# With increasing site quality asymmetric competition and mortality reduces Scots pine (*Pinus sylvestris* L.) stand structuring across Europe

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A B S T R A C T

Heterogeneity of structure can increase mechanical stability, stress resistance and resilience, biodiversity and many other functions and services of forest stands. That is why many silvicultural measures aim at enhancing structural diversity. However, the effectiveness and potential of structuring may depend on the site conditions. Here, we revealed how the stand structure is determined by site quality and results from site-dependent partitioning of growth and mortality among the trees. We based our study on 90 mature, even-aged, fully stocked monocultures of Scots pine (*Pinus sylvestris* L.) sampled in 21 countries along a productivity gradient across Europe. A mini-simulation study further analyzed the site-dependency of the interplay between growth and mortality and the resulting stand structure. The overarching hypothesis was that the stand structure changes with site quality and results from the site-dependent asymmetry of competition and mortality.

First, we show that Scots pine stands structure across Europe become more homogeneous with increasing site quality. The coefficient of variation and Gini coefficient of stem diameter and tree height continuously decreased, whereas Stand Density Index and stand basal area increased with site index.

Second, we reveal a site-dependency of the growth distribution among the trees and the mortality. With increasing site index, the asymmetry of both competition and growth distribution increased and suggested, at first glance, an increase in stand heterogeneity. However, with increasing site index, mortality eliminates mainly small instead of all-sized trees, cancels the size variation and reduces the structural heterogeneity.

Third, we modelled the site-dependent interplay between growth partitioning and mortality. By scenario runs for different site conditions, we can show how the site-dependent structure at the stand level emerges from the asymmetric competition and mortality at the tree level and how the interplay changes with increasing site quality across Europe.

Our most interesting finding was that the growth partitioning became more asymmetric and structuring with increasing site quality, but that the mortality eliminated predominantly small trees, reduced their size variation and thus reversed the impact of site quality on the structure. Finally, the reverse effects of mode of growth partitioning and mortality on the stand structure resulted in the highest size variation on poor sites and decreased structural heterogeneity with increasing site quality. Since our results indicate where heterogeneous structures need silviculture interventions and where they emerge naturally, we conclude that these findings may improve system understanding and modelling and guide forest management aiming at structurally rich forests.

## 1. Introduction

The structure of forest stands in terms of their variation in tree size is highly relevant for most ecosystem functions and services. Stand structure affects, among others, the productivity (Torresan et al. 2020, Dieler et al. 2017, Ishii et al. 2004, Juchheim et al. 2017), the mechanical stability (Dobbertin 2002) but also fire risk (Stephens and Moghaddas 2005), biodiversity (Bohn and Huth 2017, Archaux and Bakkaus 2007) and cultural services (Sutherland et al. 2016). For assessing the potential structural diversity, rating of an actual stand structure, and deriving silvicultural prescriptions, it is essential to know how the structure is pre-determined by the specific site conditions. A better understanding of the relationship between site quality and stand structure is of particular interest under changing site conditions. It may allow the prediction of how stands and associated functions and services will develop when growing conditions become harsher and how detrimental effects on stand structure may be remedied by silvicultural interventions (Schutz, 2002, Meyer 2000, Pretzsch 1996). Creation of structure by silvicultural interventions can, among others, increase mechanical stability (Griess and Knoke 2011), resistance against insect attacks (Jactel and Brock-erhoff 2007) and drought stress (Pretzsch et al. 2022, 2013). However, the effectiveness and potential of size differentiation may depend on ecological preconditions such as tree species assemblage, the initial structure, and, finally, also on the site conditions.

Starting with an initial tree size distribution, the stand structure results from the species-specific size growth and tree mortality. Site conditions may modulate both size growth and tree mortality partitioning. When dealing with the size distributions in the following, we will mainly consider the stem diameter distribution; but it should be noted that the

distribution of tree height, stem basal area, or tree volume could also be used for describing a size distribution and can be derived from the stem diameter via allometric relationships. There is a growing body of evidence that favourable environmental conditions modify the competition and growth distribution towards a more size-asymmetric mode on rich sites (Pretzsch et al. 2022, Pretzsch and Biber 2010, Wichmann 2002, Schwinning and Weiner 1998). This means that big trees grow over-proportionally more than small trees. Their high growth rate may extend the right branch of the diameter distribution (large diameter side of the distribution). This asymmetric partitioning may be quantified by the steepness of the relationship between tree growth and tree size (Pretzsch and Biber 2010), by the Gini coefficient of tree growth (Latte et al. 2016, Metsaranta and Lieffers 2010, 2008, Nord-Larsen et al. 2006), or the growth dominance coefficient, GDC, (Binkley et al., 2006). Size inequality quantifies how stand density is distributed between different sizes of trees but does not quantify how individual tree growth is distributed among different sizes (Forrester 2019); this is why GDC is useful to known in combination with the Gini coefficient.

