identity but also on the created structures (Ali et al., 2016; Dănescu et al., 2016). This underscores the importance of research into forest stand structures, ranging from even-aged mono-specific stands to uneven-aged mixed stands (Ehbrecht et al., 2017; Jucker et al., 2015). Yet, only a very few studies have demonstrated that variations in tree size and growth can influence stand-level growth, even in even-aged monospecific stands (e.g., Soares et al., 2016, Katholnig, 2012, Bravo and Guerra, 2002).

Tree size distributions and growth partitioning among trees within a forest stand have primarily been analyzed as response variables. For instance, they have been used for quantifying how many trees of which size and what assortment yield will be achieved by a defined silvicultural treatment (e.g., Nord-Larsen and Cao, 2006, Maltamo et al., 2004, Loetsch et al., 1973). Tree size distributions have also served as indicators of naturalness (Coomes and Allen, 2007), disturbances (Zenner, 2005), or forest demography (Stark et al., 2015). Studies of heterogeneous mono- and mixed-species stands have explored the effect of size structure and growth partitioning on aspects like stand growth (e.g., Binkley, 2004, Caspersen et al., 2011, Torresan et al., 2020) and stand density (Woodall et al., 2005). Forrester (2019) posited that even in stands with consistent density, the tree size distribution and inter-individual growth partitioning can modify stand productivity, emphasizing the need for deeper investigations.

Predominantly, studies on stand growth and yield rely on mean and sum values. For example, stand growth is typically described and modeled based on stand density without accounting for the distribution of size and growth among the trees in the stand (Skovsgaard and Vanclay, 2008). While individual tree models predict stand growth starting at the tree level and ending at the stand level (DeAngelis and Grimm, 2014), they don't explicitly incorporate size and growth distribution.

The need for more empirical studies exploring the connection between stand structure and dynamics prompted this investigation into the diversity of tree size and growth in even-aged Norway spruce (*Picea abies* (L.) H. Karst.) stands and their effect on various aspects of stand behavior. For our analysis we chose Norway spruce as model species because of its high representation in both forestry and long-term experiments in Europe (Pretzsch et al., 2019). Covering approximately 20% of the forest area Norway spruce is after Scots pine the second most important tree species in Europe (Brus et al., 2012; Jansen et al., 2017; Köble and Seufert, 2001). Its high productivity and economical relevance triggered many long-term thinning experiments. For no other species we have such a solid database for analyzing the effect of structural diversity on the self-thinning line, yield level, and density-growth relationship. An important aspect of forest stand structural diversity is that it can be achieved directly in existing stands by shaping the variation of size and growth distribution (Pretzsch and Zenner, 2017; Reininger, 1987). In contrast, establishing species diversity usually demands greater time and resources.

For scrutiny of structural effects in even-aged stands, we analyze the implications of the tree size and growth frequencies for the four basic relationships of forest stand dynamics, as visualized in Fig. 1. We hypothesized that the tree size and growth variation within even-aged stands could modify the basic relationships of forest stand dynamics, including the (a) self-thinning line (Reineke, 1933), (b) Eichhorn rule (Eichhorn, 1902), (c) special yield level (Assmann, 1970), and (d) the density-growth relationship (del Río et al., 2017; Assmann, 1970; Zeide, 2002). Our analysis seeks to determine the degree to which stand characteristics deviate from the average trajectory (represented by bold lines with grey band around) based on the size and growth variations of the respective tree population.

The self-thinning line (Fig. 1a) and the associated maximum stand density concept (Zeide, 1991) are also based on the mean and sum values of the stand (mean stem diameter and tree number per hectare), overlooking the effect of tree size and growth distribution. However, behind a given mean stem diameter could lie a population with uniform stem diameters (symmetric Gaussian normal distribution), a right skewed distribution, or even a Poisson distribution of stem diameters. And the course of the self-thinning line and the maximum packing density of the trees may vary with the tree size distribution (Ducey and Knapp, 2010).

Analyses of even-aged mixed species stands revealed that the intercept and slope of the relationship between mean stem diameter and tree number in fully stocked stands, as well as the maximum density, are influenced by specific traits like growth velocity, allometry, and mortality of the combined species (Rivoire and Le Moguedec, 2012). Sterba and Monserud (1993) highlighted the correlation between maximum density and size distribution in uneven-aged mixed-species stands. Yet, the ways in which size distribution and growth partitioning may differ in monospecific stands (e.g., due to spacing, thinning, genetic diversity, etc.) and how their structural diversity affects the self-thinning line and maximum stand density remain areas ripe for exploration (Forrester, 2019).

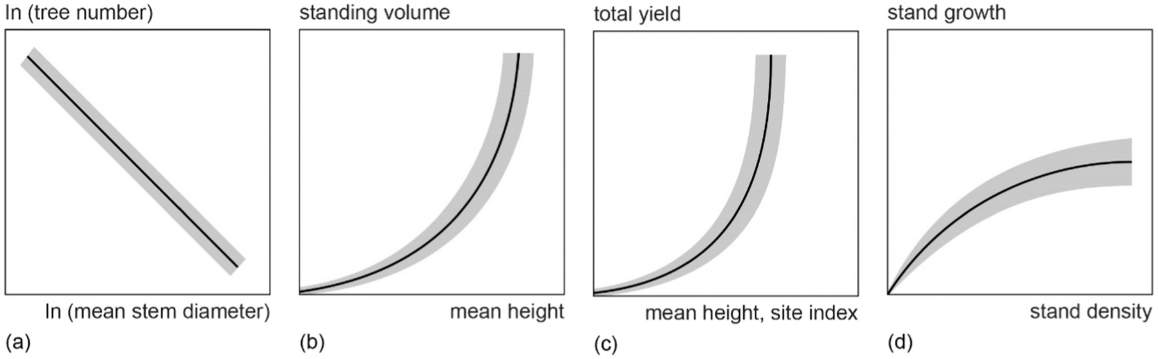

Fig. 1. Visualization of the four basic relationships of stand dynamics that we addressed in this study. (a) self-thinning line (Reineke, 1933), (b) Eichhorn rule (1902), (c) special yield level (Assmann, 1970), and (d) density-growth relationship (Assmann, 1970; Zeide, 2002). We analyze to what extent the stand characteristics vary around the mean curve (bold line with grey band around) depending on the variation of size and growth of the respective tree population.

We further analyze the effect of tree size and growth distribution on Eichhorn's rule (Eichhorn, 1902, p. 59), posing that the total standing volume in fully stocked, pure, even-aged stands solely depends on the mean stand height, independent of stand age and density (Fig. 1b). The relationship was extended by Gehrhardt (1909, 1923) to apply to total volume production or gross volume yield. The standing volume-mean height or total volume yield-mean height relationships are the backbones of many stand growth models (Skovsgaard and Vanclay, 2008), used for the indication of disturbances in forest stands (Vygodskaya et al., 2002) or as a baseline for the development of stand management rules (Trouvé et al., 2019). Other authors explained deviations from the Eichhorn rule by different productivity levels (Dhôte, 1996) or stand type, initial density, rotation length, and site quality (Newton, 2015).

Systematic deviations from Eichhorn's rule prompted Assmann (1970) to introduce the concept of the special yield level, which relates the total volume yield to mean height and site index (Fig. 1c). Recognizing that even stands with comparable mean height and site index can still exhibit differences in total yield, Assmann further introduced the concept of subdivided special yield level. According to this, the total yield can fluctuate by ±20% around the special yield level, depending on the local site conditions (Assmann, 1970, pp. 173–177).

Variations of the tree size distribution and growth partitioning have seldom been considered as factors influencing fluctuations around the special yield level. However, drawing parallels with the relationship between tree number and mean stem diameter, the kind of size distribution (whether trees within a stand have equal or unequal tree sizes and growth) might also affect the resource use, packing density, and ultimately, the standing stock and total yield of a stand at a given height. For instance, a heterogeneous size distribution may enable deeper light penetration into the canopy, promoting the growth of both small and large trees, thereby ensuring a more complete resource use and occupation of the available growing space compared to more homogeneous stands (Pretzsch, 2014).

Regarding the density-growth relationship, two contrasting theories exist: the asymptotic relationship (see Fig. 1d) assumed by Curtis et al. (1997) or Smith et al. (1997), and the unimodal relationship with an optimum point at slightly reduced stand density as introduced by Assmann (1970) or Pretzsch (2005). Notably, neither of these models accounts for the size structure of the stand as a covariable (Zeide, 2001, 2002), likely due to the historical and ongoing scarcity of data for stands with similar density but different size structure. However, Forrester (2019) showed how differences in tree size distribution and inter-individual growth partitioning can result in different stand productivity, even in stands with the same density.

In an extensive study of 11 long-term thinning experiments involving Norway spruce, encompassing 77 plots – both un-thinned and differently thinned – and 425 survey periods, we quantified the size structure, growth partitioning, and stand characteristics. We aimed to analyze how the frequency distribution of size and growth modulates stand level behavior. Specifically, we questioned how the frequency distribution of tree size and growth modulates the relationships between.

Q1: mean tree size and tree number (self-thinning line),

Q2a and b: mean tree height and standing volume (Eichhorn rule) and mean tree height and site.

index and total yield (special yield level),

Q3: stand density and stand growth.

