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RESEARCH

Structural diversity and carbon stock of forest stands: tradeoff as modified by silvicultural thinning

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Abstract

In forest management, merging stand structural diversity with carbon storage is essential for resilience and climate mitigation. This study assesses (1) how structural diversity in stands of spruce (*Picea abies* (L.) H. Karst.), pine (*Pinus sylvestris* L.), beech (*Fagus sylvatica* L.), and oak (*Quercus robur* L. and *Quercus petraea* (Matt.) Liebl.) in Central Europe varies with age, site quality, and applied thinning grade; (2) these factors' impact on carbon stock; and (3) the link between structural diversity and carbon stock. Analyzing 26 long-term thinning experiments, we used the Gini coefficient of tree heights to measure structural diversity and species-specific biomass functions for carbon stock assessments. Our results show that structural diversity, highest in beech and spruce, decreases with stand age and on richer sites. Thinning enhances structural diversity in spruce and beech but reduces it in pine and oak. Unthinned or only moderately thinned mature spruce and beech stands outperform pine and oak in carbon stock (200–300 vs. 100–150 Mg C ha^{-1}). C- and D&E-grade thinning halves carbon stock. A decrease in vertical layering with increased carbon storage varies across species. Given the same carbon stock, thinning from above maintains structural diversity in spruce and beech, while non-thinning or thinning from below promotes structural diversity in pine and oak. Based on the current silvicultural practice reflected by the NFI data of Germany, we argue that reduced thinning in previously D&E-grade thinned stands may slightly reduce their structural diversity. However, a suspension or reduction of thinning would strongly improve carbon storage (+ 100–200 Mg C ha^{-1}) in the next 3–5 decades. We discussed options for reconciling structural diversity and carbon storage by silvicultural management of the four considered species in Central Europe.

Keywords Tree size inequality · Monospecific stands · Norway spruce · Scots pine · European beech · Sessile/common oak

Introduction

Structural diversity and standing stock of wood are two essential stand characteristics driving numerous ecosystem services. Structural diversity, in terms of tree height or tree diameter inequality and associated vertical canopy stratification, can promote, e.g., habitat provision (Hilmers et al. 2018; Dieler et al. 2017; Ishii et al. 2004), growth resilience against disturbances (Nikinmaa et al. 2020; Seidl et al. 2014), or drought resistance (Pretzsch et al. 2023a; Grote et al. 2016). Meanwhile, the standing stock determines, e.g., stand growth (Zeide 2002; Assmann 1970a, b), carbon stock (Węgiel and Polowy 2020; Schaich and Plieninger 2013), and forest economy (Assmuth et al. 2018; Knoke and Plusczyk 2001). Both structural diversity and standing stock can be steered by silvicultural thinning (Duduman 2011). Unthinned stands may accumulate standing stock yet lose structural diversity. Thinning from above can boost structural heterogeneity by opening the canopy, fostering the remaining tall trees, and maintaining subdominant trees. Conversely, thinning from below may increase stand growth by eliminating less resource efficient growing trees but tends to homogenize the stand structure.

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The structural diversity of even-aged monospecific stands has been extensively documented (e.g., Oliver and Larson 1996; Knox et al. 1989; Long and Smith 1984). Initially, when established with uniform plants or naturally generated in one go, these stands exhibit homogeneity in tree size distribution. However, as soon as competition startseven-aged monospecific stands often evolve more heterogeneous size structures. This differentiation allows categorizing trees into social classes 1–5 (Kraft 1884). Later, the closing of the upper canopy and competition-induced mortality, tends to homogenize the size distribution again. In their old age, even-aged monocultures often become mono-layered or “hall-like” stands (Commarmot et al. 2005; Leibundgut 1993).

Numerous metrics exist for quantifying stand structures (del Río et al. 2016; Staudhammer and LeMay 2001), primarily utilized for analyzing and classifying specific stand development phase (Keren et al. 2019), temporal disturbances (Onaindia et al. 2004), or transition phases (Sharma et al. 2014). However, quantitative insights into structural stand development in temperate forests, particularly size differentiation with increasing stand age, its relation to site condition, and the impact of thinning, remain scarce (Kuehne et al. 2018; Pretzsch 2021; Wichmann 2001). However, Soares et al. (2017) and Sun et al. (2018) showed for forests in Brazil and China how spacing and thinning modulated structural diversity. Recently, understanding and analyzing the structure in different stand development phases has gained importance, as structural diversity is crucial for a successful transition from even-aged monocultures to uneven-aged mixed stands (Reventlow et al. 2021; Hilmers et al. 2020; Pretzsch 2019; Schütz 2001).

Combating the effects of climatic change on forests by mitigation strategies triggered numerous studies dealing with the carbon storage in the standing stock of forests (e.g., Mo et al. 2023; Köhl et al. 2010; Rötzer et al. 2010). The standing volume stock, a standard characteristic in forest management and planning, is commonly used for this purpose. Multiplying this volume by the species-specific wood density (ranging from 0.3 to 0.6 for European tree species) for mass conversion and then by the mean carbon content of 0.5 (for biomass to carbon transformation) provides a rough estimate of carbon in the standing stock. This calculation of carbon stock typically relies on observational plots, forest inventories, or existing growth and yield models. While these methods provide insights into carbon stock in representative forest stands, data on the maximum carbon stock in unmanaged stands are limited. Yet, this information on potential carbon stock without management intervention is particularly valuable as a benchmark.

Over the past half-century, strong thinning from above has become a widely applied concept in forest management (Štefančík et al.2018; del Río et al. 2017), aimed at boosting the size growth of a selected number of future crop trees through strong stand density reduction, well below the maximum standing stock. Given this trend of managing forests far below their maximum standing stock of volume and carbon stock, information about the maximum stock is crucial. Not necessarily for setting stands aside and fully exploiting the carbon storage potential but for reconsidering common thinning concepts and respective density levels in view of the carbon topic (Schwaiger et al. 2019). Especially middle aged and older stands can still have high growth rates, are often kept far below the maximum stand density, and could relatively fast (simply by changing the thinning concept) contribute to higher C sequestration, compared with other measures of C storage such as afforestation (Mo et al. 2023).

The standing stock in early thinned monospecific stands is often far below the maximum of unthinned stands on the same sites (Cavalieri et al. 2022; Mrad et al. 2020; Oliver and Larson 1996). Prior thinnings have fostered structural diversity and mechanical stability (Slodicak and Novak 2006), positioning these stands for a relatively low-risk increase in carbon stock by reducing or pausing thinning interventions. Assessing the stock of unthinned stands may reveal the extent to which stands currently exploit maximum C storage and the additional capacity they could provide by modifying thinning practices.

Structural diversification and carbon storage, in principle, represent competing objectives with inherent tradeoffs (Biber et al. 2020). On one side, the standing stock induces competition and drives structural development, leading to homogenization as lower social class trees get outcompeted by taller ones in stands with high standing stock and closed upper canopies. Conversely, the structure, characterized by tree size inequality and vertical differentiation, can positively affect the potential packing density and enhance the standing stock (Pretzsch et al. 2024; Wang et al. 2011).

In their initial phase, when the standing stock is still low, monospecific stands tend to be homogeneous, with trees assessing similar resources. As trees grow in size and resource demand, the equilibrium changes. Once the standing stock reaches a level where available resources become insufficient for all, size differentiation initiates, leading to structural heterogeneity. Predominantly, dominant trees with superior access to light survive this differentiation process, steering the stand towards homogenization. This trend results in mono-layered stands, where resource distribution may seem similar to the initial phase, but this uniformity stems from a rigorous, irreversible social selection process. In this later phase, conditions might again support understory or subdominant trees, but these have been irreversibly outcompeted decades earlier (Stimm et al. 2021; Dey et al. 2012).

During the middle age of stands, a critical phase for differentiation and loss of structure, silvicultural measures can play a pivotal role in shaping the future structural development of monospecific stands: Thinning from below tends to accelerate homogenization by removing smaller, less competitive trees, whereas thinning from above may maintain the living condition of these smaller trees by removing taller neighbors in the upper canopy. Beyond influencing various ecosystem services like aesthetic value, biodiversity, and climate stability, maintaining structural diversity can enhance a stand's potential in terms of stability and resilience. It also opens opportunities to refill the standing stock through the suspension or reduction of thinning and for transforming stands into more diverse ecosystems with multiple species and uneven-aged structures (O'Hara 2014; Schütz 2001, Kohm and Franklin 1997).

To better understand the relationship between structural diversification and carbon storage in forest stands and how the tradeoff between both is modified by thinning, we based our study on 26 long-term experiments with 164 plots in even-aged monospecific stands. This sample includes a broad spectrum of thinning grades, and unthinned reference stands. The species studied are Norway spruce (*Picea abies* (L.) H. Karst.), Scots pine (*Pinus sylvestris* L.), European beech (*Fagus sylvatica* L.), and oak (*Quercus robur* L. and *Quercus petraea* (Matt.) Liebl.). For oak, we pooled common oak (*Quercus robur* L.) and sessile oak (*Quercus petraea* (Matt.) Liebl.) as they have not been differentiated well enough in the data source.

We used “oak” as a generic term summarizing both taxa to avoid possible taxonomic pitfalls. Our comprehensive dataset, encompassing 290 surveys of the plots, covers the development of individual tree sizes over up to 150 years, providing a solid basis for quantifying structural diversity and carbon stock.

This setup was used to address three questions:

(Q1) How does the structural diversity depend on stand age, site index, and thinning grade?
(Q2) How does the stem carbon stock depend on stand age, site index, and thinning grade?
(Q3) How is the structural diversity related with the carbon stock?

Especially the unthinned plots provided reference data for rethinking the potential of carbon stock. For showing the difference between the potential carbon stock and the current carbon stock in forest practice we used the NFI data of Germany. Based on this comparison we discussed options for reconciling structural diversity and carbon storage by silvicultural management.

Material and methods

Long-term experimental plots as empirical basis

This study leveraged 26 long-term thinning experiments located in southern Germany, involving 164 plots and 290 surveys in even-aged, monospecific stands of N. spruce, S. pine, E. beech, and oak (Fig. 1). The plots, originating from either planting or seeding, are situated across diverse environmental conditions, with elevations ranging from 340 to 840 m above sea level, annual precipitation between 640 and 1200 mm, and mean temperatures of 6–8 °C. Soil quality across these sites varies from poor to rich (Table 1).

Plot sizes varied, with the smallest being 0.09 ha and the largest extending to 0.36 ha. Each experiment consisted of up to 24 plots. Depending on the timing of the first (ranging between 1870 and 2004) and last (occurring between 1990 and 2022) surveys, each experiment underwent 4 and 18 surveys. The length of observation lasted up to 150 years, and the age differed between 36 and 198 years (Table 2), thereby offering a comprehensive dataset for our analysis.

Applied thinnings

The experiments encompassed plots subjected to various thinning grades as defined by Wiedemann (1935) and elaborated in detail by Kramer (1988, pp. 179–183), implemented in this study’s experimental plots (Table 2). The thinning grades are categorized as A-, B-, and C-grade, representing slight, moderate, and intense 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 and subdominant trees, with B-grade leaving only co-dominant and dominant trees and C-grade retaining only the dominant trees.