However, mortality rates also often increase with site quality (Eid and Tuhus 2001). Thus, even if the growth partitioning became more asymmetric with increasing site quality, the stand structure may, in the end, be less heterogeneous (Gracia and Retana 1996, Aber et al. 1982). This means that despite a more unequal competition and growth distribution, the tree size structure may become more equal on rich and more unequal on poor sites. Whereas many studies dealt with the site-dependency of the mode of competition and partitioning of biomass, only little research is done about the site-dependency of the mode of mortality (the pattern of dropout of small compared to big trees) and its effect on size distribution in addition to the structuring effect of growth

partitioning (Bigler et al. 2007). In the following, we will use the term dropout trees for those trees that were dead at the time of the inventory. Both the partitioning of growth and mortality shape the size distribution dynamics; both may be site-dependent. Their interaction may result in the counterintuitive decrease of stand heterogeeity with increasing site quality despite the initial increase of inequality growth distribution.

Against this background, the overarching hypothesis of this study was that the stand structure changes with site quality and results from site-dependent partitioning of both growth and mortality. We used a set of 90 medium and evenly aged, fully stocked Scots pine (*Pinus sylvestris* L.) stands distributed along a productivity gradient across Europe to answer the following questions:

Q I: How does the stand structuring, characterized by, e.g. the co-efficient of variation, and the Gini coefficient of stem diameter, change with increasing site quality across Europe?

Q II: How does the inter-individual symmetry/asymmetry of competition, growth partitioning, and mortality depend on the site quality?

Q III: How does the site-dependency of the stand structure result from the interplay between growth partitioning and mortality?

## 2. Material and methods

### 2.1. Material

A series of EU funded projects such as EuMIXFOR, REFORM, and CARE4C backed by national projects of the included institutions, created a Trans-European network of triplets covering mono- and mixed species stands of Scots pine and European beech (*Fagus sylvatica* L.; Pretzsch et al. 2015, 2016), Scots pine and Norway spruce (*Picea abies* (L.) Karst.; Ruiz-Peinado et al. 2021), and Scots pine and sessile and common oak (*Quercus robur* L., *Quercus petraea* (Matt.) Liebl.; Pretzsch et al. 2020a). The triplets are located in 21 countries (Austria, Belgium, Bosnia-Herzegovina, Bulgaria, Czech Republic, Denmark, Estonia, France, Georgia, Germany, Italy, Latvia, Lithuania, Norway, Poland, Serbia, Slovakia, Spain, Sweden, Netherlands, and Ukraine). Here, we used the 90 monospecific Scots pine stands established and inventoried in 2013–2017 in these countries across Europe (Fig. 1).