We discuss the modification of the stand-level relationships by the tree size frequency distributions of the respective stands and the implications for understanding, theory and model building, and silvicultural steering of stand dynamics.

2. Material and Methods

2.1. Basic characteristics of the included long-term thinning experiments

We have chosen 11 long-term thinning experiments in southern Germany (Fig. 2) to examine the effect of tree size and growth diversity on aspects such as the self-thinning line, Eichhorn rule, yield level, and density-growth relationship. Each stand is monospecific, even-aged, and originated from planting or seeding. We only included experiments without severe biotic or abiotic disturbances (e.g., by wind, snow-breakage, bark beetle); mortality on all plots was mainly driven by competition. At the time of the most recent survey, their ages varied between 44 and 143 years (Table S1). The elevation above sea level of these plots spans from 510 m to 810 m. All plots' combined long-term mean annual temperature is between 6 °C and 7.5 °C, while the mean annual precipitation ranges from 800 mm to 1200 mm (Table 1). Predominantly, these plots feature loamy soils. Regarding soil types, the spruce plots were predominantly established on parabrown and brown soils (Table 1). The 11 long-term thinning experiments comprise varying numbers of plots. For instance, while experiment DEN 5 consists of only three plots, experiment FFB 612 encompasses 21 plots. The plot sizes vary, with the smallest being 0.09 ha and the largest extending to 0.25 ha. Depending on the timing of the first (ranging between 1882 and 1993) and last (occurring between 1990 and 2022) surveys, each experiment underwent between 6 and 18 surveys (Table S1), thereby offering a temporally comprehensive dataset for our analysis.

The experiments encompassed plots subject to various predefined thinning grades, following Wiedemann (1935), explained in detail by Kramer (1988, pp. 179–183), and applied on the experimental plots of this study (Table S1). The A-, B-, and C-grades denote slight, moderate, and intense thinning from below. On A-grade plots, only dead or dying trees were removed. On B- and C-grade plots, mainly small and subdominant trees were eliminated; B-grade retained only co-dominant and dominant trees, while C-grade preserved solely the dominant trees. The D- and E-grades represent moderate and strong thinning from above. Both grades eliminate mainly dominant trees to promote the growth of the remaining dominant trees. The difference between D- and E-grade thinning is rather the horizontal distribution of the interventions (D-grade homogeneously, E-grade around future crop trees) than the stand density reduction. For a more comprehensive explanation of the internationally defined thinning grades, refer to Assmann (1970) and Verein Deutscher Forstlicher Versuchsanstalten (1902, 1873).

2.2. Stand data evaluation

In this study, the characteristics at the stand level were derived from successive inventories, which included tree diameters, tree heights, and records of the dropout trees (Table 2). 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") (Johann, 1993; Biber, 2013). The calculation of stem volume was conducted using regional-specific stem form equations and coefficients. 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 (1936/42). 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. To describe stand density, we used the stand density index (SDI) according to Reineke (1933). In calculating the SDI for this study into Norway spruce, the exponents of $\alpha_{N,d}$ was set to -1.664, as recommended by Pretzsch and Biber (2005).

Delving deeper into the data presented in Table 2, it is evident that the experimental plots exhibited a diverse range of growth and yield characteristics. These differences were observed between the different experiments and within the plots of a single experiment.

The expected stand height at age 100 (SI) demonstrated a variation, with values oscillating between 30 and 46 m, and an average height of 38.75 m was recorded across all plots. Furthermore, the number of stems per hectare showcased a wide range, from a minimal 150 to a

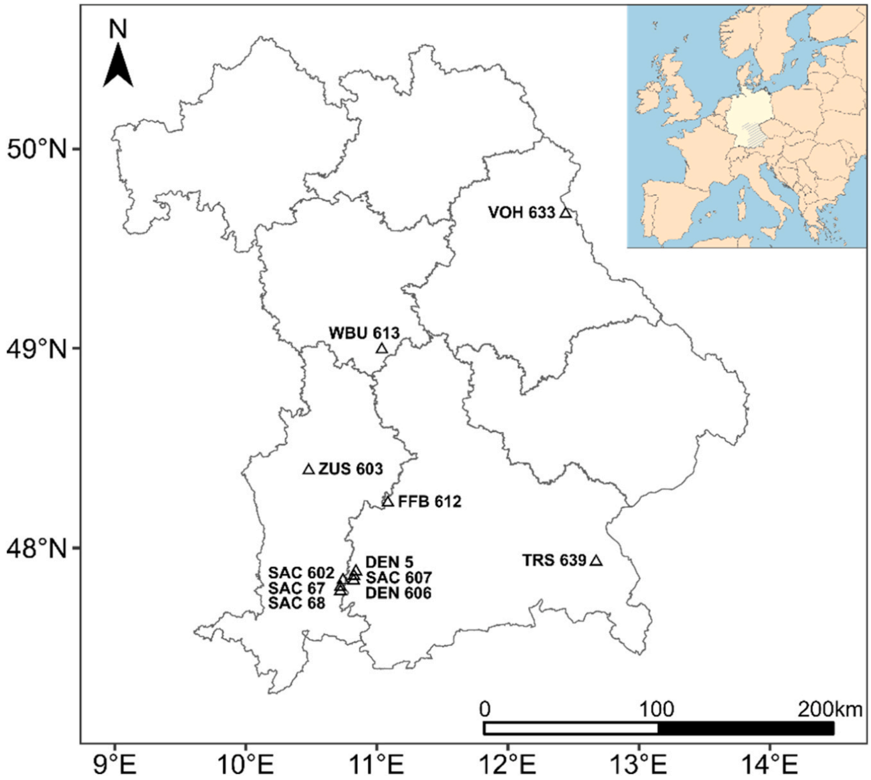

Fig. 2. Map with the distribution of the 11 thinning experiments of Norway spruce in Southern Germany. Abbreviations near the symbols refer to the location and number of the experiments (see Table 1).

Table 1
Geographical information and site characteristics of the long-term thinning experiments involving Norway spruce sampled in this study. E, elevation (m a.s.l.); T, mean annual temperature (°C); P, annual precipitation (mm). Soil texture and type as described in the world reference base for soil resources (FAO, 2014).

Experiment No.	E. lon	N. lat	E	T	P	Soil texture	Soil type
DEN 5	10.841	47.873	770	6.8	1100	loam	parabrown soil
SAC 67	10.752	47.834	840	6.2	1200	loam	parabrown soil
SAC 68	10.753	47.834	840	6.2	1200	loam	parabrown soil
ZUS 603	10.480	48.397	510	7.5	800	loamy sand	brown soil
DEN 606	10.825	47.868	760	6.8	1120	loam	parabrown soil
SAC 607	10.823	47.867	770	6.8	1120	sandy loam	parabrown soil
FFB 612	11.094	48.239	550	7.5	825	loam	parabrown soil
WBU 613	11.040	49.002	560	7	800	loam	parabrown soil
VOH 622	12.438	49.684	730	6	900	loam	brown soil
TRS 639	12.673	47.940	590	7.3	1200	loam	Pseudogley

substantial 2524 trees per hectare. Similarly, the quadratic mean stem diameter (dq) and mean stem height (hq) varied markedly, ranging from 16.9 to 56.9 cm and 12 to 41.5 m, respectively. Regarding standing stem volume (V), values fluctuated between 128 and 1461 m^3ha^{-1}, indicating the variations in merchantable stem volume across the different plots. Here we define merchantable volume as volume with diameter $>$ 7 cm at the smaller end. The stand density index (SDI) also exhibited a broad spectrum of values, ranging from 273 to 1575 trees per hectare, further emphasizing the diversity in stand density across the experimental plots. Analyzing the periodic mean annual volume growth (IV) and total yield (TY), it was observed that these values also varied considerably between the plots, with IV ranging from 10.3 to 38.8 $m^3ha^{-1}year^{-1}$ and TY between 160 and 2258 m^3ha^{-1}.

In conclusion, the detailed analysis of the experimental plots, as outlined in Table 2, reveals a multifaceted picture of growth and yield characteristics. The diversity observed within and among the experiments underscores the suitability of this data to examine the effects of tree size distribution and growth partitioning on aspects such as the self-thinning line, Eichhorn rule, yield level, and density-growth relationship.

2.3. *Characterizing the size distribution and the growth partitioning among trees*

In this study, to characterize the tree size distribution and growth partitioning, we utilized two key metrics: the Gini Coefficient of the stem volume (*GC*) and the Growth Dominance Coefficient (*GDC*) based on stem volume and stem volume growth. These metrics were applied across all plots and surveys to provide a comprehensive understanding of how variations in tree size distribution and growth partitioning can influence stand dynamics and overall forest productivity.

Gini coefficient of tree size, GC: The Gini coefficient for a cumulative stock of trees is generally calculated as follows: $GC = \frac{\sum_{i=1}^{n}\sum_{j=1}^{n}|x_i - x_j|}{2n(n-1)\times\bar{x}}$ (see de Camino, 1976; Kramer, 1988). Where x_i and x_j denote the size (or growth or other tree characteristics) for the i'th and the j'th tree in the stand, with $i = 1\ldots n$ trees, and $\bar{x}$ is the mean value of the characteristic being measured across all trees. The Gini coefficient, *GC*, of tree size (e.