D- and E-grade thinning denote moderate and strong thinning from above, targeting mainly dominant trees to promote the growth of the remaining dominant 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). We therefore grouped D- and E-grade plots in our evaluation. For a more comprehensive explanation of the internationally defined thinning grades, refer to Assmann (1970a, b), Hummel (1953), and Verein Deutscher Forstlicher Versuchsanstalten (1902, 1873).

Metrics for quantifying tree size distribution and stand structure

We utilized common metrics such as the Gini Coefficient of the tree heights (*GCh*), stem diameter (*GCd*), and stem

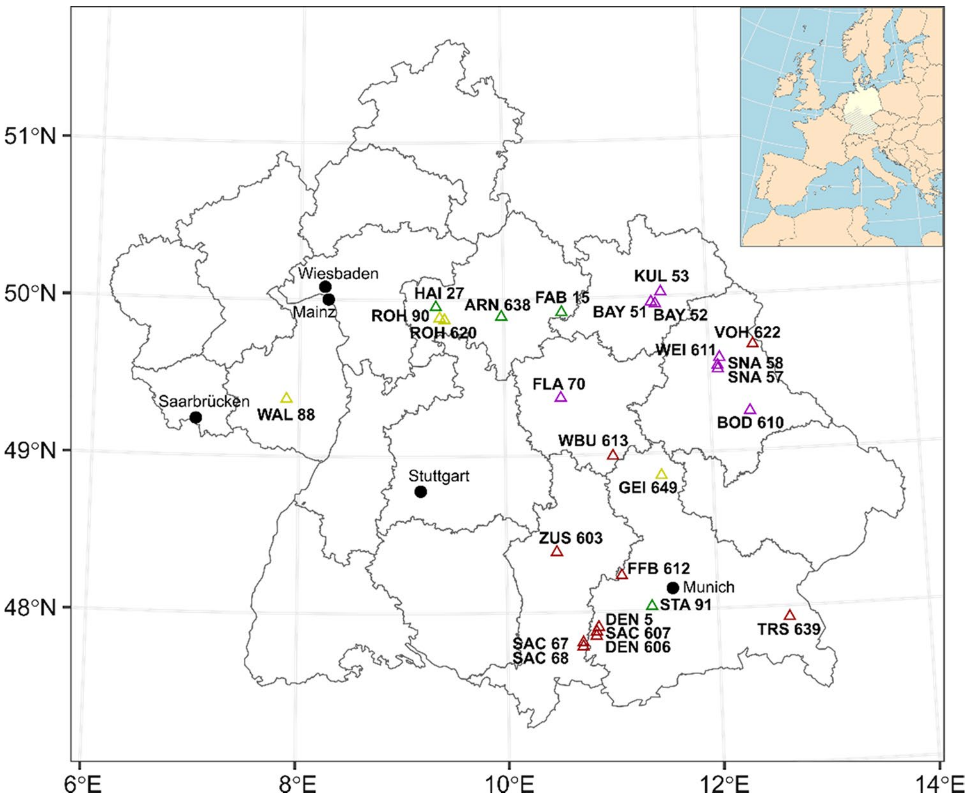

Fig. 1 Map with the distribution of the 26 long-term thinning experiments of Norway spruce (red), Scots pine (purple), European beech (green), and sessile/common oak (green) in southern Germany. Abbreviations near the symbols refer to the location and number of the experiments (see Table 1)

volume (GCv) across all plots and surveys to provide a comprehensive insight into the stand structure and their dependency on the applied thinnings.

Gini coefficient of stem diameter, GCd: 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, p. 82). 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 charactersitic being measured across all trees. The Gini coefficient, GC, of tree size (e.g., based on stem diameter) 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., $GC = 0.5$). It can be visualized by plotting the cumulative tree diameter against the cumulative tree number after ranking the trees according to their diameter. 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. We calculated the Gini coefficients in terms of tree height (GCh), stem diameter (GCd), and stem volume (GCv).

Evaluation of growth, standing stock, and carbon stock at tree and stand level

In this study, the characteristics at the stand level were derived from the successive inventories, which included tree diameters, tree heights, and records of the dropout trees. 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 (merchantable stem volume > 7 cm at the smaller end) was based on the regional-specific stem form equations by Franz et al. (1973). The results of the standard evaluation included the quadratic mean tree diameter, stand volume, and volume growth.

For above ground biomass estimation we used the stem biomass equations by Pretzsch (2005) $\ln(m) = a + b \times \ln(d)$ with stem mass, m, and stem diameter, d, and coefficients for N. spruce ($a = -3.839$, $b = 2.861$), S. pine ($a = -3.580$, $b = 2.693$), E. beech ($a = -2.856$, $b = 2.678$), and oak ($a = -1.179$, $b = 2.173$). These equations are based on sample tree measurements from the experimental plots of this study and represent different thinning regimes. So they should represent the local stem shapes better than generalized biomass equations (e.g., by Forrester et al. 2017), which might be more suitable for studies including regions

Table 1 Geographical information and site characteristics of the long-term thinning experiments in Norway spruce, Scots pine, European beech, and sessile/common oak 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)

Species	Experiment no.	E. lon	N. lat	E	T	P	Soil texture	Soil type
N. spruce	DEN 5	10.841	47.873	770	6.8	1100	Loam	Parabrown soil
N. spruce	SAC 67	10.752	47.834	840	6.2	1200	Loam	Parabrown soil
N. spruce	SAC 68	10.753	47.834	840	6.2	1200	Loam	Parabrown soil
N. spruce	ZUS 603	10.480	48.397	510	7.5	800	Loamy sand	Brown soil
N. spruce	DEN 606	10.825	47.868	760	6.8	1120	Loam	Parabrown soil
N. spruce	SAC 607	10.823	47.867	770	6.8	1120	Sandy loam	Parabrown soil
N. spruce	FFB 612	11.094	48.239	550	7.5	825	Loam	Parabrown soil
N. spruce	WBU 613	11.040	49.002	560	7	800	Loam	Parabrown soil
N. spruce	VOH 622	12.438	49.684	730	6	900	Loam	Brown soil
N. spruce	TRS 639	12.673	47.940	590	7.3	1200	Loam	Pseudogley
S. pine	BAY 51	11.454	49.976	355	7.7	670	Loam	Parabrown soil
S. pine	BAY 52	11.493	49.964	350	7.7	670	Loam	Pseudogley
S. pine	KUL 53	11.551	50.038	370	7.7	700	Loamy sand	Brown soil
S. pine	SNA 57	12.085	49.557	395	7	650	Loamy sand	Brown soil
S. pine	SNA 58	12.087	49.535	400	7	650	Loamy sand	Brown soil
S. pine	FLA 70	10.547	49.378	470	8	680	Loamy sand	Brown soil
S. pine	BOD 610	12.383	49.261	390	6.9	640	Loamy sand	Brown soil
S. pine	WIE 611	12.106	49.607	400	7.5	680	Loamy sand	Brown soil
E. beech	FAB 15	10.570	49.924	460	7.5	820	Loamy sand	Brown soil
E. beech	HAI 27	9.333	49.991	400	7	1080	Loamy sand	Brown soil
E. beech	STA 91	11.373	48.038	635	7.5	1040	Loamy sand	Brown soil
E. beech	ARN 638	9.977	49.901	340	8	670	Loam	Parabrown soil
s/c oak	WAL 88	7.874	49.377	430	7.8	810	Loamy sand	Brown soil
s/c oak	ROH 90	9.418	49.882	475	7	1120	Loamy sand	Brown soil
s/c oak	ROH 620	9.370	49.894	450	7	1120	Loamy sand	Brown soil
s/c oak	GEI 649	11.503	48.870	475	7.8	700	Loam	Parabrown soil

for which local equations are not available. The carbon content was calculated by multiplying the biomass by the mean carbon content of 0.5 (Körner 2002). Martin et al. (2018) showed that the wood carbon content can vary among species and biomes, however, we had no species-specific values for our study region n available.

To determine an integrated measure for site quality, the site index for each plot and survey was determined using yield tables specific to each species: N. spruce by Wiedemann (1936/1942), S. pine by Wiedemann (1943), E. beech by Schober (1975), and oak by Jüttner (1955). It's crucial to clarify that the site indexes referenced in this study represent the expected mean stand heights at an age of 100 years.

Standing volume and carbon stock according to the National Forest Inventory for comparison

To assess the potential of an additional volume and carbon stock by suspension or reduction of thinning, we used the standing stock of the four species according to the current National Forest Inventory in Bavaria/Germany (BWI III 2023). We calculated the difference between the potential carbon stock (based on the unthinned and only moderately thinned experimental plots) and the current carbon stock in forest practice (based on the NFI data of Bavaria, Germany).

This data is particularly relevant as it pertains to the region where our experimental areas are situated. For even-aged monocultures of N. spruce, S. pine, E. beech, and sessile/common oak, respectively, the standing stock was on average 631, 429, 440, and 390 $m^3\ ha^{-1}$ in age class 80–100, and 644, 432, 468, and 372 $m^3\ ha^{-1}$ in age class 100–120. Interestingly, also at the state level, the standing stock was still increasing at that age. To convert this volume data to carbon stock, specific wood densities (dry weight/fresh volume) were applied: 0.38 Mg m^{-3} for N. spruce, 0.43 Mg m^{-3} for S. pine, 0.55 Mg m^{-3} for E. beech, and 0.56 Mg m^{-3} for sessile/common oak (Knigge and Schulz 1966). With the assumption of a 50% carbon content in the biomass, we roughly estimated the carbon stock to be 120, 92, 121, and 109 Mg C ha^{-1} in the 80–100 year-old stands and 122, 93, 129, and 104 Mg C ha^{-1} in the 100–120 year-old stands (always carbon stock in stem volume > 7 cm at the smaller end).