The plots were established in mature, even-aged, fully stocked stands without signs of recent thinning interventions so that they represent stands close to maximum stand densities (Pretzsch et al. 2015). Most of the plots were established in even-aged plantation forests. Plot sizes were highly variable and ranged from 0.014 to 1.55 ha. On each plot, the diameter of all trees>7 cm was measured, and two increment cores per tree were taken at 1.3 m stem height in a sample of around 20 living trees per species and plot (covering the diameter range). For each standing tree, we recorded whether it was alive or dead. Annual ring widths were measured from each increment core, and the growth series were cross-dated using standardized dendrochronological techniques. Mean values of annual ring widths of the two cores per tree were used for further analysis. Using data from cored trees, tree diameter increment-diameter models were fitted by year, species and plot to estimate diameter increments of non-cored trees for the studied period (Steckel et al. 2019). The studied 5-years growth periods were 2009–2013 for the
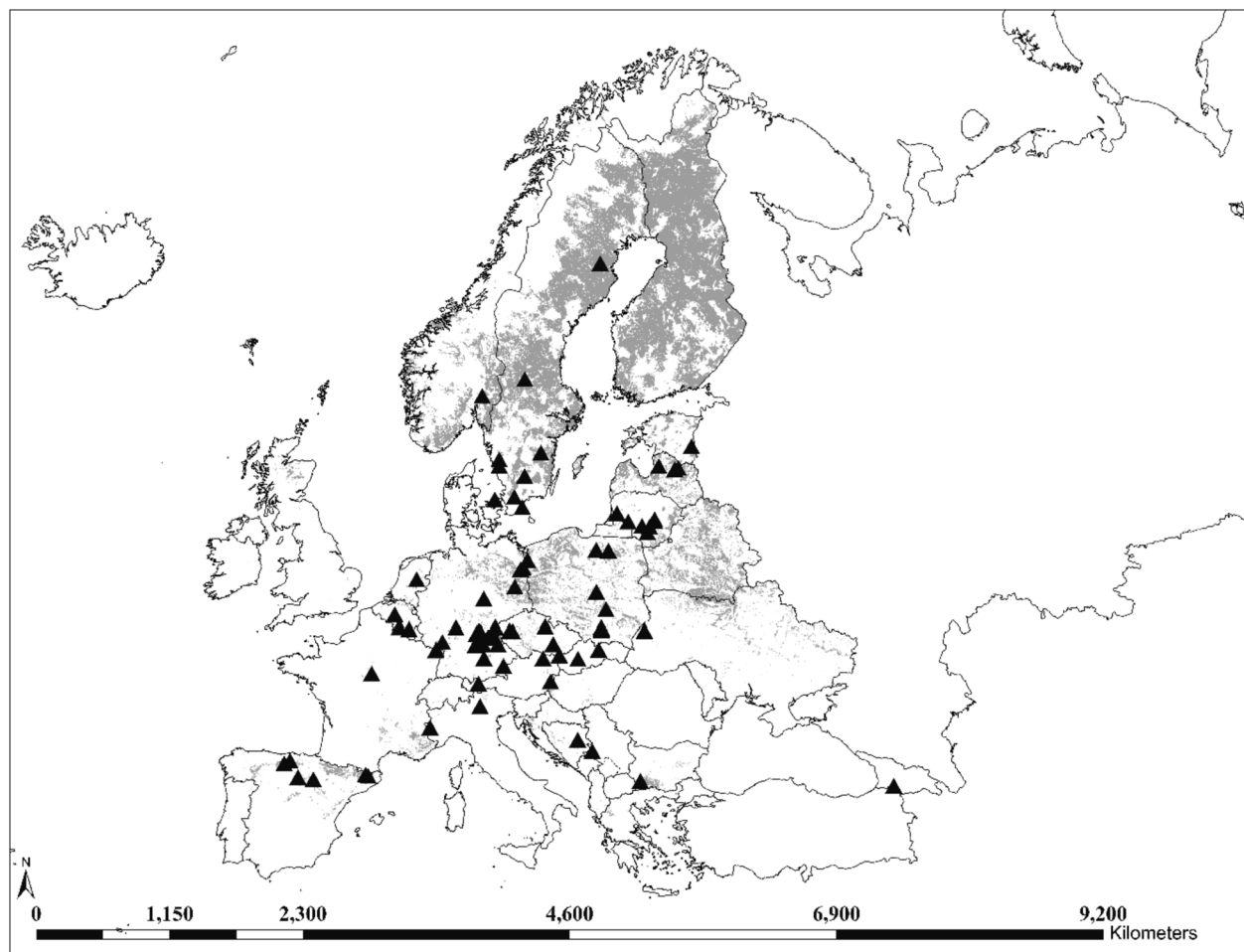


**Fig. 1.** The locations of the 90 plots with monospecific Scots pine (black triangles) in Europe and the species distribution of Scots pine (grey) according to EUFORGEN (www.euforgen.org).

beech-pine transect and 2013–2017 for the oak-pine and the spruce-pine transects, the last year corresponding to triplet establishment. See Pretzsch et al. (2015, 2020) and Ruiz-Peinado et al. (2021) for more details on field measurements and main stand characteristics calculations. Note that stand state inventory data from the year of plot establishment was available for all 90 Scots pine plots. In contrast, retrospective growth data was limited to 88 plots due to inconsistent measurements. A description of the main tree and stand characteristics is presented in Table 1.

**T, P:** mean annual temperature and annual precipitation based on annual climate data were obtained from meteorological weather stations near each plot. When local station data were not available, or observations did not cover the studied period, gridded data provided by national meteorological services or the Climatic Research Unit (CRU) Time-Series (TS) Version 3.10 database (Harris et al. 2020) were used.