Table 2
Overview of the growth and yield characteristics on the plots (mean, minimum, maximum) of the 11 thinning experiments in Norway spruce shown for the last survey. SI, site index based on hq; N, tree number; dq and hq, quadratic mean stem diameter and mean tree height; V, standing stem volume (merchantable volume > 7 cm); SDI, stand density index; IV, periodic mean annual volume growth; TY, total yield, i. e. gross volume growth since stand establishment.

Experiment No.		age (years)	SI (m)	N (trees ha^{-1})	dq (cm)	hq (m)	V (m^3 ha^{-1})	SDI (trees ha^{-1})	IV (m^3 ha^{-1} year^{-1})	TY (m^3 ha^{-1})
DEN 5	mean	132	36	397	50.4	32.3	1260	1236	13.5	1980
	min	132	35	276	44.7	38.6	1076	1028	12.8	1925
	max	132	36	528	55.1	39.5	1372	1389	14.1	2036
SAC 67	mean	119	38	365	51.6	34.1	1321	1186	16.4	2194
	min	119	37	252	47.1	39.5	1156	990	15.6	2160
	max	119	39	472	56.9	41.5	1461	1354	17.9	2258
SAC 68	mean	118	38	396	48.9	33.9	1193	1142	15.3	2032
	min	118	38	236	43.0	39.9	1004	919	14.6	2004
	max	118	39	556	56.6	40.9	1394	1371	16.3	2070
SAC 602	mean	46	40	1226	24.8	15.7	615	1152	36.1	1002
	min	46	38	740	22.2	22.2	524	931	33.4	961
	max	46	40	1919	28.7	23.7	828	1575	38.4	1036
ZUS 603	mean	42	42	1598	22.6	13.3	576	1122	29.4	780
	min	42	40	480	16.9	21.3	493	812	26.7	733
	max	42	46	2524	34.3	25.2	674	1405	32.4	832
DEN 606	mean	50	37	1242	23.5	16.7	554	1031	21.9	908
	min	50	36	560	20.2	22.5	360	676	15.2	759
	max	50	39	2144	28.0	24.6	784	1504	27.2	1023
SAC 607	mean	53	37	722	28,4	17,8	494	843	22,7	780
	min	53	34	443	21,8	22,2	327	600	18.0	571
	max	53	39	1668	31.8	26.2	675	1328	30.0	901
FFB 612	mean	37	41	941	24.9	14.5	357	795	27.7	489
	min	37	38	200	17.1	17.7	161	370	17.7	220
	max	37	44	1989	39.8	20.9	517	1171	33.6	695
WBU 613	mean	86	32	615	33.3	25.3	675	931	14.4	1182
	min	86	30	300	27.3	27.4	476	615	10.3	1048
	max	86	34	900	38.7	31.2	942	1263	18.8	1275
VOH 622	mean	33	40	498	23.0	12.0	161	417	15.7	244
	min	33	39	286	19.4	15.7	128	316	12.8	160
	max	33	42	638	29.2	17.8	198	497	18.9	303
TRS 639	mean	36	45	682	29.8	16.0	339	699	23.3	540
	min	36	45	150	23.0	20.8	142	273	11.6	364
	max	36	45	1600	35.8	21.3	665	1393	38.8	706

g., based on stem diameter or stem volume) can be used for quantification of whether a tree size distribution is homogeneous and equal ($GC = 0$), maximal unequal ($GC = 1$), or in between (e.g., $GC = 0.5$). After ranking the trees according to their volume, it can be visualized by plotting the cumulative tree volume against the cumulative tree number. In Fig. 3a, the curves for $GC = 0, 0.5$, and 1 are shown. A Gini coefficient of 0.5 might be observed in mature, even-aged forest stands, indicating a moderate level of inequality in tree size distribution. In this study, the tree volume was used to characterize tree size (GCv). The Gini coefficient as indicator variable was chosen, as it is frequently used in forest science, and it makes our results comparable with other studies into stand structure. In addition the Gini coefficient has a higher sensitivity to a range of non-normal distributions relative to alternatives such as Shannon’s H’ applied to diameter classes (Lexerød and Eid, 2006).

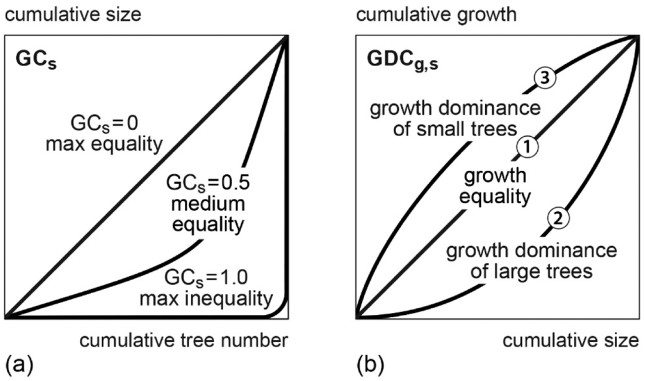

Fig. 3. Visualization of the approaches and applied metrics to quantify the effects of tree size distribution and growth partitioning on stand dynamics and yield. (a) The Gini coefficient, GC_s, of tree size reflects the degree of equality of the stem size distribution. (b) The Growth Dominance coefficient, $GDC_{g,s}$, indicates equality of growth partitioning (curve 1, GDC=0) and the growth dominance of large (curve 2, GDC>0) or small trees (curve 3, GDC<0).

Growth Dominance Coefficient, GDC: The Growth Dominance Coefficient is a measure used to evaluate the growth partitioning among trees within a forest stand. It was proposed by Binkley et al. (2006) and further detailed by West (2014). The GDC describes the partitioning of the annual or periodic size growth of n individual trees (e.g., stem diameter growth, id, or tree volume growth iv) relative to their size at the beginning of the growth period (Fig. 3b). Thus, it provides a measure of the growth dominance within forest stands. For the calculation of the GDC, the following statistic was used:

$$GDC = 1 - \sum\nolimits_{k=1}^{n} (cv_k - cv_{k-1}) \times (civ_k - civ_{k-1})$$

where n is the number of trees in the stand, k represents the relative position (rank) of a tree in ascending order of tree volumes, whereas cv_k and civ_k denote the cumulative proportion of trees ranked 1 to k in the total stand volume and in the total stand volume increment, respectively. If $GDC = 0$, it indicates that all trees contribute proportionally to the total growth relative to their stem size. If the value is negative ($GDC < 0$), smaller trees contribute over-proportionately high to the total growth; if $GDC > 0$, larger trees contribute over-proportionally to the total growth (Fig. 3b). The GDC was calculated for all the growth periods used in the analysis. GDC can vary with increasing growth period length (Dye et al., 2019). However, on our plots the growth period lengths varied only between 4–6 years and were 5 years on average.

2.4. Statistical models, derivatives

For analyzing the effects of *GC* on the stand density in terms of tree number per hectare (Q1), we used model (1), where *GC* and *SI* were included as additional covariables in the self-thinning line equation. For SI, we found no interaction with *GC*.

$$\ln(N_{ij}) = a_0 + a_1 \times \ln(dq_{ij}) + a_2 \times \ln(GC_{ij}) + a_3 \times GC_{ij} + a_4 \times \ln(SI_{ij}) + a_5 \times \ln(dq_{ij}) \times \ln(GC_{ij}) + \varepsilon_{ij}. \tag{1}$$

The effect of *GC* on the relationship between standing volume, *V*, (Q2a) and the total yield, *TY*, (Q2b) with mean height, *hq*, was analyzed by models (2) and (3). The site index was included in the model (3) as the total yield may vary with site index (Supplement S1)

$$\ln(V_{ij}) = b_0 + b_1 \times \ln(hq_{ij}) + b_2 \times \ln(GC_{ij}) + b_3 \times GC_{ij} + b_4 \times \ln(hq_{ij}) \times \ln(GC_{ij}) + \varepsilon_{ij} \tag{2}$$

$$\ln(TY_{ij}) = c_0 + c_1 \times \ln(hq_{ij}) + c_2 \times \ln(GC_{ij}) + c_3 \times GC_{ij} + c_4 \times \ln(SI_{ij}) + c_5 \times \ln(hq_{ij}) \times \ln(GC_{ij}) + \varepsilon_{ij} \tag{3}$$

For analyzing the effect of *GC* on the stand growth-density relationship (Q3), we used as dependent variable stand volume growth, *IV*, and as independent variable stand density, *SDI*, Gini coefficient of tree size, *GC*, and their interaction. Moreover, we included mean tree volume, *vq*, as it reflects the stand development phase. Site index and stand age had no additional significant effect on the stand growth-density relationship.

$$\ln(IV_{ijk}) = d_0 + d_1 \times \ln(vq_{ijk}) + d_2 \times \ln(GC_{ijk}) + d_3 \times GC_{ijk} + d_4 \times \ln(SDI_{ijk}) + d_5 \times \ln(SDI_{ijk}) \times GC + b_i + b_{ij} + \varepsilon_{ijk} \tag{4}$$

For analyzing the effect of *GDC* on stand volume production, *IV*, (Q3) we used the same model structure but replaced the Gini coefficient of tree volumes, *GC*, by the growth dominance coefficient, *GDC*. Model (5) does not use *GDC* directly, but the natural logarithm of *GDC*+ *1* to permit log-transformation. For about a third of the stands *GDC* was below 0 in certain observation intervals. By adding 1 before taking the logarithm, the variable $\ln(GDC+1)$ always exceeds zero for all trees. By integrating *GDC* in logarithmic and non-logarithmic representation the model is able to indicate any unimodal relationship between *GDC* and IV. In this model, the effect of age was significant.

$$\ln(IV_{ijk}) = b_0 + b_1 \times \ln(age_{ijk}) + b_2 \times \ln(vq_{ijk}) + b_3 \times \ln(GDC_{ijk} + 1) + b_4 \times GDC_{ijk} + b_5 \times \ln(SDI_{ijk}) + b_i + b_{ij} + \varepsilon_{ijk} \tag{5}$$

The models (1) – (3) were fitted by the quantile regression using $\tau = 0.75$. In contrast to model (4), which described the effect of different density levels on IV, models (1) - (3) address the N-, V-, and TY-values in fully stocked stands. By choosing $\tau = 0.75$, we based the regression on the upper 25% of the tree number, standing volume, and total yield values. Model calculations with $\tau = 0.90,\ 0.80,$ and 0.70 yielded similar results. However, we chose $\tau = 0.75$ as about a quarter of the included plots were unthinned or just slightly thinned.