Table 2 Number of plots and surveys, year of the first and last survey, stand age at the last survey, and covered thinning grades of the long-term thinning experiments of Norway spruce, Scots pine, European beech, and sessile/common oak sampled in this study. The prescription of A–E-grades is based on Wiedemann (1935) and summarized by Kramer (1988, pp. 179–183)

Species	Experiment	No. of plots	Plot size (ha)	No. of sur-veys	First survey	Last survey	Age at last survey	Thinning grade
N. spruce	DEN 5	3	0.25	18	1882	1990	143	A, B, C
N. spruce	SAC 67	3	0.25	14	1902	1990	130	A, B, C
N. spruce	SAC 68	3	0.25	14	1902	1990	130	A, B, C
N. spruce	ZUS 603	6	0.10	9	1974	2017	54	3 × A, 3 × D&E
N. spruce	DEN 606	6	0.09–0.12	9	1977	2022	69	2 × A, 4 × D&E
N. spruce	SAC 607	13	0.10	9	1977	2020	67	2 × A, 2 × C, 9 × D&E
N. spruce	FFB 612	21	0.09	6	1991	2017	48	2 × A, 19 × D&E
N. spruce	WBU 613	7	0.09–0.10	7	1974	2016	100	1 × A, 2 × A, 4 × D&E
N. spruce	VOH 622	11	0.11	6	1993	2018	44	5 × A, 6 × D&E
N. spruce	TRS 639	4	0.10	7	1988	2018	48	1 × A, 3 × D&E
S. pine	BAY 51	1	0.30	15	1899	2014	171	B
S. pine	BAY 52	2	0.25	15	1899	2014	171	B, C
S. pine	KUL 53	2	0.22	15	1899	2014	155	B, C
S. pine	SNA 57	1	0.25	15	1901	2014	157	B
S. pine	SNA 58	2	0.25	15	1901	2014	148	B, C
S. pine	FLA 79	2	0.25	13	1912	2018	133	B, C
S. pine	BOD 610	14	0.10	8	1976	2021	69	2 × A, 12 × D&E
S. pine	WEI 611	24	0.10	7	1987	2021	51	8 × A, 16 × D&E
E. beech	FAB 15	3	0.36	20	1870	2020	198	A, B, C
E. beech	HAI 27	3	0.36	19	1870	2014	182	A, B, C
E. beech	STA 91	5	0.10	8	1971	2019	92	A, 4 × D&E
E. beech	ARN 638	4	0.25	6	1991	2019	82	A, 3 × D&E
s/c oak	WAL 88	6	0.21	14	1934	2022	136	2 × A, 4 × D&E
s/c oak	ROH 90	3	0.28	10	1934	2013	149	A, 2 × D&E
s/c oak	ROH 620	6	0,16	7	1980	2018	92	A, 5 × D&E
s/c oak	GEI 649	9	0.16	4	2004	2019	36	3 × A, 6 × D&E

Statistical models and evaluation

To analyze the overall effect of site index and stand age on the Gini coefficient of tree heights (*GCh*) in unthinned stands (A-grade), we employed model 1. This model incorporates the four species as a factorial variable (basic model for spruce, and factor 1 = pine, 2 = oak, 3 = beech). We used the coefficients a_0–a_3 to show the model results.

$$\ln\left(GCh_{ij}\right) = a_0 + a_1 \times \ln\left(SI_{ij}\right) + a_2 \times \ln\left(age_{ij}\right) + a_3 \times \text{species} + b_i + \varepsilon_{ij} \tag{1}$$

For analyzing the effect of different thinning grades on the Gini coefficient of tree heights (*GCh*) within each species, we applied model 2. This model treats different thinning grades as a factorial variable (basic model for A-grade, and factor 1 = B-grade, 2 = C-grade, 3 = D&E-grade). To present the results, we employed specific coefficients for each species: c for N. spruce, d for S. pine, f for E. beech, and g for oak.

$$\ln\left(GCh_{ij}\right) = c_0 + c_1 \times \ln\left(SI_{ij}\right) + c_2 \times \ln\left(age_{ij}\right) + c_3 \times \text{thinning} + b_i + \varepsilon_{ij} \tag{2}$$

Model 3 was applied for analyzing the effect of site index and stand age on the carbon stock in A- and B-grade plots for each species separately. To ensure a stable, conservative estimation of the carbon storage capacity of unthinned stands, and due to the relative scarcity of A-grade plots (Table 2), we pooled A- and B-grade plots. We used the coefficients h, l, m, and n to show the results for N. spruce, S. pine, E. beech, and oak, respectively.

$$\ln\left(Cstock_{ij}\right) = h_0 + h_1 \times \ln\left(SI_{ij}\right) + h_2 \times \ln\left(age_{ij}\right) + b_i + \varepsilon_{ij} \tag{3}$$

For analyzing the effect of site index, stand age, and thinning grade on the carbon stock for each species, we used model 4. In contrast to model 3, where we pooled the data from A- and B-grade thinning for analysis, model 4 exclusively used data from C and D&E-grade thinned plots. It's important to note that only D&E-grade data were included in Model 4 for oak, as C-grade data were not available for this species (Table 2). We used the coefficients o, p, q, and r to show the results for N. spruce, S. pine, E. beech, and oak, respectively.

$$\ln\left(Cstock_{ij}\right) = o_0 + o_1 \times \ln\left(SI_{ij}\right) + o_2 \times \ln\left(age_{ij}\right) + o_3 \times \text{age} + o_4 \times \text{thinning} + b_i + \varepsilon_{ij} \tag{4}$$

Model 5 was implemented to analyze the relationship between carbon stock and the Gini coefficient of tree heights (GCh) for each species and how this relationship is influenced by site index and thinning grade. The coding for the thinning grade in model 5 was consistent with that in model 2. We used the coefficients s, t, u, and v to show the results for N. spruce, S. pine, E. beech, and oak, respectively.

$$\ln\left(GCh_{ij}\right) = s_0 + s_1 \times \ln\left(SI_{ij}\right) + s_2 \times \ln\left(Cstock_{ij}\right) + s_3 \times \text{thinning} + b_i + \varepsilon_{ij} \tag{5}$$

With ε_{ij}, we denoted the residual error with mean zero and unknown variance of σ^2. To account for the grouped structure in terms of repeated surveys of the same plot, random effect b_i was implemented at the level of plot in alignment with the standard assumptions of mixed-effects models (e.g., Mehtätalo and Lappi 2020). The included experimental plots represent different site conditions (Table 1). In order to capture the effect of the site conditions on the stand structure and carbon stock, we included the site index as a fixed effect in all models. The experiment was not used as a random effect as it would have eliminated the effect of the site index.

In the models $a_0, \ldots, a_n$–$s_0, \ldots, s_n$ are the parameters of the fixed effects. Restricted likelihood was used to estimate 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 (Supplementary Figures S1–S4). Likewise, the normality of errors was verified by making normal *q–q* plots of the residuals (Supplementary Figures S1–S4). For all calculations, we used the statistical software R 4.1.0 (R Core Team 2021), explicitly employing the packages *nlme* (Pinheiro et al. 2021), *lme4* (Bates et al. 2015), and *lmfor* (Mehtätalo and Kansanen 2022).

Results

Overview of tree size distribution, standing volume, and carbon stock on the experimental plots

Table 3 shows that the included experimental plots encompassed a broad spectrum of stand ages (11–178 years) and site indexes (17–48 m hq at age 100). Our primary focus was on the Gini coefficient of tree heights (GCh) due to its effective representation of vertical stand structuring. However, for comparative purposes, we also report Gini coefficients for tree diameter (GCd) and volume (GCv), which are commonly used in other studies. Across all species, the mean level of Gini coefficients follows the trend $GCh < GCd < GCv$. In addition to reporting the standing stock in terms of carbon (Mg C ha^{-1}), we also provided data on the standing volume in $\text{m}^3\ \text{ha}^{-1}$ (Table 3). E. beech, on average, exhibited the highest standing stock at 543 m3 ha^{-1}, followed by N. spruce, oak, and S. pine. The average carbon stock value range was 35–112 Mg C ha^{-1}, maintaining the same species ranking as that for volume.

Notice, that Table 3 (last two rows) displays the stem volume, V, in terms of merchantable wood (wood with > 7 cm at the smaller end), whereas carbon stock, C, is reported for total stem volume. Merchantable wood constitutes about 99–99.5% of the total stemwood in trees with stem diameters of 20–30 cm but only 80% of the total stemwood in trees with stem diameters of 10 cm (Prodan 1965, pp. 199,

Table 3 Overview of stand age, site index, tree size distribution, standing volume, and carbon stock on the experimental plots. Mean, minimum, and maximum of the stand age, site index, Gini coefficients based on tree height, diameter, and volume (GCh, GCd, GCv), standing merchantable stem volume (wood with > 7 cm at the smaller end), and carbon stock of stem volume

	Norway spruce			Scots pine			European beech			Sessile/common oak		
	Mean	Min	Max	Mean	Min	Max	Mean	Min	Max	Mean	Min	Max
Stand age	47	11	132	47	17	138	110	45	178	81	21	132
Site index	38	27	48	24	17	33	31	25	37	28	22	32
GCh (./.)	0.057	0.012	0.129	0.055	0.011	0.099	0.060	0.016	0.176	0.034	0.018	0.084
GCd (./.)	0.129	0.038	0.218	0.138	0.068	0.211	0.145	0.076	0.292	0.100	0.065	0.202
GCv (./.)	0.299	0.083	0.506	0.337	0.155	0.536	0.315	0.539	0.168	0.241	0.159	0.483
V ($\text{m}^3\ \text{ha}^{-1}$)	436	5	1461	157	24	837	543	156	1069	314	79	695
C (Mg ha^{-1})	96	1	308	35	8	125	112	31	223	83	32	170

Table 107). Therefore, the proportions between C and V are similar for mean and maximum tree sizes (see values in columns mean and max) but higher for minimum tree sizes (see values in min column).This ranking can be attributed to the different mean ages of the included stands: 47 years for N. spruce and S. pine and 81 and 110 years for oak and E. beech, respectively. However, the maximum carbon stock values proved more informative for our study, with N. spruce reaching 308 Mg C ha^{-1} and E. beech, oak, and S. pine achieving 223, 170, and 125 Mg C ha^{-1}, respectively. *GCh* showed a strong correlation with both *GCd* and *GCv* (Fig. 2). The Pearson correlation coefficients between *GCd* and *GCh* were notably high, recorded at r = 0.81, 0.92, 0.88, and 0.95 for N. spruce, S. pine, E. beech, and oak, respectively. Similarly, the correlation coefficients between *GCv* and *GCh* were r = 0.91, 0.96, 0.91, and 0.96.

Surely, standing volume and carbon stock also displayed a close correlation (Supplementary Figures S5). The Pearson correlation coefficients between standing stem volume and carbon stock were remarkably high, at r = 0.99, 0.97, 0.99, and 0.98 for N. spruce, S. pine, E. beech, and oak, respectively.

Structural diversity depending on stand characteristics and thinning (Q1)

Figure 3 shows the Gini coefficients of tree height (a–d) and stem volume (e–h) plotted against stand age for N. spruce, S. pine, E. beech, and oak. The various thinning grades in the data are represented by letters a, b, c, and d, corresponding to A-grade, B-grade, C-grade, and D&E-grade thinning, respectively. Horizontal lines in the graph illustrate the mean Gini coefficients for each thinning grade, as observed in the experiments.

To address the first research question (Q1) regarding the dependence of structural diversity on stand age, site index, and thinning grade, we focused on the Gini coefficients of tree height. The results of analyzing Q1 are presented in terms of statistical characteristics in Tables 4 and 5 and visualized in Figs. 4 and 5. Initially, we examined the decline in height variation (measured by *GCh*) with stand age in unthinned stands. This analysis is crucial as it highlights the baseline level of *GCh* values in untreated stands, serving as a reference point for comparing the effects of thinning in stands.

The analysis revealed that in their younger stages, stands of all four species—E. beech, N. spruce, oak, and S. pine—exhibited relatively heterogeneous structures. However, with progressing age, they tended to evolve towards a more monolayered structure (Fig. 4a, Table 4). Among these species, E. beech maintained the most pronounced vertical structuring throughout the timespan. The order of decreasing vertical structuring was observed as E. beech > N. spruce > oak > S. pine.

Additionally, the vertical structuring of the stands was found to diminish with increasing site index (Fig. 4b). The same ranking (E. beech > N. spruce > oak > S. pine) in terms of structuring was noted; we found no interactions between the independent variables age and SI (Table 4). E. beech and N. spruce exhibited similar patterns in their vertical structuring, and a parallel behavior was observed between oak and S. pine.

Figure 5, derived from Model 2 (Table 5), illustrates the decline in structural diversity with increasing stand age for all four species. Our results highlight the significant effect of thinning practices on both the level and drift of structural diversity within forest stands.