**MA:** For characterizing the climatic conditions in the last 30 years before the plot establishment, we used the de Martonne aridity index (M = P/(T + 10)) (Martonne 1926). We selected these annual climate variables as it describes in a simple way the large variability of climates covered by study sites, from Mediterranean to boreal climates, and is related to productivity variation at large scales (Huang and Xia 2019) (Table 1).

**SI:** For site indexing (Table 1), we used the mean tree height at age 100 and applied the yield table (moderate thinning) for Scots pine by Wiedemann (1943), as this yield table covers the most fertile but also the poorest sites of Scots pine in Europe. When calculating the mean tree height we followed the standard procedure by Johann (1993); we first calculated the quadratic mean stem diameter ($d_q$), second derived the current diameter-height curve by regression (h-d relationship), and third entered with $d_q$ into the h-d relationship to read off the mean height $h_q$ which was used for site indexing. In this way trees of all sizes are considered when deriving the mean tree height of the stands and the respective SI (Kramer and Akça 1995).

### 2.2. Measures and metrics

#### 2.2.1. Classical tree and stand variables

For characterizing and analyzing the effect of site conditions on the tree and stand growth and structure, we used the following tree and stand characteristics (Table 1):

**d, h:** measured individual stem diameter at 1.30 m above ground level and tree height.

**v:** merchantable stem volume (>7 cm at the smaller end) calculated based on stem diameter, tree height and form factors according to Franz et al. (1973).

**dq, hq:** quadratic mean stem diameter and height of the tree with dq.

**do, ho:** mean stem diameter do of the 100 largest stem diameter trees per hectare and height of the trees with do.

**N, BA:** tree number and stand basal area per hectare.

**SDI:** stand density index according to Reineke (1933) calculated with exponent −1.593 according to Pretzsch and Biber (2005).

**V:** Standing stem volume of the stand.

#### 2.2.2. Characteristics of size distribution and partitioning of growth and mortality

For characterizing the size distribution and partitioning of growth and mortality on the plots we used the following variables and metrics (Table 1):

**CVd, CVh, CVba:** coefficient of variation of stem diameter, tree height, and stem basal area.

**GINId, GINIh, GINIba:** Gini coefficient of stem diameter, tree height, and stem basal area. The Gini coefficient for a cumulative stock of trees is generally calculated as follows GINI $= \frac{\sum_{i-1}^{n}\sum_{j=1}^{n} x_i - x_j}{2n(n-1)\times \overline{x}}$ (see de Camino, 1976, Kramer, 1988, p 82). Variables $x_i$ and $x_j$ denote size or growth (or other tree characteristics) for the $i^{th}$ and the $j^{th}$ tree in the stand with $i$ and $j = 1…n$ trees (see Supplementary Fig. 1).

**skew, kurt:** skewness and kurtosis of stem diameter distribution.

**GDCba:** Growth Dominance Coefficient based on stem basal area and basal area growth (Binkley et al., 2006). The GDC can be calculated directly based on the individual tree records of stem basal area and stem basal area growth of all trees of a population sorted by size as GDC $= 1 - \sum_{k=1}^{n}(ba_k - ba_{k-1})(iba_k + iba_{k-1})$ (see Supplementary Fig. 1).

**a0, a1:** intercept and slope of the plotwise linear regression $id = a_0 + a_1 \times d$, with $id$ being the stem diameter increment in a given 5-years-period and $d$ being the stem diameter at the beginning of this period.

**dratio:** the ratio between the mean stem diameter of the dropped out trees ($d_{mort}$) caused by natural mortality and the mean stem diameter ($d_{total}$) of all trees of a stand. As we inventoried both the stem diameters of the standing dead and living trees, we were able to calculate the variable dratio. The collective of dropped out trees included only dead trees that were still standing.

Our study covered mainly medium-aged stands; we did not strive for analysing the change of structure with increasing stand age. We nevertheless included stand age and quadratic mean stand diameter in the regression models. However, as expected, these two variables proved to be not significant due to the sampling of mainly medium aged stands.

#### 2.2.3. Overview of the empirical basis of this study

Due to their location across Mediterranean, Atlantic, temperate, and continental regions, the mean values of annual temperature and precipitation show a very wide range; this results in site index (SI) values at age 100 from SI = 14.44 to 35.74 m (Table 1).