With ε_{ijk}, we denoted the residual error with mean zero and unknown variance of σ^2. In the course of our analyses, while random effects were incorporated in models (4) and (5) to account for grouped structure, they were deliberately excluded from the quantile regression. Quantile regression focuses on estimating conditional quantiles of the response variable, and introducing random effects could complicate the interpretation of these quantile estimates.

In models (4) and (5), the indexes *i*, *j*, *k* refer to the levels experiment, plot, and single observation, respectively. Assumptions about uncorrelated remaining errors, ε_{ij}, are as before in models (1)-(3). To account for the grouped structure, random effects b_i and b_{ij} were implemented at the level of experiment and plot in alignment with the standard assumptions of mixed-effects models (e.g., Mehtätalo and Lappi, 2020). The random effects are independent across experiments and plots, and residual errors are independent across observations.

In the Eqs. (1) - (5) $a_0, \ldots, a_n$ - $e_0, \ldots, e_n$ are the parameters of the fixed effects. All modeling results were evaluated with the basic fit statistics: AIC, BIC, and − 2Log likelihood and were subject to the usual visual residual diagnostics. For all models, the residuals were plotted against the fitted values. In no case the plots suggested a violation of variance homogeneity. Likewise, the normality of errors was verified by making normal *q-q* plots of the residuals. See Supplement S1 for additional information about the building procedures regarding models (1)-(5). For all calculations, we used the statistical software R 4.1.0 (R Core Team, 2023), explicitly employing the packages *nlme* (Pinheiro and Bates, 2000, 2023), *lme4* (Bates et al., 2015), and *quantreg* (Koenker et al., 2017).

By setting the first derivation of the fitted models (1) – (5) to zero and retransforming it to *GC*, we deduced for which *GC* values the *N*-, *V*-, *TY*-, and *IV*-values achieve a maximum (see Table S2 and S3).

3. Results

3.1. Description of stand characteristics and their tree size and growth distribution

Fig. 4 provides an overview of the development of the size distribution in terms of volume, *GCv*, and size-growth partitioning, *GDCiv*, *v*, with the progression stand age, and the relationship between *GCv*, and *GDCiv*, *v*. The value spectrum is 0.1–0.5 for *GCv* and − 0.3–0.15 for *GDCiv*, *v*. *GCv*, values were higher in the young phase and exhibited a decline with progressing stand development (Fig. 4a). The hierarchy of mean *GCv*, values regarding the thinning grades was discernible as the A≅ D&E > B≅C (see Fig. 4a, horizontal lines). In case of *GDCiv*, *v* we found A> B>C>D&E (see Fig. 4b, horizontal lines). We pooled the plots of D- and E-grade thinning as the difference is rather the horizontal distribution of the interventions than the stand density reduction.

Fig. 4c reveals a hump-shaped relationship between *GDCiv*, *v* and *GCv*,. Stands characterized by average *GCv*, values achieve the highest *GDCiv*, *v* values. The very low *GDCiv*, *v* values in the lower right corner of Fig. 4a result from very widely spaced young stands (solitary plots) where smaller trees are rather facilitated than competed by larger neighbors. We exclusively show *GDC* and *GCv* owing to their prevalent usage in literature and their subsequent correlation to stand growth and yield. Both *GDCiv*, *v* and *GCv* were based on stem volume. Notice that *GDC* and *GC*, when based on variables such as stem diameter, stem basal area, or tree mass, demonstrated analogous behavior.

Fig. 5 shows relationships between variables at the stand level and the size distribution. Stand growth and yield characteristics, when plotted against *GCv* show hump-shaped relationships, with maxima at intermediate levels of size and growth inequality (Fig. 5, a-d). The *SDI*, standing volume (*V*), and total yield (*TY*) represent state variables and were consequently plotted over *GCv*, which represents the state of size distribution (Fig. 5, a-c). As the mean periodic stand volume growth is a rate variable associated to *GDCiv*, *v*, which quantifies the partitioning of this rate, it was plotted over *GCv* (Fig. 5d) and *GDCiv*, *v* (Fig. S1). All three relationships *SDI-GCv*, *V-GCv*, and *TY-GCv*, showed a hump-shaped distribution with a maximum at mean size inequality. Interestingly, stands either un-thinned or thinned from above presented comparable *GCv* values, markedly higher than those of stands thinned from below (see vertical lines in Fig. 5, a-c).

In addition to the visualization of the state of the stand growth and structure characteristics, Fig. S2 shows the trajectories of (a) *IV* over *GCv*, (b) *IV* over *GDC*, and (c) *GDCiv*, *v* over *GCv* for experimental plots

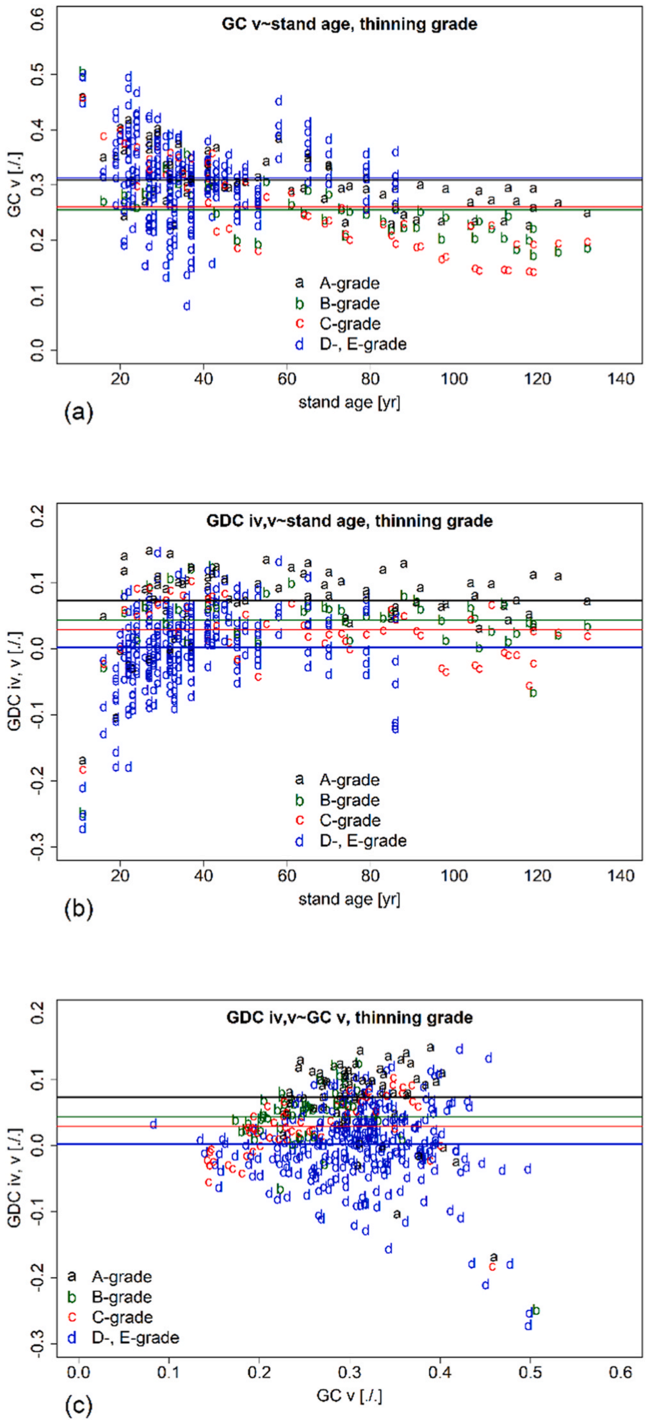

Fig. 4. Visualization of the GCv and $GDCiv, v$ values of stands with thinning grades A, B, C (light, moderate, strong thinning from below) and D and E (thinning from above) and ranking of the mean GCv and $GDCiv, v$ values (horizontal lines). (b) hump-shaped relationship between $GDCiv, v$ and GCv.

with thinning grades A, B, C (light, moderate, strong thinning from below) and D and E (thinning from above). The trajectories substantiate the unimodal relationships between IV and GCv, IV and $GDCiv, v$, and the negative correlation between GCv and $GDCiv, v$.