For N. spruce and E. beech (Fig. 5a, c), thinning from above (D&E-grade) is demonstrated to effectively counteract the loss of structural diversity that typically occurs with aging. In contrast, thinning from below (B- and C-grade) tends to exacerbate the reduction in structural diversity. Notably, thinning from above not only mitigates the decline in diversity but, interestingly, can increase it above the level observed in the A-grade (unthinned) plots. For Scots pine and sessile/common oak (Fig. 5b, d), unthinned plots (A-grade) maintain the highest levels of structural diversity. In contrast, all other thinning practices significantly diminish this diversity. Among the four tree species studied, E. beech exhibited the most pronounced response to thinning in terms

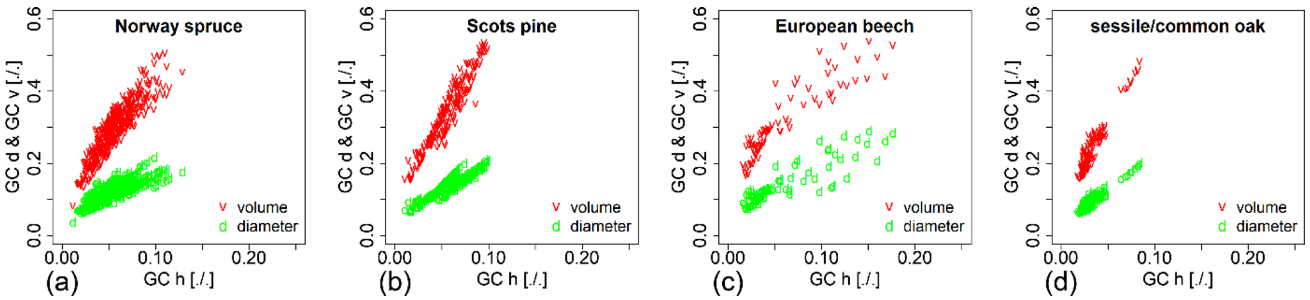

Fig. 2 Relationship between Gini coefficient of stem diameter and tree height (green) and the relationship between Gini coefficient of stem volume and tree height (red) visualized for **a** Norway spruce, **b** Scots pine, **c** European beech, and **d** sessile/common oak

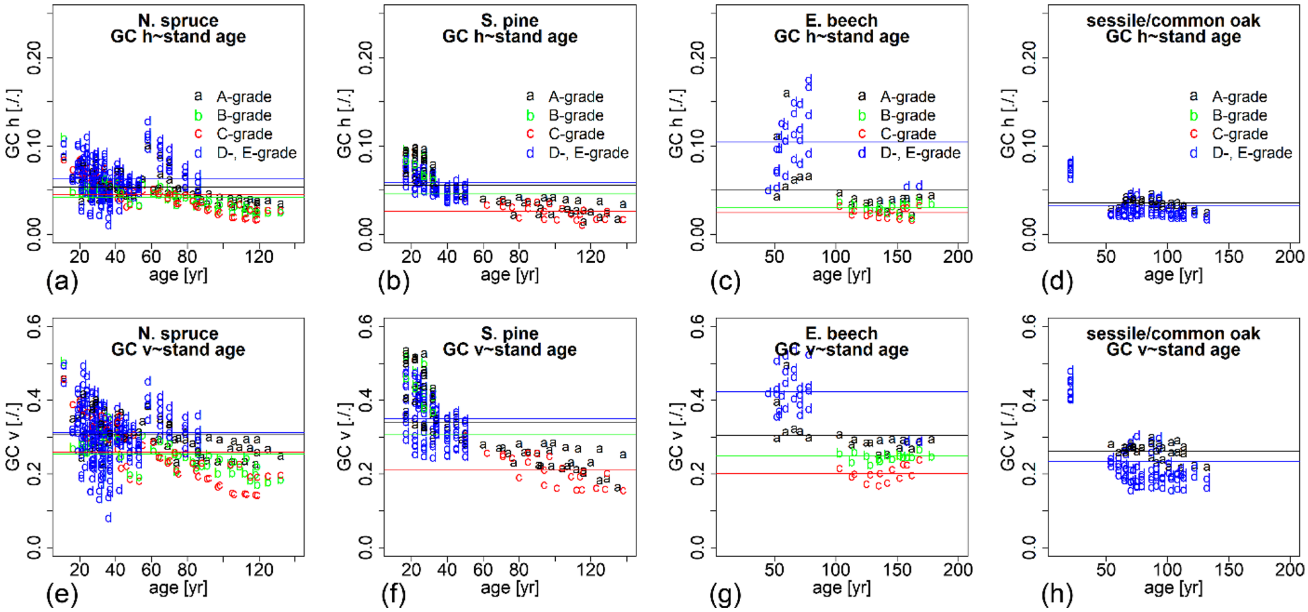

Fig. 3 Gini coefficients of tree height (**a**–**d**) and Gini coefficients of stem volume (**e**–**h**) plotted over stand age for the tree species (from left to right) Norway spruce, Scots pine, European beech, and sessile/common oak. The different thinning grades are indicated by a, b, c, and d (A-grade, B-grade, C-grade, and D&E-grade). The horizontal lines reflect the mean Gini coefficients for the different thinning grades

Table 4 Results of fitting the linear mixed effect model 1 for Gini coefficient *GCh* depending on site index, stand age, and tree species $\ln(GCh) = a_0 + a_1 \times \ln(SI) + a_2 \times \ln(age) + a_3 \times \text{species}$. N = 219

Fixed effect	Coeff	est	se(est)	*p* value
Fixed part				
	a_0	1.96	0.52	< 0.001
Site index	a_1	− 0.94	0.15	< 0.001
Stand age	a_2	− 0.53	0.03	< 0.001
Species [s/o oak]	a_3	0.16	0.06	0.013
Species [N. spruce]	a_3	0.53	0.09	< 0.001
Species [E. beech]	a_3	0.61	0.08	< 0.001
Random part and residual				
	var(b_i)	0.08^2		
	σ^2	0.21^2		

of the Gini coefficient of tree height (*GCh*). Thinning interventions in E. beech stands have the potential to double *GCh* values. Conversely, for the other species—N. spruce, S. pine, and oak—the impact of thinning on *GCh* values was more modest, leading to modifications in the range of 10–20%.

Standing stock of carbon depending on stand characteristics and thinning (Q2)

The results of analyzing Q2 are presented in terms of statistical characteristics in Table 6 and visualized in Fig. 6. The carbon stock continuously increases until advanced ages in stands of all four tree species (Fig. 6). Notably, N. spruce stands can accumulate up to 300 Mg C ha^{-1}, while S. pine stands typically plateau around 100 Mg C ha^{-1}. This leads to the species-specific carbon stock ranking of N. spruce > E. beech > oak > S. pine. Regarding thinning grades, A- and B-grade plots generally achieve the highest carbon stocks. Conversely, plots thinned under D&E-grades, and particularly those under C-grade, exhibit lower carbon storage. Note the difference in the age axis for E. beech and oak (200 years) compared to N. spruce and S. pine (140 years) in Fig. 6.

Unthinned stands of N. spruce and E. beech reached carbon stocks of 200–300 Mg C ha^{-1} in their advanced ages. In contrast, S. pine and oak stands achieved approximately 100–150 Mg C ha^{-1}. Thinning at the C- and D&E-grade levels halved the carbon stock (Fig. 7, Table 6).

Trade-off between carbon stock and structural diversity (Q3)

The results of analyzing Q3 are presented in terms of statistical characteristics in Table 7 and visualized in Fig. 9. Figure 8 shows a discernible decrease in the Gini coefficient of tree height (*GCh*) as carbon stock accumulates for all four species. D&E-grade plots, despite having the highest *GCh* values, exhibit the lowest carbon stock. Conversely, C-grade plots show both low structural diversity and low

Table 5 Results of fitting the linear mixed effect model 2 for Gini coefficient *GCh* depending on site index, stand age, and thinning $\ln(GCh) = c_0 + c_1 \times \ln(SI) + c_2 \times \ln(age) + c_3 \times \text{thinning}$ (Question 1). The coefficients c, d, f, and g show the model 2 results for spruce, pine, beech, and oak, respectively

Fixed effect	N. spruce (n = 452)				S. pine (n = 219)			
	Coeff	est	se(est)	*p* value	Coeff	est	se(est)	*p* value
Fixed part					*Fixed part*			
	c_0	7.58	0.40	< 0.001	d_0	1.96	0.52	< 0.001
Site index	c_1	− 0.44	0.02	< 0.001	d_1	− 0.94	0.15	< 0.001
Stand age	c_2	− 2.46	0.10	< 0.001	d_2	− 0.53	0.03	< 0.001
Thinning [B-grade]	c_3	0.02	0.04	0.690	d_3	0.16	0.06	0.013
Thinning [C-grade]	c_3	− 0.08	0.04	0.027	d_3	0.53	0.09	< 0.001
Thinning [D&E-grade]	c_3	0.11	0.03	< 0.001	d_3	0.61	0.08	< 0.001
Random part and residual					*Random part and residual*			
	$var(b_i)$	0.10^2			$var(b_i)$	0.08^2		
	σ^2	0.19^2			σ^2	0.21^2		
Fixed effect	E. beech (n = 77)				sessile/common oak (n = 114)			
	Coeff	est	se(est)	*p* value	Coeff	est	se(est)	*p* value
Fixed part					*Fixed part*			
	f_0	− 7.74	2.60	0.004	g_0	1.18	0.79	0.137
Site index	f_1	1.68	0.63	0.009	g_1	− 0.53	0.23	0.023
Stand age	f_2	− 0.23	0.15	0.143	g_2	− 0.61	0.05	< 0.001
Thinning [B-grade]	f_3	− 0.30	0.15	0.043	g_3	–	–	–
Thinning [C-grade]	f_3	− 0.70	0.16	< 0.001	g_3	–	–	–
Thinning [D&E-grade]	f_3	0.54	0.13	< 0.001	g_3	− 0.29	0.05	< 0.001
Random part and residual					*Random part and residual*			
	$var(b_i)$	0.13^2			$var(b_i)$	0.08^2		
	σ^2	0.30^2			σ^2	0.20^2		