The mean individual stem diameters (23.6 cm), tree heights (20.2 m), and stem volumes (0.55 m³) but also mean and variation of stand age reflect that our study stands cover mainly medium-aged trees. The standard deviation, the minimum and maximum values show a

**Table 1**
Characteristics of the 90 plots in monospecific Scots pine stands with altogether 8610 sample trees measured in 2013–2017 used in this study (see variable explanation in sections 2.2.1 and 2.2.2).

| variable | unit | mean | sd. dev | min | max |
|---|---|---|---|---|---|
| *site conditions* | | | | | |
| T | °C | 8.09 | 1.30 | 2.80 | 11.47 |
| P | mm yr⁻¹ | 735.72 | 172.78 | 456.02 | 1250.03 |
| MA | mm °C⁻¹ | 40.98 | 10.49 | 21.24 | 69.23 |
| SI | m | 25.55 | 4.47 | 14.44 | 35.74 |
| *tree characteristics* | | | | | |
| d | cm | 23.59 | 9.83 | 0.70 | 72.70 |
| h | m | 20.22 | 6.23 | 0.60 | 40.00 |
| v | m³ | 0.55 | 0.60 | 0.001 | 6.61 |
| *stand characteristics* | | | | | |
| plot size | m² | 1332.97 | 1882.34 | 140.00 | 15500.00 |
| stand age | yr | 66.49 | 22.58 | 40.00 | 150.00 |
| dq | cm | 21.77 | 5.62 | 11.70 | 40.58 |
| hq | m | 19.21 | 4.03 | 8.56 | 30.39 |
| do | cm | 34.20 | 10.33 | 19.26 | 71.94 |
| ho | m | 24.10 | 4.91 | 10.60 | 38.00 |
| N | ha⁻¹ | 839 | 604 | 50 | 3200 |
| BA | m² ha⁻¹ | 35.66 | 15.41 | 4.35 | 83.08 |
| SDI | ha⁻¹ | 688.35 | 302.97 | 87.02 | 1561.56 |
| V | m³ ha⁻¹ | 382.41 | 191.19 | 44.17 | 959.33 |
| *stand structure* | | | | | |
| CVd | ./. | 0.31 | 0.09 | 0.10 | 0.56 |
| CVh | ./. | 0.20 | 0.10 | 0.04 | 0.45 |
| CVba | ./. | 0.51 | 0.16 | 0.14 | 0.82 |
| GINId | ./. | 0.17 | 0.05 | 0.06 | 0.31 |
| GINIh | ./. | 0.11 | 0.05 | 0.02 | 0.25 |
| GINIba | ./. | 0.33 | 0.09 | 0.15 | 0.55 |
| skew | ./. | −0.01 | 0.56 | −1.98 | 2.04 |
| kurt | ./. | 2.88 | 1.23 | 1.39 | 9.52 |
| *partitioning* | | | | | |
| GDCba | ./. | 0.00 | 0.09 | −0.43 | 0.20 |
| a0 | ./. | 1.17 | 0.77 | −0.43 | 2.85 |
| a1 | ./. | 0.57 | 0.25 | 0.12 | 1.10 |
| dratio | ./. | 0.80 | 0.21 | 0.48 | 1.39 |

considerable variation in size, indicating a variation of the stand structure. The upscaling from small plot sizes to hectare values may cause over- or underestimation of stand values. The plots represent unthinned and fully stocked stands; the various measures of stand density such as tree number, stand basal area, SDI or standing volume indicate the wide range of covered site conditions.

All stand structural characteristics show a wide variation; e.g. the coefficient of variation of the stem diameter was 0.31 on average. However, it was very low in homogeneous stands (CVd = 0.10) or even 5-fold in heterogeneous stands (CVd = 0.56). The variation of CVh, GINId, GINIba was even wider. The shape of the diameter distribution was nearly symmetric on average (skew = -0.01) but reached from strongly left-skewed (skew = -1.98) to right-skewed (skew = 2.04).

The variation of growth and mortality partitioning was of particular interest. The GDC based on the individual stem basal area indicated size-proportional partitioning on average (mean GDCba = 0); however, there were stands with an overproportional contribution of small trees to the stand growth (GDCba = -0.43) and stands with clear growth dominance of big trees (GDCba = 0.20). The intercept (a0) and slope (a1) of the plot-specific id-d relationships corroborated this wide variation of growth partitioning; e.g., a0-values could be far below zero (a0 = -0.43), indicating size-asymmetric partitioning with a preference of big trees but also far above zero (a0 = 2.85) indicating size-asymmetric partitioning with a preference of small trees. The dratios were 0.80 on average and covered a range between dratio = 0.48 and 1.39; this means that on some plots, mortality eliminated mainly small trees with a mean diameter below the average stem diameter; on other plots, mortality eliminated mostly big trees.