For further information about how the stand volume growth and the stand density index, SDI, develop with increasing age under different thinning grades (A-C thinning from below, D-E thinning from above), see Fig. S3.

3.2. Self-thinning line modulated by tree size distribution (Q1)

Fig. 6a presents the dataset for answering question 1; it delineates observed tree numbers plotted against mean tree diameters and the commonly expected self-thinning lines of Norway spruce with allometric slope $\alpha = -1.664$ and density levels SDI= 500, 1000, and 1500 trees ha^{-1}. The expected self-thinning lines ($\ln(N) = a + \alpha \times \ln(dq)$) are used in Fig. 6b as a reference for showing how the self-thinning line is modulated by the tree size distribution in terms of the Gini coefficient GCv (Table 3). In case of very unequal size distribution (GCv =0.40), the predicted line aligns closely with the expected self-thinning line with $\alpha = -1.664$; however, the more equal the size distribution, the more shallow the modeled self-thinning lines (for values of GCv =0.40, 0.30, 0.20 the steepness of self-thinning line decreases). Fig. 6c shows that there is a unimodal optimum relationship between GCv and tree number; given the same mean tree diameter and site index. The tree number (and respective maximum stand density) is the highest for mean GCv -values, i.e., mean tree size inequalities. For both more homogeneous and heterogeneous size distributions the stand density is below the maximum achieved by medium size variation.

The GCv value that allows maximum stand density for a given quadratic mean stem diameter was derived in Table S2. The GCv -values where stand density achieves the optimum change slightly with stand development. The optimal GCv depends on the quadratic mean stem diameter. $GC_{opt} = 0.287, 0.262, 0.245$ for dq= 25, 35, 45 cm. The derived optimal GC_{opt} and maximum tree number are visualized in Fig. 6c.

3.3. Eichhorn's rule and yield level as modulated by size distribution within the stand (Q2, a and b)

Fig. 7a shows the exponential increase of the standing volume with increasing mean stand height. The strong variation of V-values for given hq values results, among others, from the different thinning grades represented by the plots and the different GCv -values. Fig. 7b visualizes the results of model 2, based on quantile 75% to exclude non-fully stocked stands. We found a strong variation of V-values over stand mean height caused by the Gini coefficient (Table 4). Fig. 7c displays that there is a unimodal optimum relationship between V and GCv. Maximum standing volume is achieved at a mean degree of size inequality. The maximum of the curve is shifting to the left with progressing stand development, expressed by hq, i.e., in older stands, the maximum standing volume is achieved in more homogeneous stands, whereas in younger stands, the maximum is reached under more heterogeneous conditions (Fig. 7c). The site index did not significantly modify this relationship between V and GCv.

The GCv value that allows maximum standing volume for a given mean height was derived analogously to Table S2. The GCv -values where standing volume achieves the optimum change slightly with stand development. The optimal GCv depends on the mean tree height. $GC_{opt} = 0.547, 0.467, 0.414$ for hq= 15, 25, 35 m. The derived optimal GC_{opt} and maximum tree number are visualized in Fig. 7c.

The effect of the Gini coefficient on the special yield level was similar to its effect on the standing volume (Fig. 8). The total yield increased exponentially with increasing mean stand height (Fig. 8a) but varied for given hq values (Table 5). A part of this variation can be explained by the site index and the size structure variation in the stands in terms of the Gini coefficient of stem volume. Fig. 8b visualizes the results of model 3. After excluding the thinning effects by quantile regression ($\tau = 0.75$) there is a strong variation of TY-values over stand mean height and site index caused by the Gini coefficient. Fig. 8c indicates that there is a unimodal optimum relationship between TY and GCv. Maximum total yield is achieved at a mean degree of size inequality. Analogously, as shown for the standing volume, the maximum of the curve is shifting to the left with progressing stand development (Fig. 8c).

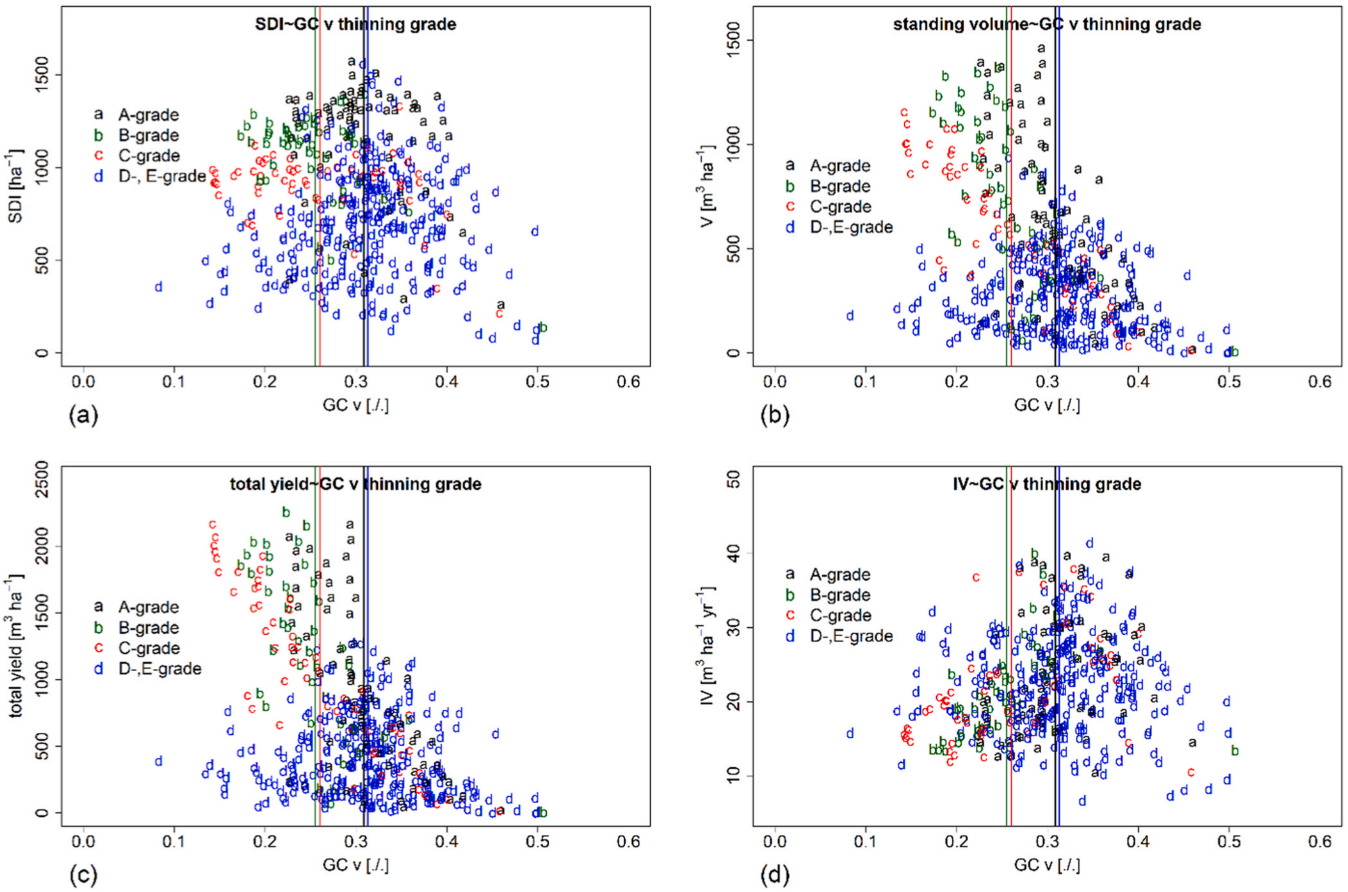

Fig. 5. Stand growth and yield characteristics plotted over *GCv*. The vertical lines reflect the mean *GCv* values for the different thinning grades (A-, B-, C-grade, i.e. self-thinning and moderate and strong thinning from below; D-, E-grade thinning from above). (a) Stand density index plotted over *GCv*. (b and c) Both standing volume and total yield, respectively over *GCv*. (d) Stand volume growth over *GCv*.

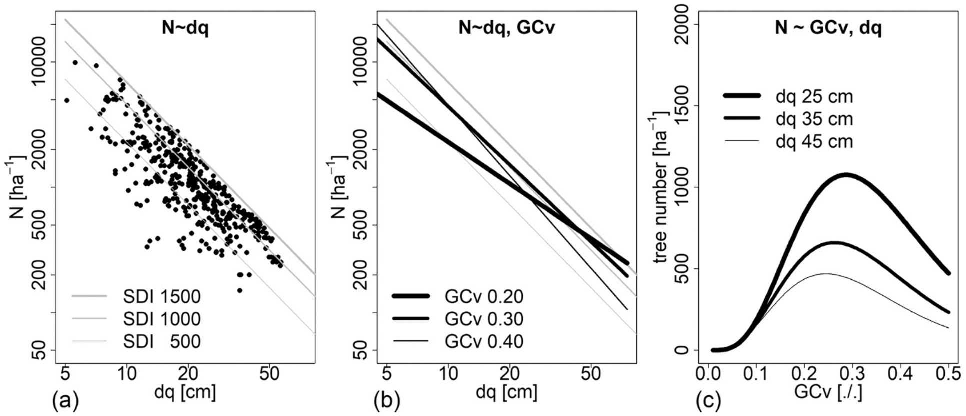

Fig. 6. Modification of the self-thinning line by the tree size distribution in terms of the Gini coefficient of stem volume; visualization of model 1 (see Table 3). (a) Observed tree numbers, *N*, plotted over mean diameter and expected self-thinning lines with allometric slope $\alpha = -1.664$ and density levels *SDI*= 500, 1000, and 1500 trees ha^{-1}. (b) self-thinning lines according to model 1 for *GCv* values of 0.20, 0.30, and 0.40. (c) unimodal relationship between *GCv* and tree number per hectare for *dq* levels of *dq*= 25, 35, and 45 cm. Note that the site index, *SI*, was uniformly maintained at the mean for this predictions.