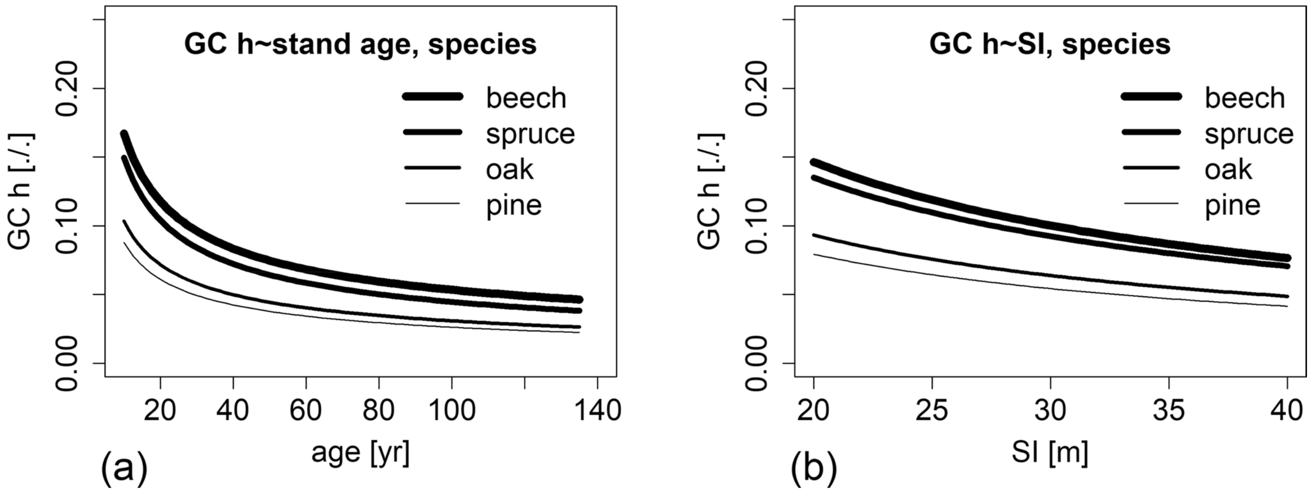

Fig. 4 Effect of stand age and site index on the vertical structural diversity *GCh* of unthinned stands (A-grade) of European beech, Norway spruce, sessile/common oak, and Scots pine. Visualization of the behavior of model 1 (see coefficients in Table 4). For visualization, we modified the respective variables and kept the other covariables constant **a** SI = 30 m and **b** stand age 25 years

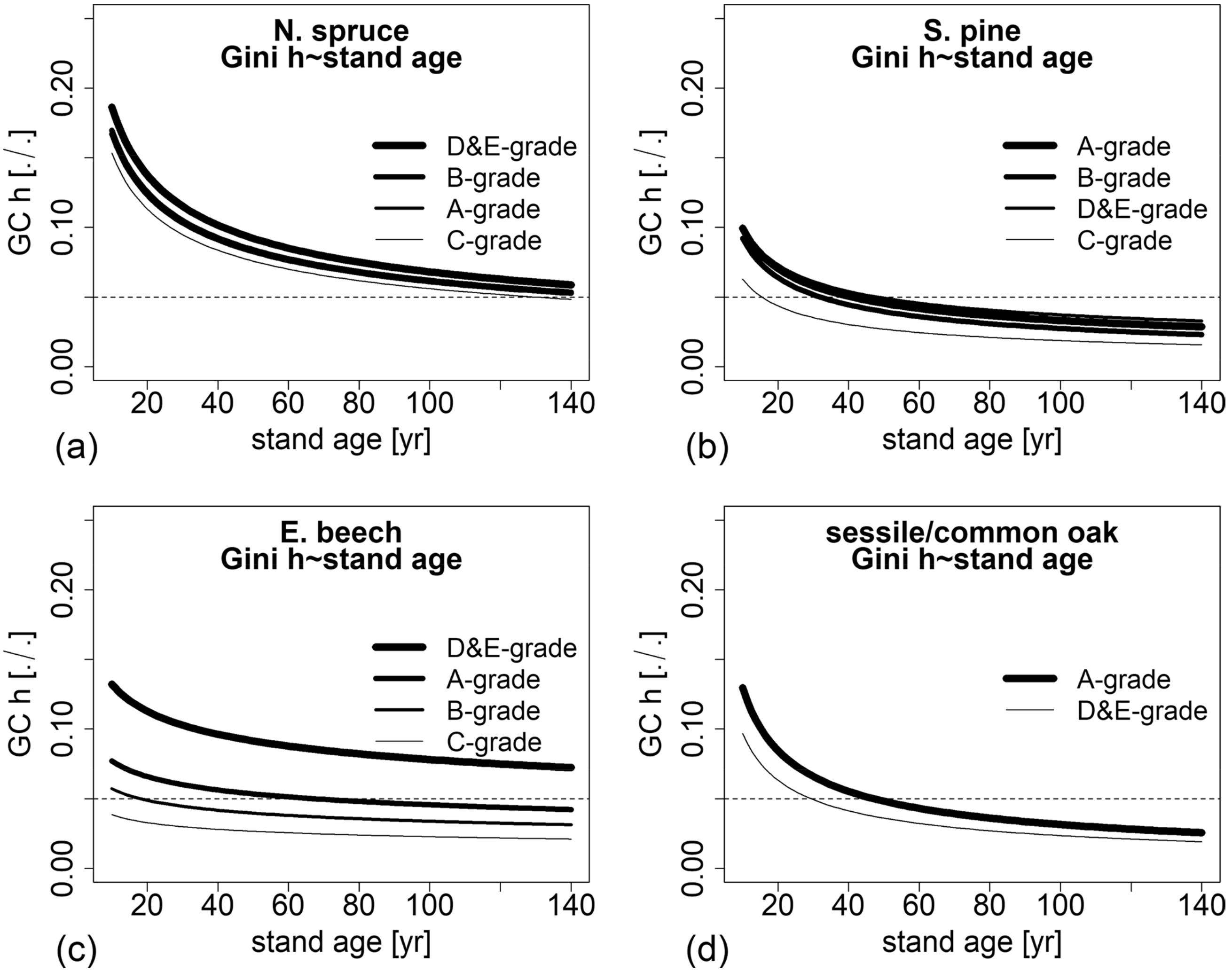

Fig. 5 Effect of stand age and thinning grade (A-, B-, C-, D&E-grade) on the vertical structural diversity *GCh* of **a** Norway spruce, **b** Scots pine, **c** European beech, and **d** sessile/common oak. The visualization is based on model 2 and the coefficients given in Table 5; we modified the respective variables and fixed the covariable SI = 30

carbon stock. A- and B-grade plots typically fall in the middle, with high carbon stock and moderate structural diversity. For oak (shown in Fig. 8d), B- and C-grade plots were not represented, but the trends for A- and D&E-grades mirror those observed in the other species (Fig. 8a–c).

Our findings revealed a general trend where vertical layering, as measured by the Gini coefficient of tree height (*GCh*), decreased with an increase in the standing stock of carbon (Fig. 9, Table 7). However, this trend varies by species in terms of the average level of *GCh*, its reduction with carbon accumulation, and the reaction to different thinning practices.

For a medium standing stock of 150 Mg C ha^{-1}, N. spruce and E. beech (Fig. 9a, c) exhibited higher *GCh* levels than S. pine and oak (Fig. 9b, d). The decline in tree height diversity with increasing carbon stock was relatively modest for N. spruce and E. beech but more pronounced for S. pine and oak. Regarding thinning effects, for N. spruce and E. beech, thinning from above (D&E-grade) was found to be most favorable for maintaining height structuring. In contrast, A-, B-, and C-grade significantly reduced structural diversity in these species. On the other hand, for S. pine and oak, thinning from below (A-, B-grade) led to more diverse structures compared to thinning from above (D&E-grade).

Discussion

The drift of structural diversity with progressing age and counteracting silvicultural measures

As even-aged forest stands age, they tend to become more structurally homogeneous, a process that occurs more rapidly on richer sites compared to poorer ones. As the stock

Table 6 Results of fitting the linear mixed effect model 3 for carbon stock, Cstock, depending on site index and stand age for A- and B-grades $\ln(Cstock) = h_0 + h_1 \times \ln(SI) + h_2 \times \ln(age)$ and model 4 for Carbon stock depending on site index, stand age, and thinning degree $\ln(Cstock) = o_0 + o_1 \times \ln(SI) + o_2 \times \ln(age) + o_3 \times \text{age} + o_4 \times \text{thinning}$ (Question 2). The coefficients h, l, m, and n show the model 3 results, and the coefficients o, p, q, and r show the model 4 results for N. spruce, S. pine, E. beech, and oak, respectively

Fixed effect	N. spruce (model 3; n = 180)				S. pine (model 3; n = 146)			
	Coeff	est	se(est)	*p* value	Coeff	est	se(est)	*p* value
Fixed part					*Fixed part*			
	h_0	−8.43	0.58	<0.001	l_0	−6.94	0.48	<0.001
Site index	h_1	2.38	0.14	<0.001	l_1	2.17	0.12	<0.001
Stand age	h_2	1.22	0.06	<0.001	l_2	1.04	0.06	<0.001
Random part and residual					*Random part and residual*			
	var(b_i)	0.36^2			var(b_i)	0.36^2		
	σ^2	0.37^2			σ^2	0.31^2		

Fixed effect	E. beech (model 3; n = 131)				sessile/common oak (model 3; n = 139)			
	Coeff	est	se(est)	*p* value	Coeff	est	se(est)	*p* value
Fixed part					*Fixed part*			
	m_0	−7.74	0.58	<0.001	n_0	−7.17	0.61	<0.001
Site index	m_1	2.27	0.13	<0.001	n_1	2.12	0.13	<0.001
Stand age	m_2	1.12	0.06	<0.001	n_2	1.11	0.07	<0.001
Random part and residual					*Random part and residual*			
	var(b_i)	0.43^2			var(b_i)	0.31^2		
	σ^2	0.31^2			σ^2	0.32^2		

Fixed effect	N. spruce (model 4; n = 566)				S. pine (model 4; n = 524)			
	Coeff	est	se(est)	*p* value	Coeff	est	se(est)	*p* value
Fixed part					*Fixed part*			
	o_0	−7.32	0.48	<0.001	p_0	−7.93	0.45	<0.001
Site index	o_1	1.21	0.09	<0.001	p_1	1.21	0.10	<0.001
ln(Stand age)	o_2	2.28	0.11	<0.001	p_2	2.23	0.12	<0.001
Stand age	o_3	−0.02	0.002	<0.001	p_3	−0.02	0.002	<0.001
Thinning [D&E-grade]	o_4	−0.43	0.14	0.002	p_4	0.29	0.11	0.006
Random part and residual					*Random part and residual*			
	var(b_i)	0.10^2			var(b_i)	0.09^2		
	σ^2	0.40^2			σ^2	0.41^2		

Fixed effect	E. beech (model 4; n = 515)				Sessile/common oak (model 4; n = 84)			
	Coeff	est	se(est)	*p* value	Coeff	est	se(est)	*p* value
Fixed part					*Fixed part*			
	q_0	−7.15	0.33	<0.001	r_0	2.98	0.51	<0.001
Site index	q_1	1.20	0.11	<0.001	r_1	−0.12	0.13	0.382
ln(Stand age)	q_2	2.16	0.03	<0.001	r_2	0.31	0.07	<0.001
Stand age	q_3	−0.02	0.06	<0.001	r_3	0.01	0.001	<0.001
Thinning [D&E-grade]	q_4	−0.23	0.16	0.140				
Random part and residual					*Random part and residual*			
	var(b_i)	0.09^2			var(b_i)	0.12^2		
	σ^2	0.42^2			σ^2	0.08^2		