### 2.3. Statistical analysis

To analyze how the stand structure is modified by the site conditions (Q I), we scrutinized by ordinary linear regression how the Coefficients of variation of the stem diameter and tree height distribution, CVd, and CVh, and the Gini Coefficient of stem diameter and tree height, GINId, GINIh depend on the site index, SI, of the stands. We used the climate variables T, P, and MA to characterize the range of site conditions of the plots; however, these variables did not significantly contribute to explaining the variation of the stand structure along the transect across Europe.

$$ln(CVd_k) = a_0 + a_1 \times ln(SI_k) + \varepsilon_k \tag{1a}$$

$$ln(CVh_k) = a_0 + a_1 \times ln(SI_k) + \varepsilon_k \tag{1b}$$

$$ln(GINId_k) = a_0 + a_1 \times ln(SI_k) + \varepsilon_k \tag{1c}$$

$$ln(GINIh_k) = a_0 + a_1 \times ln(SI_k) + \varepsilon_k \tag{1d}$$

where $\varepsilon_k \sim N(0, \sigma^2)$ is the residual for the $k$th forest plot. We chose double-logarithmic relationships in all four cases (models 1a-1d) as they appeared biologically more plausible than linear relationships and they also resulted in higher $R^2$ values.

To analyze how the stem diameter growth and the partitioning of growth and mortality change with site index (Q II), we fitted models 2–7 to the data. Model 2 was fitted to quantify the plotwise relationship between the stem diameter increment in a given 5-years-period and d being the stem diameter at the beginning of this period. The evaluations resulted in the plotwise intercepts and slopes $a_0$ and $a_1$, respectively. In models 3–5, we tested the potential influence of site index and quadratic mean diameter (as an indicator of the stand stage development) on growth partitioning. In model 3, we explored these relationships using all the tree data by expanding the id-d model. In models 4–5, we tested the effect of site index and quadratic mean diameter on the intercepts and slopes of plotwise id-d relationships. We also tested the interactions between the variables and included them in case of significant contribution at $p < 0.05$.

$$id_k = a_0 + a_1 \times d_k + \varepsilon_k \tag{2}$$

$$id_{ik} = a_0 + a_1 \times d_{ik} + a_2 \times SI_{ik} + a_3 \times dq_{ik} + b_i + \varepsilon_{ik} \tag{3}$$

$$a0 = a_0 + a_1 \times SI_k + a_2 \times dq_k + a_3 \times SIq_k \times dq_k + \varepsilon_k \tag{4}$$

$$a1 = a_0 + a_1 \times SI_k + a_2 \times dq_k + a_3 \times SIq_k \times dq_k + \varepsilon_k \tag{5}$$

Notice that in models (1) - (7), we used $a_0 - a_3$ as regression coefficients, whereas $a0$ and $a1$ in models (4) and (5) are dependent variables. We tested the effects of all available stand variables and their respective interactions on dratio; only the following two models, 6 and 7, yielded significant results.

$$dratio_k = a_0 + a_1 \times SI_k + a_2 \times dq_k + \varepsilon_k \tag{6}$$

$$dratio_k = a_0 + a_1 \times GDC_k + \varepsilon_k \tag{7}$$

We applied ordinary linear regression (models 1–2 and 4–7) and linear mixed effect models (3). The lower letters $i$ and $k$ represent the $k$th observation on the $i$th triplet in the previous equations. All fitted models 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. In model 3, a random effect $b_i \sim N(0, \tau^2)$ was implemented at the plot level to consider the hierarchical data structure, and that we sampled several trees on the same plot. In this way, we covered any spatial correlation between the neighbouring trees on a given plot. With $\varepsilon_{ik} \sim N(0, \sigma^2)$ we denoted independently and identically distributed errors. In all equations $a_0, ..., a_n$ are the fixed effects parameters.

For all calculations, we used the libraries nlme (Pinheiro et al., 2021) and lme4 (Bates et al. 2015) within the statistical software environment R 4.1.0 (R Core Team, 2021).