The *GCv* value that allows maximum special yield level for a given mean height was derived analogously to the derivation shown in Table S2. The *GCv* -values where the special yield level achieves the optimum change slightly with stand development. The optimal value of *GCv* depends on the mean tree height. $GC_{opt} = 0.611, 0.444, 0.334$ for *hq*= 15, 25, 35 m. The optimal *GCv* and maximum tree number are visible in Fig. 8c.

3.4. Stand density-stand growth relationship modulated by size inequality and growth partitioning (Q3)

Here, we analyzed the codetermination of stand growth by the Gini coefficient, *GCv*. Fig. 9 visualizes the modification of the stand volume by stand density and tree size inequality in terms of *GCv*. Fig. 9a shows the underlying observations grouped according to *GCv* levels. Fig. 9b, based on model 4 (Table 6), reflects that the well-known *IV-SDI*

Table 3
Results of fitting model (1) of tree numbers per hectare depending on mean tree diameter, *dq*, Gini coefficient of stem volume, *GCv*, and site index, *SI*. $\ln(N) = a_0 + a_1 \times \ln(dq) + a_2 \times \ln(GC) + a_3 \times GCv + a_4 \times \ln(SI) + a_5 \times \ln(dq) \times \ln(GCv)$. Number of observations = 425.

Fixed Effect Variable	Fixed Effect Parameter	Estimate	se	p-value
intercept	a_0	28.219	1.649	< 0.001
ln(dq)	a_1	-2.859	0.210	< 0.001
ln(GCv)	a_2	7.896	0.939	< 0.001
GCv	a_3	-15.294	1.499	< 0.001
ln(SI)	a_4	-0.589	0.141	< 0.001
ln(dq)× ln(GCv)	a_5	-1.091	0.168	< 0.001

relationship is additionally shaped by *GCv* conditions within the respective stands. Most interesting are the unimodal *IV- GCv* relationships in Fig. 9c. They reveal that certainly, the stand volume growth increases with *SDI* level. However, new is the optimum relationship between tree size inequality and stem volume growth. For a given *SDI* level, stand growth is at maximum at mean size inequality; the growth-optimal *GCv* level shifts towards higher size inequality with increasing *SDI* level.

By setting the first derivation of model 4 to zero and retransforming it to *GCv* we can show that *GCv* = 0.269, 0.338, and 0.396 enable maximum stand productivity for *SDI* levels of 500, 1000, and 1500 trees per hectare, respectively (Table S3). The position of *GCv* where *IV* is at maximum changes with *SDI*, other variables did not show any interactions with *GCv*.

We further show the codetermination of stand volume growth by the Growth Dominance Coefficient, *GDC*. Fig. 10a is based on model 5 and substantiates that volume growth increases logarithmically with stand density. Given the same stand density, stand volume growth differs depending on the growth partitioning *GDC* (Fig. 10a). The logarithmic model approach means a multiplicative effect of *GDC* on stand density. Though, the effect of *GDC* on stand growth is greater for high compared to low density levels. By setting the first derivation of formula 5 to zero and retransforming it to *GDC,* we can show that *GDC*= 0.08 enables maximum stand productivity (Table S3). The logarithmic *IV-SDI* relationship is the steepest for values of *GDC*= 0.08 and decreases for higher and smaller *GDC* values. Fig. 10b shows the variation of *IV* with *GDC* for different ages, with the maximum at *GDC*= 0.8. GDC= 0.08 indicates an only slightly unequal growth partitioning in favor of tall trees, whereas a more preferential partitioning in favor of tall or small trees results in suboptimal stand growth. The position of *GDC* where *IV* is at maximum is invariant regarding *SDI, vq*, and *age*.

4. Discussion

We revealed an optimum relationship between the inequality of tree size and the stand density, standing volume, total yield, and stand volume growth in Norway spruce. This suggests that stand density and yield, as well as stand growth, are the highest at mean structural diversity in terms of inequality of tree size. Accordingly, we found that stand growth is the highest, with slightly unequal growth partitioning in favour of tall trees. Strongly homogeneous or very heterogeneous stand structures turned out as disadvantageous regarding growth and yield. Many present silvicultural prescriptions are aiming at diversification by structuring monospecific stands or mixing tree species to improve ecosystem services and functions such as stability, resilience, biodiversity, or recreational value. Interestingly, we found a tradeoff between heterogeneity of stand structure and stand growth and yield. As stand growth and yield are the main drivers of carbon uptake, this also means a tradeoff between the heterogeneity of structure and carbon sequestration. The parameterized functions enable us to calculate how much stand growth is lost if structural diversity is maximized for other purposes.

4.1. The general importance of stand structure along the continuum from even-aged mono-specific stands to uneven-aged mixed stands

Our results corroborate the essential role of structural diversity also for even-aged monocultures. Growth, density, and yield were the highest at mean structural diversity in terms of inequality of tree size and growth. Ceteris paribus, in strongly heterogeneous stands, the Gini and *GDC* coefficients were higher, i.e., the volume and volume growth was concentrated on the large trees. In very homogeneous stands, both coefficients were lower, i.e., the small trees had a higher share of the standing volume and volume growth. We found that both strongly homogeneous and very heterogeneous stand structures turned out as

Table 4
Results of fitting model (2) of standing volume depending on stand mean tree height, hq, and Gini coefficient of stem tree volume, *GCv*. $\ln(V) = b_0 + b_1 \times \ln(hq) + b_2 \times \ln(GCv) + b_3 \times GCv + b_4 \times \ln(hq) \times \ln(GCv)$. Number of observations = 425.

Fixed Effect Variable	Fixed Effect Parameter	Estimate	se	p-value
intercept	b_0	4.999	0.985	< 0.001
ln(hq)	b_1	1.183	0.178	< 0.001
ln(GCv)	b_2	2.545	0.546	< 0.001
GCv	b_3	-2.619	1.146	0.002
ln(hq)× ln(GC)	b_4	-0.411	0.130	< 0.001

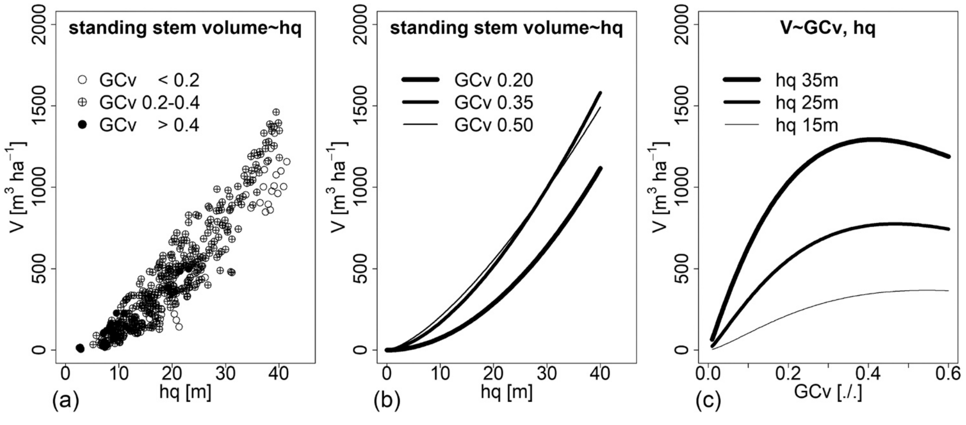

Fig. 7. Modification of the Eichhorn relationship by the tree size distribution in terms of the Gini coefficient of stem volume, *GCv*; visualization of model 2 (see Table 4). (a) Observed standing volume plotted over mean stand height for different levels of Gini coefficients. (b) Eichhorn relationship according to model 3 for *GCv* values of 0.20, 0.35, and 0.50. (c) unimodal relationship between *GCv* and standing volume given for defined levels of *hq*= 15, 25, and 35 m.