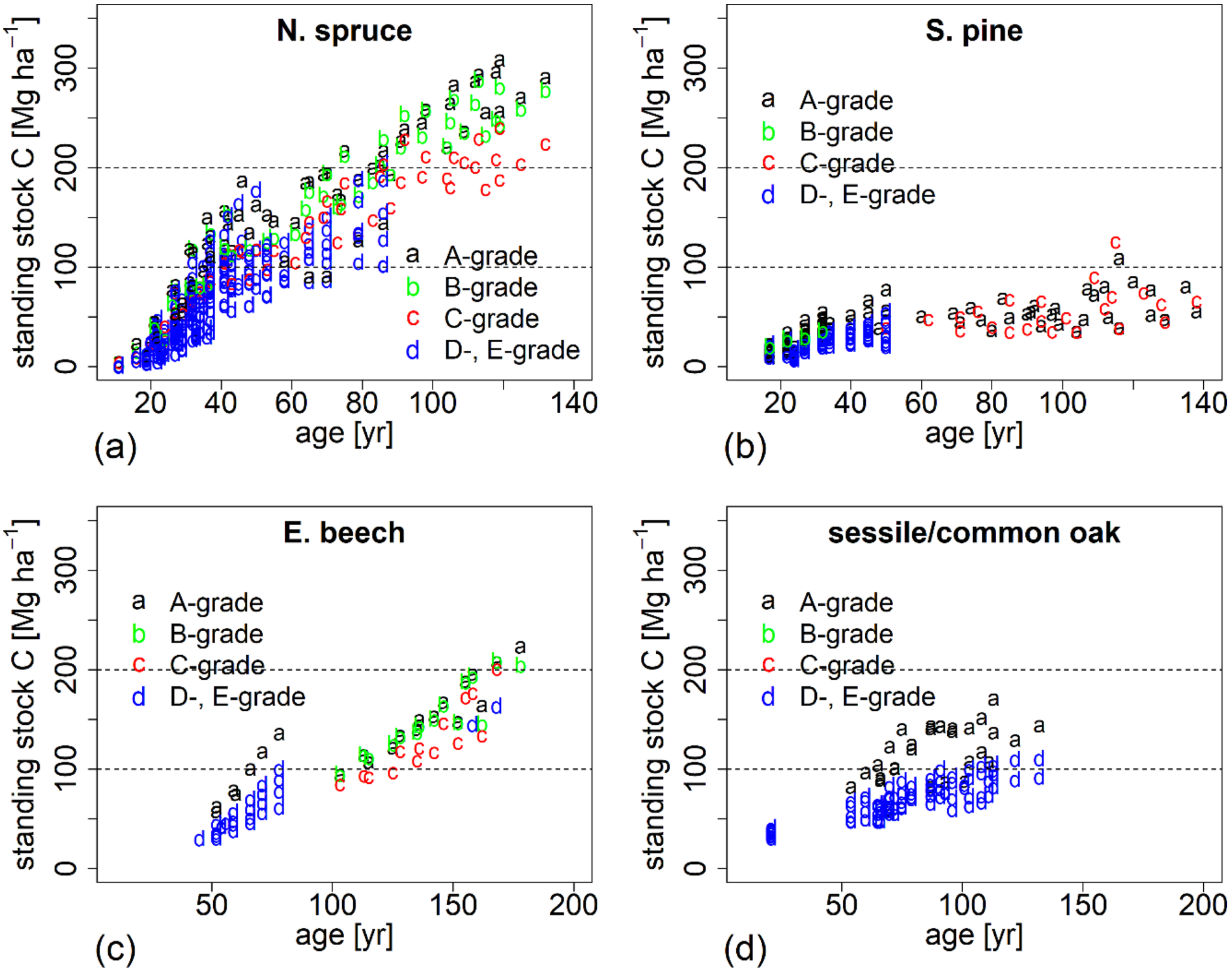

Fig. 6 Standing stock of carbon in stem wood plotted over age in differently thinned stands of **a** Norway spruce, **b** Scots pine, **c** European beech, and **d** sessile/common oak. The horizontal lines at the levels of 100 and 200 Mg C ha^{-1}, respectively, serve for comparing the species

accumulates, competition for resources intensifies, leading to self-thinning, particularly of smaller trees within the stand. This increased competition and density do not directly cause tree mortality. Instead, the reduced carbon balance in dominated trees heightens their vulnerability to pathogens, more likely resulting in the death of smaller trees than their taller counterparts (Long and Smith 1984). The loss of understory or subdominant trees is essentially irreversible, as these trees are outcompeted due to temporary resource scarcity and weakening. However, under more open canopies in later developmental stages, these smaller trees might have a renewed opportunity to survive and even contribute to maintaining higher levels of stand growth. Such loss can be mitigated through silvicultural practices like thinning from above, which supports the growth of smaller and medium-sized trees by removing taller ones. This approach can help preserve structural diversity in the forest stands, though it may come at the cost of reduced accumulation of standing volume and carbon stock.

The accumulation of standing stock is a crucial factor driving stand homogenization, highlighting a challenging tradeoff between structural diversity and standing stock in even-aged and monospecific stands we were considering here. Although this tradeoff may be difficult to completely resolve monospecific stands, it can be mitigated through targeted silvicultural interventions. For species such as N. spruce and E. beech, thinning from above has been shown to be effective. On the other hand, for S. pine and oak, adopting a strategy of no thinning or only moderate thinning is preferable (Fig. 9). Interestingly, the variability of the *GCh* values of oak is not higher than of the other species (Figs. 8, 9), although the data is based on two species (*Quercus robur* L. and *Quercus petraea* (Matt.) Liebl.) compared to the other species of this study.

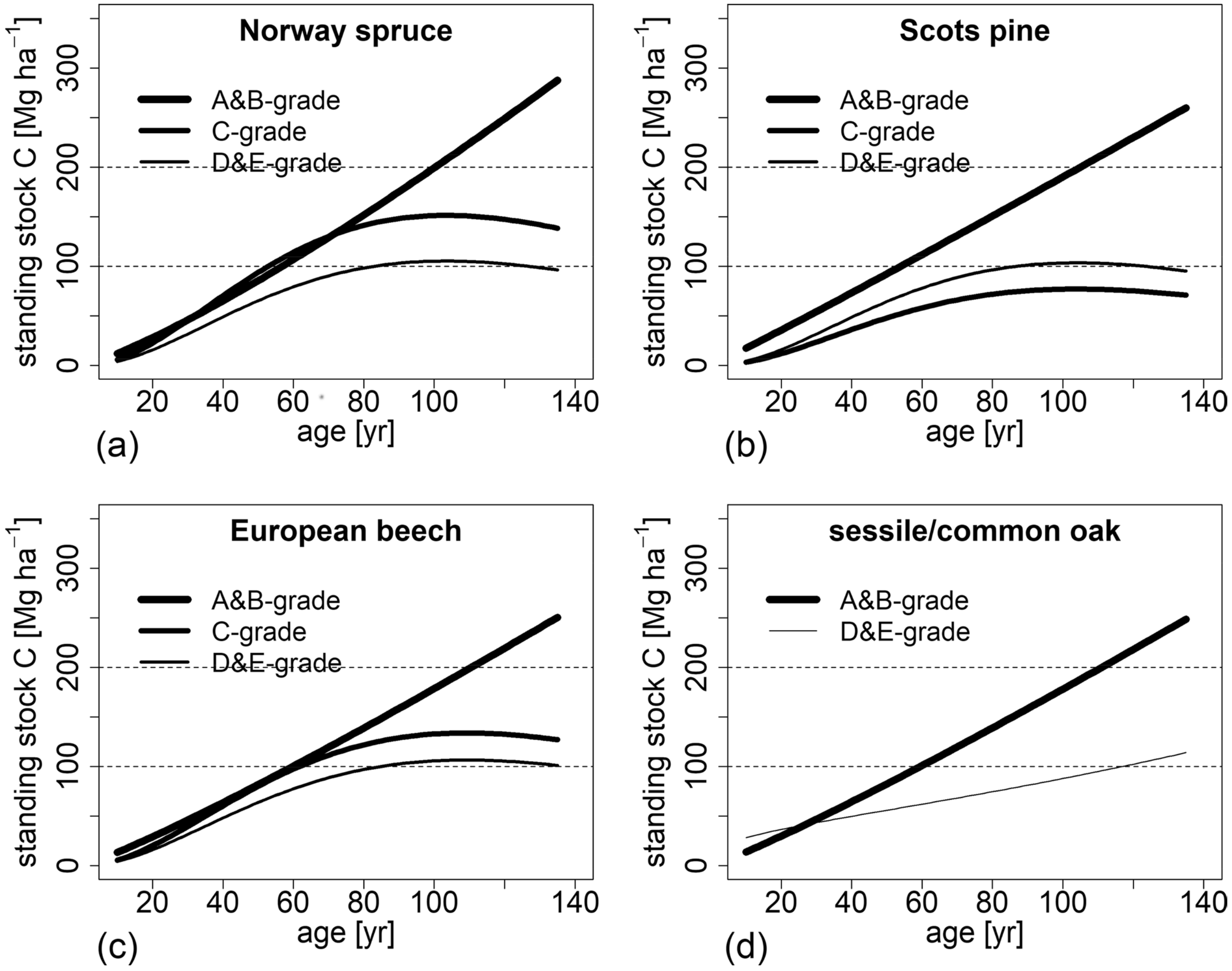

Fig. 7 Visualization of models 3 and 4 for the dependency of the standing stock of C and stand age for **a** Norway spruce, **b** Scots pine, **c** European beech, and **d** sessile/common oak. For model coefficients, see Table 6; the site index was set to SI = 30 m for all model runs

Differences between the standing stock on unthinned and differently thinned plots

The standing stock of volume and carbon of the unthinned or moderately thinned stands was far above the level of stands with usual thinning from below (C-grade) or above (D&E-grade) (Fig. 7). This reveals a high potential for further carbon stock accumulation in the latter stands, especially in the case of the structural heterogeneous stands. They are stabilized and equipped with trees of various dimensions that may maintain the stand growth on a high level if the thinning is reduced or suspended in the next decades for the purpose of carbon neutrality (Melikov et al. 2023; Rybar and Bosela 2023).