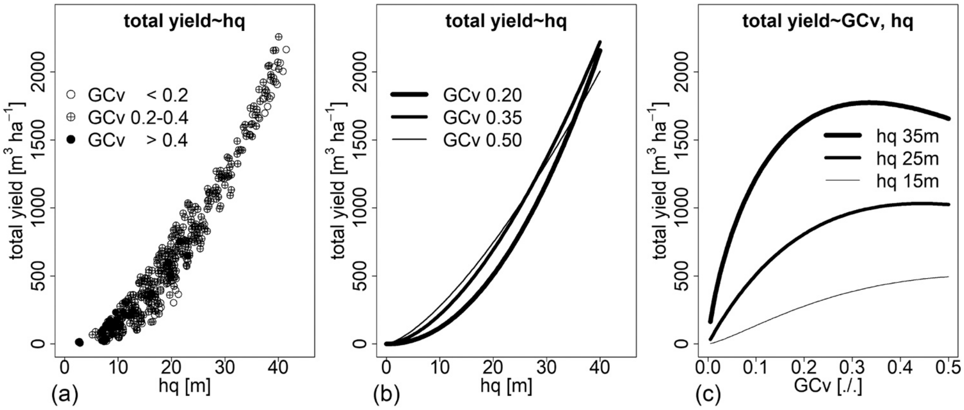

Fig. 8. Modification of the special yield level by the tree size distribution in terms of the Gini coefficient of stem volume, *GCv*; visualization of model 5 (see Table 5). (a) Observed total yield plotted over mean stand height, *hq*, for different levels of Gini coefficients. (b) total yield according to model 4 for *GCv* values of 0.20, 0.35, and 0.50. (c) unimodal relationship between *GCv* and total yield given for defined levels of *hq*= 15, 25, and 35 m. The site index was fixed for the visualization to the mean of *SI*= 30.

Table 5

Results of fitting model (5) of total volume yield, *TY*, depending on stand mean tree height, hq, Gini coefficient of stem tree volume, *GCv*, and site index, SI. $\ln(TY) = c_0 + c_1 \times \ln(hq) + c_2 \times \ln(GCv) + c_3 \times GCv + c_4 \times \ln(SI) + c_5 \times \ln(hq) \times \ln(GCv)$. Number of observations = 425.

Fixed Effect Variable	Fixed Effect Parameter	Estimate	se	p-value
intercept	c_0	5.051	0.857	< 0.001
ln(hq)	c_1	0.926	0.128	< 0.001
ln(GCv)	c_2	3.310	0.387	< 0.001
GCv	c_3	-2.212	0.842	< 0.001
ln(SI)	c_4	0.193	0.110	0.007
ln(hq)× ln(GCv)	c_5	-0.723	0.086	< 0.001

disadvantageous regarding growth and yield, as also found by Soares et al., (2020, 2016). Another implication of our findings is that previous studies only looking at simple linear growth-structural complexity relationships may have not captured these non-linear nuances. Examples from the literature on conifer-dominated systems that considered only a linear response-structural complexity relationship are Aspinwall et al. (2011), Long and Shaw (2010), and Yáñez et al. (2017).

As the diversity of tree species and stand structure can increase various forest ecosystem functions and services, mixed species stands have recently attracted increased attention (e.g., Brockerhoff et al., 2017, Felton et al., 2016 , Pretzsch et al., 2017). Due to the niche complementarity of the species combined in a stand, the size and growth distribution range can be wider in mixed compared with mono-specific stands. In mixed stands, superior growth velocities of one species may extend the tree size distribution to the right (range of large trees), whereas higher shade tolerance may extend the tree size distribution to the left (range of small trees). In this way, the variation of co-occurring tree size and growth rates in a stand may increase (Varga et al., 2005). This widening of the size distribution increases the vertical layering and structural heterogeneity (Katholnig, 2012). Ali et al. (2016) identified stand structural diversity rather than species diversity as the major determinant for the standing stock. They recommend the maintenance of tree size diversity through silvicultural operations as an effective approach for enhancing aboveground C storage in these forests (Mo et al., 2023; Warner et al., 2023).

Size structure is considered an important characteristic in uneven-aged and mixed forests (del Río et al., 2016). Our results emphasize that information on the frequency distribution of tree size and growth provides essential additional information beyond the classical mean tree and sum values at the stand level, also for even-aged spruce monocultures.

4.2. Relevance for classical rules and relationships

We revealed an optimum relationship between the inequality of tree size in forest stands and the maximum density, standing volume, yield

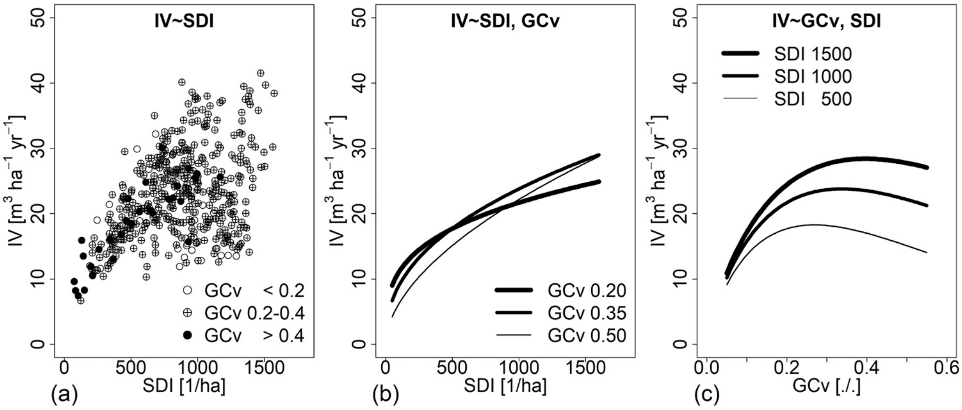

Fig. 9. Stand volume growth, *IV*, increases with stand density, *SDI*, and is additionally modulated by the tree size variation, represented by *GCv*; Visualization according to model 4 (see model coefficients in Table 6). (a) Observed *IV* values plotted over *SDI* and visualization of different *GCv* groups. (b) *IV-SDI*-relationships for *GCv* values of 0.20, 0.35, and 0.50. (c) unimodal relationship between *GCv* and *IV* for *SDI* levels of *SDI*= 500, 1000, and 1500. Note that the mean stem volume, *vq*, was uniformly maintained at the mean for this predictions.

Table 6
Results of fitting the linear mixed effect model (4) of stand volume growth depending on quadratic mean tree volume, *vq*, Gini coefficient of tree volume, *GCv*, and stand density index, *SDI*. $\ln(iv) = d_0 + d_1 \times \ln(vq) + d_2 \times \ln(GCv) + d_3 \times GCv + d_4 \times \ln(SDI) + d_5 \times \ln(SDI) \times GCv$. AIC comparisons suggested using random effects at the experiment and the plot level. Number of observations = 425, AIC= −384.98.

Fixed Effect	Parameter	Estimate	se	p-value
Fixed part				
Intercept	d_0	4.018	0.632	< 0.001
ln(vq)	d_1	-0.022	0.010	0.026
ln(GCv)	d_2	0.802	0.174	< 0.001
GCv	d_3	-8.378	1.332	< 0.001
ln(SDI)	d_4	0.119	0.077	0.120
ln(SDI) × GCv	d_5	0.869	0.199	< 0.001
Random part and residual				
Experiment level	var(b_i)	0.135^2		
Plot level	var(b_{ij})	0.066^2		
	σ^2	0.223^2		

Table 7
Results of fitting the linear mixed effect model of stand volume growth depending on stand age, *age*, quadratic mean tree volume, *vq*, *GDC*, and stand density, *SDI*. $\ln(IV) = b_0 + b_1 \times \ln(age) + b_2 \times \ln(vq) + b_3 \times \ln(GDC+1) + b_4 \times GDC + b_5 \times \ln(SDI)$. AIC comparisons suggested using random effects at the experiment and the plot level. Number of observations = 425, AIC= −426.832.

Fixed Effect	Parameter	Estimate	se	p-value
Fixed part				
Intercept	b_0	2.622	0.325	< 0.001
ln(age)	b_1	-0.586	0.076	< 0.001
ln(vq)	b_2	0.101	0.020	< 0.001
ln(GDC+1)	b_3	15.656	3.801	< 0.001
GDC	b_4	-14.502	3.752	< 0.001
ln(SDI)	b_5	0.415	0.037	< 0.001
Random part and residual				
Experiment level	var(b_i)	0.124^2		
Plot level	var(b_{ij})	0.051^2		
	σ^2	0.129^2		

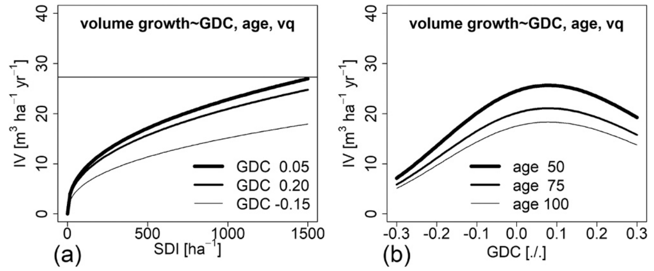

Fig. 10. Stand volume growth, *IV*, increases with stand density, *SDI*, and is additionally modulated by the growth partitioning, *GDC*. Visualization according to model 5 (see model coefficients in Table 7). (a) *IV-SDI* relationship shown for *GDC*= 0.05, 0.20, − 0.15 (*vq* set to 1.0, stand age to the mean of 50 years). (b) unimodal *IV-GDC* relationship shown for age 50, 75, and 100.

level, and stand productivity (Fig. 11). The optimal diversity changed slightly with the development state of the stand, the mean height, and the stand density; however, the optimum was always achieved under mean structural diversity in terms of *GC* or *GDC*. The self-thinning line, representing the maximum stand density, the Eichhorn rule, yield level, and density-growth relationship are the backbones of the theory of stand dynamics (e.g., Skovsgaard and Vanclay, 2008, Zeide, 2001, 2002, Assmann, 1970). That these basic relationships are, ceteris paribus, strongly co-determined by the frequency distribution of tree size and growth diversity underlines the important role of stand structure even in even-aged mono-specific stands.

A modulation of the stand growth by structural characteristics in addition to stand density means that stand growth of un-thinned stands can vary depending on their structure, and that growth is the result of steering density and structure. Given the same stand density, a growth-optimal structure may out-yield stands with suboptimal structure. Even if the density of an un-thinned stand with a growth-suboptimal structure is reduced, the growth and yield can increase if the stand is converted from a suboptimal to a more advantageous structure. In this way, the unimodal density-growth relationship becomes just a special case of a more general density-structure-growth-relationship (Fig. 11c).

Literature presents for the density-growth relationship two competing concepts (Zeide, 2001, 2002), the asymptotic relationship assumed by Curtis et al. (1997) or Smith et al. (1997) versus the unimodal relationship with an optimum at slightly reduced density introduced by Assmann (1970) or Pretzsch (2005). The extension of the density-growth relationship towards a density-structure-growth relationship consolidates these so far diverging concepts. It also means that deviations from the Eichhorn rule or yield level may be caused by stand structure, whereas so far, they were attributed to differences in site conditions (Assmann, 1970, pp. 173–177).

4.3. Mechanistic explanation of the revealed patterns

In case all trees in a stand would be similar in size and located in one layer, they would strongly compete with each other and outcompete smaller neighbors, as a one-layered canopy hardly allows light getting through to lower layers. Due to this monolayered structure, all crowns would be somewhat similar in lateral and vertical extension (Pretzsch, 2014). This means a similarity of the allometry, space requirement, and growth rate, implying a low complementarity in space occupation and a low maximum packing density (Jucker et al., 2015). Equal growth rates mean that the stand has a rather clear peak of stand growth, as the trees have a similar course of growth over age. They peak and decrease synchronously. Analyses of mixed stands showed that size inequality can increase the packing density due to the species' complementarity. It can also smooth and extend the stand growth (lower the peak at mean age, extend the decrease in old age) (e.g., Zeller and Pretzsch, 2019, Pretzsch et al., 2015, Mitscherlich, 1970, Kennel, 1965). Species-specific crowns in mixed stands may be more complementary (small trees closer to or below tall neighbors), growth rates more asynchronous (rates of tall trees decrease while small trees increase).

Our results show that analogous to uneven-aged and mixed-species stands, even-aged monoculture stands feature a variety of trees with different sizes structures, and growth rates, caused, for example, by genetic variation, different initial size or tree age, variation in planting technique and success, micro-site, or biotic and abiotic disturbances. Even in fully stocked unmanaged monocultures, some openings of the canopy might be caused by crown shyness, as abrasion of neighboring crowns is most evident when they are not complementary but swinging at the same height (e.g., Van Der Zee et al., 2021, Pretzsch, 2019, Fish et al., 2006). Such openings cause some size and growth heterogeneity. Indeed, also management, in terms of different thinning grades, may contribute to an inequality of sizes and growth. And the more variable the size distribution, the stronger the structuring of the canopy space and the light penetration also into the lower canopy space, enabling survival also of subdominant and suppressed trees.

Even-aged, monospecific stands of Norway spruce may have an optimal ensemble of small and tall trees that allows a maximum packing density or growth by combining trees of different sizes. A stand with a heterogeneous, unequal size distribution, i.e., a combination of high growth rates of a restricted number of tall trees with lower growth rates of a high number of smaller trees, may result in a maximum stand growth that more homogeneous structures might not achieve. Too high size variation, with too many small trees, may also be disadvantageous

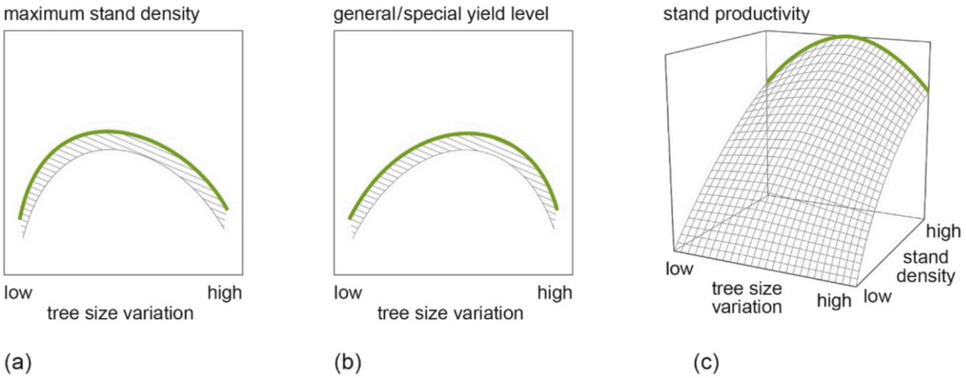

Fig. 11. Schematic representation of the main findings. The stand characteristics maximum stand density (a), general and special yield level (b), and stand productivity in terms of stand volume growth (c) show a unimodal dependency on tree size variation with an optimum level at mean size variation.

for stand growth. Small, suppressed trees usually have a lower resource use efficiency than large trees and may, even if they are more frequent, decrease the stand growth. However, the presence of small trees could also reduce stand growth reduction under drought as they are less affected than large trees (Grote et al., 2016, Pretzsch et al., 2022).

For selection forest, de Liocourt (1898) showed that a certain inequality of the size frequency distribution keeps the stand growth and structural diversity constantly on a high level. Optimal conditions require an exponential decline in tree numbers from the lowest to the highest diameter classes, according to the law of de Liocourt (1898). An overabundance or deficit of tall trees disrupts this balance, either diminishing or amplifying the proportion of smaller trees, thus thwarting the equilibrium. The general theory of forest structure and dynamics posited by West et al. (2009) and Enquist et al. (2009) shows that tree growth and allometry results in tree size-frequency distribution that ensures a steady state of growth structure, standing stock, etc., at the stand level. Despite their strong simplification, such as the presumption of allometrically ideal plants and generalized metabolic rates, this theoretical framework provides a conceptual link between tree level, size frequency distribution, and stand growth. Notwithstanding their simplifications, these concepts offer pathways to keep selection forests in a steady state regarding growth, regeneration, and standing volume (Bachofen, 1999, O'Hara, 1998) or for the transition of monocultures into selection forests (e.g., Sterba and Zingg, 2001, Schütz, 2001, 2002, Reininger, 1987).

Drawing parallels to those theoretical and empirical findings gathered from uneven-aged mixed forests, it's conceivable that even-aged stands may also possess an optimal size distribution for maximum growth and yield. In contrast to selection forest, where a continuous demography is essential, the criteria for optimality are simpler (optimal diversity lower) if the aim is a maximum productivity. However, if there is an ambition to transform mono-specific stands into demographic systems with ingrowth, the optimal inequality of the size distribution might necessitate a higher threshold. Such a configuration would not only promote heightened productivity but would also ensure a continuous natural regeneration (Bachofen, 2009, Pretzsch, 2019).

4.4. Implications for forest management

In essence, when all other factors are kept constant, a strong homogenization in tree size and growth, perhaps brought about by heavy thinning from below, may reduce growth, maximum density, standing stock, and yield level. Excessive heterogenization, potentially caused by strong thinning from above, can also lead to suboptimal growth and yield on the opposite end of the spectrum. It is the stands with a medium inequality of tree size and growth, potentially achieved via moderate thinning interventions from either direction, that come off the best in terms of growth and yield.

That such medium structured stands don't provide the most homogeneous stem sizes and assortment, the largest mean stem dimensions, and regular tree ring pattern may be disadvantageous for classical wood dominated forest management (Bauhus et al., 2010). However, for modern multi-purpose forest management, they are superior as subdominant trees endure drought better than dominant trees (Pretzsch et al., 2018); multi-layering can buffer growth losses caused by dropouts in the upper layer (e.g., by windthrow, ice breakage), and heterogeneous structures enable transitioning to uneven-aged stands (Pretzsch et al., 2022b). Diversity of tree sizes implies a variation in growth rates, ensuring sustained and potentially higher levels of growth into advanced stand ages (e.g., Pretzsch, 2019, Mitscherlich, 1970, Kennel, 1965). Conversely, stands characterized by more homogeneous structures synchronize the courses of individual growth, which may boost productivity in the youth but decrease it in the advanced stand development phase.

5. Conclusions

Information of the frequency distribution provides essential additional information, surpassing the classical mean tree and sum values at the stand level, even for even-aged spruce monocultures. The profound influence of stand structure on stand growth and yield, even when the classical stand attributes are analogous, warrants further scientific attention when analyzing mono- and mixed species stands. Neglecting differences in stand structure can lead to skewed interpretations of growth reactions to density regulation or species mixing. From a forest management perspective, our results unveil the untapped potential of structural diversification, even for mono-specific stands.

CRediT authorship contribution statement

Pretzsch Hans: Writing – review & editing, Writing – original draft, Visualization, Methodology, Formal analysis, Conceptualization. **del Río Miren:** Writing – review & editing, Methodology, Conceptualization. **Hilmers Torben:** Writing – review & editing, Visualization, Formal analysis.

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.

Data availability

Data will be made available on request.

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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.2024.121736.

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