The A-grade plots demonstrate a remarkable potential for carbon storage, which continues to increase even in old stands, and have not yet reached the maximum level of above-ground standing stock, often referred to as the constant final yield (Cavalieri et al. 2022; Weiner and Freckleton 2010). Indeed, there are many practical reasons to reduce their standing stock early, such as realizing intermediate yield and income, mechanical stabilization against storms and snow-breakage, or establishment and promotion of natural regeneration. Other reasons may be the export of intermediately thinned wood to substitute fossil fuels and construction materials by wood (Biber et al. 2020; Schwaiger et al. 2018, 2019). The continuously increasing stocks on the A-grades may be slowed down in the future by climate change effects, especially in N. spruce and E. beech stands (Lévesque et al. 2013, Mette et al. 2013, Geßler et al. 2007), which are more susceptible to drought than S. pine and oak (Meyer et al. 2020; Merlin et al.2015). Despite these considerations, it is evident that the A-grade stands in our study have not yet reached their full carbon storage potential. This observation aligns with a Europe-wide study involving 476 A-grade plots, which revealed a consistent

Table 7 Results of fitting the linear mixed effect model 5 for the Gini coefficient *GCh* depending on the site index, carbon stock and thinning grade for all species separately $\ln(GCh) = s_0 + s_1 \times \ln(SI) + s_2 \times \ln(Cstock) + s_3 \times thinning$ (Question 3). The coefficients s, t, u, and v show the model 5 results for N. spruce, S. pine, E. beech, and sessile/common oak, respectively

Fixed effect	N. spruce (n = 452)				S. pine (n = 219)			
	Coeff	est	se(est)	*p* value	Coeff	est	se(est)	*p* value
	Fixed part				*Fixed part*			
	s_0	4.58	0.43	<0.001	t_0	−0.42	0.48	0.381
Site index	s_1	−0.17	0.01	<0.001	t_1	−0.37	0.04	<0.001
Carbon stock	s_2	−1.87	0.12	<0.001	t_2	−0.36	0.16	0.028
Thinning [B-grade]	s_3	−0.07	0.05	0.153	t_3	0.19	0.10	0.045
Thinning [C-grade]	s_3	−0.16	0.05	<0.001	t_3	−0.78	0.08	<0.001
Thinning [D&E-grade]	s_3	0.09	0.04	0.016	t_3	−0.07	0.05	0.168
	Random part and residual				*Random part and residual*			
	$var(b_i)$	0.12^2			$var(b_i)$	0.17^2		
	σ^2	0.23^2			σ^2	0.21^2		

Fixed effect	E. beech (n = 84)				Sessile/common oak (n = 114)			
	Coeff	est	se(est)	*p* value	Coeff	est	se(est)	*p* value
	Fixed part				*Fixed part*			
	u_0	−10.92	2.72	<0.001	v_0	1.14	0.97	0.241
Site index	u_1	−0.13	0.14	0.348	v_1	−0.79	0.09	<0.001
Carbon stock	u_2	2.51	0.70	<0.001	v_2	−0.21	0.29	0.462
Thinning [B-grade]	u_3	−0.33	0.18	0.065	v_3	–	–	–
Thinning [C-grade]	u_3	−0.78	0.21	<0.001	v_3	–	–	–
Thinning [D&E-grade]	u_3	0.53	0.18	0.005	v_3	−0.51	0.07	<0.001
	Random part and residual				*Random part and residual*			
	$var(b_i)$	0.24^2			$var(b_i)$	0.16^2		
	σ^2	0.37^2			σ^2	0.24^2		

increase in standing stock with no evident flattening even in older stands across all major European tree species (Pretzsch et al. 2023b).

On the thinned plots, the carbon stock is kept far below the maximum, as indicated by the A-grade plots. Especially on the C- and D&E-grade plots, the stock levels plateau at medium ages due to the removal of biomass through thinning, resulting in stock levels that are only 50–70% of those seen in A-grade plots. Without A-grades in long-term experiments, this plateauing effect in C- and D&E-grades could be misinterpreted as a natural development, representing the maximum storage potential. The existence of continuously monitored A-grade plots is crucial, as they provide a benchmark for understanding the true potential of carbon storage. Without these plots, there is a significant risk of underestimating the carbon storage capacity of forest stands. This underscores the importance of A-grade plots in research despite their instability against storm and ice-breakage or lack of economic feasibility (Paul et al. 2019; Pretzsch et al. 2019).

The thinned stands typically remain below the constant final yield level, but those stabilized through thinning from above exhibit potential for low-risk carbon stock accumulation in the coming decades. D&E-grade plots, often reflecting common thinning practices in forestry, result from continuous crop tree promotion through strong thinning from above. This approach involves maintaining stand density below the level that would achieve maximum growth rates. Reducing thinning in these stands could increase the standing stock relatively fast, as growth rates are likely to rise alongside the increasing stock until the maximum stand density is reached (Assmann 1970a, b; Zeide 2001, 2002).

The potential of higher C accumulation in the standing stock

To further substantiate the potential of carbon storage in mature forest stands in South Germany, we used the standing stock of the four species according to the current National Forest Inventory in Bavaria/Germany (BWI III 2023). This data represents the site conditions, current

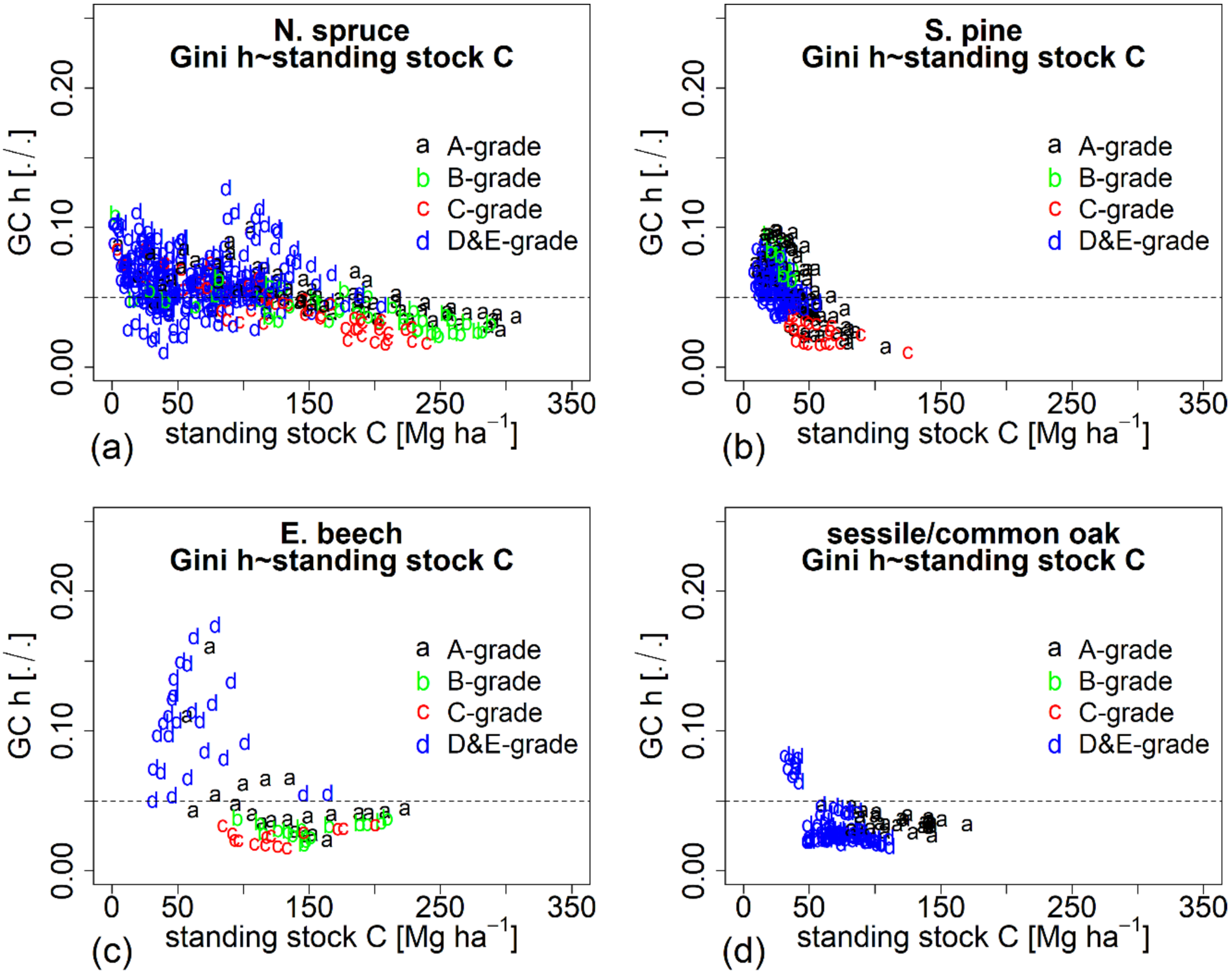

Fig. 8 Gini coefficient of tree height plotted against the standing stock of carbon in stem wood in differently thinned stands of **a** Norway spruce, **b** Scots pine, **c** European beech, and **d** sessile/common oak. The horizontal lines at the levels of $GCh = 0.05$ serve for comparing the species

silvicultural practice, and standing stock of the region where our experimental areas are situated. Comparing the mean carbon storage on the A- and B-grade plots with the National Forest Inventory data (Sect. "Standing volume and carbon stock according to the National Forest Inventory for comparison") showed that the carbon storage potential is far from exploited. For the 80–100 age class, the mean carbon storage on experimental plots was 244, 176, 233, and 122 Mg C ha^{-1} for N. spruce, S. pine, E. beech, and oak, respectively, and 260, 193, 271, and 147 Mg C ha^{-1} for the 100–120 age class. These values were derived using Model 3, based on the ages of 90 and 110 and the mean site index values for the species in Bavaria (SI = 32.1, 26.8, 31.0, 24.4 for N. spruce, S. pine, E. beech, and oak, respectively).

For N. spruce, only 47–50% of its carbon storage potential is currently being utilized. In S. pine, E. beech, and oak, the exploitation rates are 48–53%, 47–55%, and 71–78% respectively. This translates to an under-exploitation of 22–53%, with N. spruce showing the most significant gap and oak the least. A reduction in thinning, particularly in stands previously managed with D&E-grade thinning, might lead to a decrease in structural diversity. However, it could be an effective strategy for enhancing carbon storage in stands of the four considered species in Central Europe until their level of constant final yield is reached. This approach could potentially add an additional 100–200 Mg C ha^{-1} to the carbon stock over the next 3–5 decades.

Methodological considerations

In their early stages, planted stands typically exhibit a very uniform tree size distribution due to the selection of similarly sized plants from nurseries. This similarity

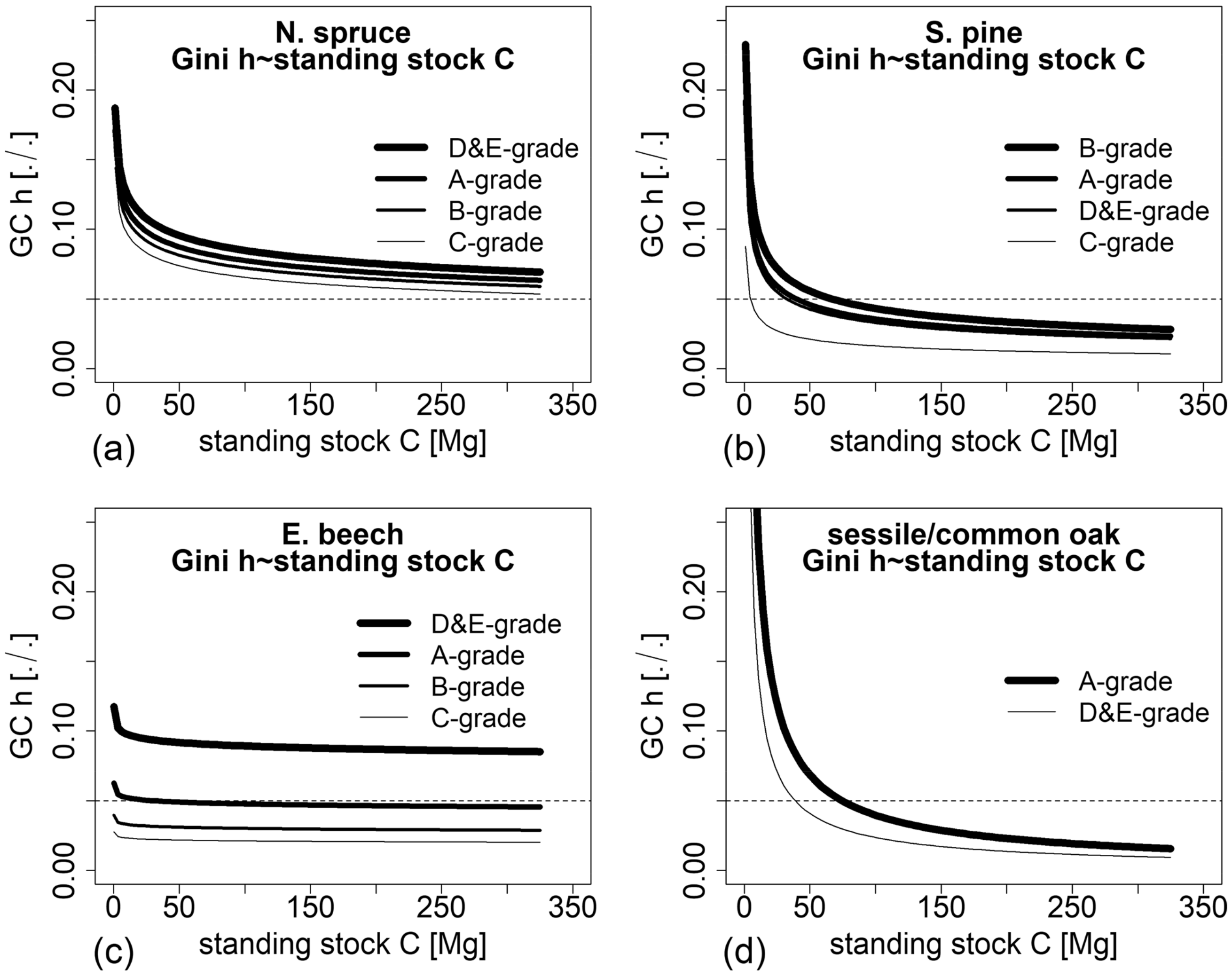

Fig. 9 Trade-off between standing stock in terms of carbon and tree height diversity in terms of Gini coefficient of height for **a** Norway spruce, **b** Scots pine, **c** European beech, and **d** sessile/common oak for different thinning grades. The visualization is based on model 5. The site index was set to hq = 3 m. The horizontal line of *GCh* = 0.05 serves as a reference when comparing the species' behavior

in size would result in the Gini coefficient for tree height (*GCh*) being close to zero at the outset. However, the initial surveys and measurements on experimental plots are usually conducted 5–10 years after planting, by which time the trees have grown beyond 1.30 m in height, and their stem diameter at breast height becomes measurable. During this phase, intense competition and significant size differentiation among trees lead to high *GCh* values. This competitive growth phase is why the curves depicting structural diversity over stand age, as shown in Figs. 4, 5, and 9, start from a peak at ages 5–10. Had measurements been taken earlier, the structural diversity would likely display an optimum curve, starting with low *GCh* values in the initial phase, peaking at ages 5–10, and then showing a decline in heterogeneity in subsequent years.

Our analysis primarily utilized the Gini coefficient of tree height (*GCh*) as it most effectively represents the vertical structuring of stands. However, we also included the Gini coefficients of tree diameter (*GCd*) and tree volume (*GCv*) for comprehensive insights and comparability with other studies. For all species, the average level of these Gini coefficients followed the sequence: $GCh < GCd < GCv$. Notably, *GCh* was found to correlate closely with both *GCd* and *GCv* (Fig. 1). Furthermore, there was a strong correlation between the standing stock in terms of volume (m^3 ha^{-1}) and the carbon stock (Mg C ha^{-1}) (Fig. 2). This correlation suggests that the relationships identified between the Gini coefficient of tree height and carbon stock are similarly applicable to relationships involving Gini coefficients based on other tree attributes (such as diameter and volume) and the standing volume stock.

The comparison of maximum carbon stock in unthinned and moderately thinned stands from the experimental plots with the mean carbon stock reported in the National Forest

Inventory (BWI III 2023) might be subject to a slight bias. The inventory data primarily accounts for merchantable wood, focusing on standing stem volume greater than 7 cm at the smaller end, which is then converted into biomass and carbon stock. In contrast, our biomass and carbon stock calculations were based on stemwood functions. As noted by Prodan (1965, pp. 199, Table 107), merchantable wood constitutes about 99–99.5% of the total stemwood in trees with stem diameters of 20–30 cm. This suggests that a correction factor of approximately 1% could be applied to our values to account for the difference between merchantable and total stemwood. This study analyzed the above ground stock of tree volume and carbon; to et a complete picture of the stock below ground values may be accessed by expansion factors or models (Rötzer et al. 2009).

Implications for silviculture and forest management

On the underlying experimental plots, we strictly follow the prescribed thinning grades to learn more about the behavior of different treated stands in old ages. However, for the management of forest stands in practice, we can draw some conclusions or derive some scenarios for climate change mitigation considering the revealed tradeoff between structural diversity and carbon storage and its modification by silvicultural thinning.

Figure 10 illustrates three primary scenarios for enhancing the carbon stock in forest stands. Stands that have undergone substantial thinning, either from below (C-grade) or from above (D&E-grade), might be stable enough (due to low height-to-diameter ratios from past density reductions) to accumulate more stock. This accumulation could feasibly occur from middle to old age. This approach might slow the promotion of diameter growth in selected future crop trees, delay harvesting, and potentially lead to economic drawbacks.

Scenario 1 (Fig. 10a) proposes increasing density through the reduction or suspension of thinning. This approach is expected to gradually bring the standing stock closer to the constant final yield level, potentially over the course of several decades. Stands treated with D&E-grade thinning typically have sufficient trees across various layers, allowing growth to continue at a relatively high level into older ages.

Scenario 2 (Fig. 10b) suggests that future forest generations might maintain a higher standing stock from the beginning on. Given the current challenges in carbon storage, the demand for energy wood, and the minimal price differences between low and high dimension timber, the traditional practice of strong density reductions to promote a limited number of future crop trees and accelerate their diameter growth may be re-evaluated. These past practices of reducing density to favor individual tree growth often came at the cost of overall stand growth, as well as reduced carbon storage.

Scenario 3 (Fig. 10c) involves initiating regeneration early, either through natural regeneration or by planting different cohorts below the overstory. This process could be executed in stages, forming groups or clusters with various species, depending on their light requirements and canopy

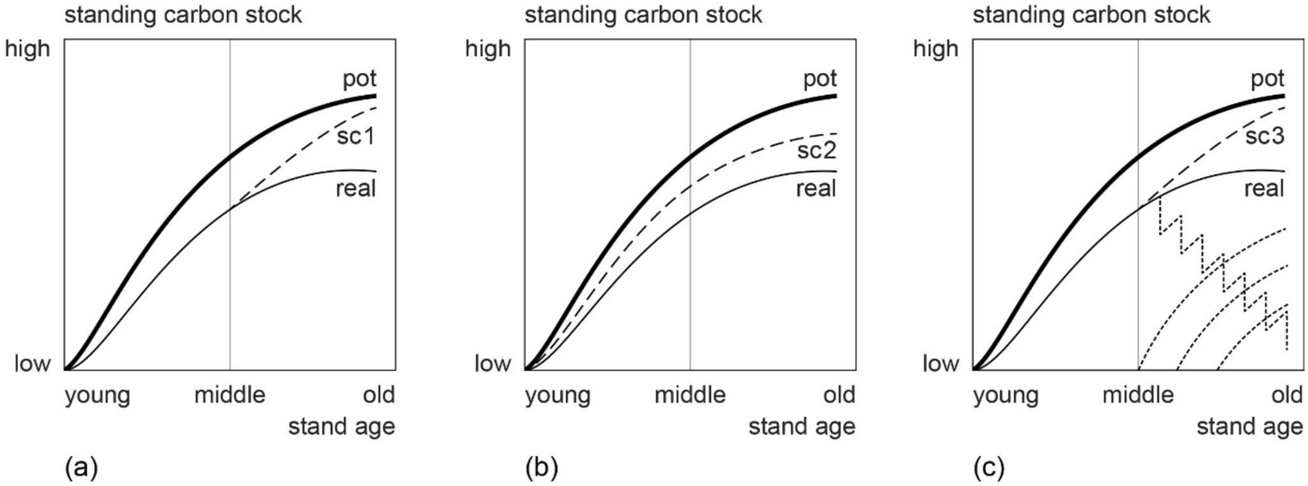

Fig. 10 Concepts for better utilizing the carbon storage potential of forest stands by scenarios 1–3 (broken lines). The upper bold lines (pot) indicate the potential carbon storage according to our findings on A- and B-grade plots. The lower thin lines (real) represent the current carbon storage according to our findings on C- and D&E-grade plots. **a** Increase of the stock in middle aged stands by reducing the harvest and increasing the density. **b** Continuous increase of the carbon stock by raising the stand density since the young stand phase. **c** Increase of the total standing stock (overstory + regeneration) since the middle stand age by continuous reduction of the overstory and establishment and promotion of the regeneration

openings. The standing stock from this new regeneration may offset the carbon exported when thinning the upper layer to facilitate and encourage the growth of the new generation. Over the long term, the standing stock of these uneven-aged stands may be lower compared to the old phase of even-aged stands. However, this approach can transform the forest into a continuously covered forest system, where the stock is consistently maintained at a relatively high level (Reventlow et al. 2021; Hilmers et al. 2020; O'Hara 2014; Schütz 2001).

Disturbances, both by human interventions and nature, are creating numerous canopy openings in forests globally (Patacca et al. 2023; Reis et al. 2022; McCarthy 2001), leading to increasingly gappy and fragmented forests (Biber and Pretzsch 2022; Senf and Seidl 2018). As a result, forests are experiencing a notable reduction in standing stock. In response to this trend, a strategic approach could be to reduce thinning in forest areas that still retain normal and closed structures. Such a management strategy would help preserve the diversity in horizontal patterns of forest areas, maintaining a balance between closed and open zones.

Conclusions

Knowledge-based silvicultural design can reconcile initially seemingly diverging management goals. Reconciliation of stand structure diversity and carbon storage is essential for stress resilience and climate mitigation through sustainable forest management. We found, that in general stand structure diversity decreased with increasing carbon stock. Silvicultural treatment, and especially the kind of thinning and stand density management modified the tradeoff between stand structure diversity and carbon storage. When the carbon stock was increased from a low to a mean level we found a drastic reduction of stand structure diversity. Further accumulation of the carbon stock above the mean level hardly exacerbated the losses of stand structural diversity. Comparing the carbon stock of stands under the current standard of strong thinning with the potential carbon stock of unthinned or only moderately thinned stands showed that the carbon storage potential is far from exploited. A reduction in thinning, particularly in stands previously heavily thinned from above, might cause slight losses of structural diversity. However, it could add an additional 100–200 Mg C ha^{-1} to the carbon stock of these species over the next 3–5 decades. Our study emphasizes the relevance of silvicultural measures and their modulating effect on the relationship between stand structure diversity and carbon storage. This and also further knowledge is essential for a better integration of nature conservation and biodiversity aspects into sustainable forest management.

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Data availability The datasets analyzed during this study are available from the corresponding author upon reasonable request.

Code availability Not applicable.

Declarations

Conflict of interest The authors have no conflict of interest to declare that is relevant to the content of this article. The authors have no relevant financial or non-financial interests to disclose.

Ethics approval Not applicable—no living material is included.

Consent to participate Not applicable—no living material included.

Consent for publication Not applicable—no living material included.

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