### 2.4. Model development and scenario analyses

In addition to the empirical analyses, we developed and applied a simulation model to understand better the effect of both partitioning of growth and mortality between the trees on the size structure of the stand (Q III). The model was used to study the interplay between the site-dependency of the partitioning of growth and mortality. It was applied to answer Question 3, i.e., how the partitioning of mortality (in terms of the size distribution of dropout trees and its dependency on site conditions) in addition to the growth partitioning shapes the size variation and thereby the stand structure.

The main model components were algorithms to generate the initial size distributions, model the growth partitioning between the trees depending on the site conditions, and model the mortality depending on site conditions. The initial size distribution was generated by random numbers from Gaussian normal distribution with a defined tree number, mean stem diameters and standard deviation using the R routine rnorm (). The whole model was developed as a script in R. We used realistic start parameters extracted from the empirical dataset of the 90 Scots pine plots. For the growth partitioning, we used equation (3), which estimates the annual stem diameter growth depending on the stem diameter at the beginning of the period, the quadratic mean stem diameter, and the site index, SI. The mortality was modelled in two steps; first, we estimated the number of dropout trees based on the self-thinning line and second, we selected the dropout trees from the size distribution. As the self-thinning line, we applied the equation $ln(N) = 12 - 1.593 \times ln(d_q)$. The intercept was based on an SDI = 1000, and for the exponent, we chose the species-specific value reported by Pretzsch and Biber (2005). 

We implemented a uniform selection of the number of dropout trees (number of trees exceeding the self-thinning line) within defined diameter ranges of the stand. So, the simulation model allowed selecting

the dropout trees from different percentiles of the diameter distribution or over the whole range. In this way, we could analyze how different modes of mortality (e.g., dropout only at the smaller end or over the entire range of the distribution) affect the size variation of the stand in addition to the growth partitioning. In accordance with the empirical analyses, we assumed a restriction to the smaller end of the size distribution on rich sites, a wider range on medium sites, and mortality covering uniformly the whole diameter range on poor sites.

In annual steps, the resulting scenario runs show how various (default values) assumptions of site-dependent partitioning of growth and mortality shape stand characteristics such as the GINI and GDC coefficient, the variation coefficient of stem diameter distribution, and the relationships between these values for different SI values.

## 3. Results

### 3.1. Overview of tree and stand characteristics

The metrics for the stand structure, such as coefficient of variation (CVd, CVh, and CVba), GINI, and GDC, showed that the 90 Scots pine plots vary considerably in stand heterogeneity, size distribution, and growth partitioning (Table 1). Fig. 2 visualizes this finding by the Gini coefficients of (a) cumulative stem basal area and (b) basal area growth, plotted against the cumulative tree number, ordered after increasing tree size. The bundle of curves reveals the broad range of size and growth partitioning patterns on the 90 plots. The curves close to the bisecting line reflect an equal size or size growth distribution on the plots; the further the curves deviate from the bisecting line, the stronger the inequality of size or growth on the respective plots.

The Growth Dominance coefficient can be visualized by the cumulative distribution of stem basal area growth over stem basal area, e.g., stem basal area growth over the initial stem basal area (Fig. 2c). For this purpose, all trees of a stand are ranked from smallest to largest basal area; the cumulative basal area of the trees is registered on the abscissa, their cumulative basal area growth on the ordinate. The resulting curves illustrate how tree size distribution contributes to total stand growth. The lines in Supplement Fig. 1c indicate a growth dominance of big trees (lower curve, GDC > 0), small trees (upper curve, GDC < 0), or a proportional contribution of growth according to their size (straight line, GDC = 0).

The 90 Scots pine plots include stands where small trees grow overproportionally related to their share in the stand (Fig. 2c, curves above the bisecting line) and stands where trees of all sizes grow proportional to their relative share of the stand basal area (curves close to the bisecting line). The curves below the bisecting line represent stands

with an overproportional growth partitioning favouring big trees.

The stands also varied considerably in the partition of mortality. The mean stem diameters on the plots (Fig. 3a) vary due to the strongly differing site conditions, although the stand ages are somewhat similar. We show both the mean stem diameters of the total and dropout trees (Fig. 3a and b) to stress that mortality does not operate exclusively at the smaller end of the diameter distribution. The ratios $dratio = d_{mort}/d_{total}$ show that in many cases, the dropout trees' stem diameter is, on average smaller than those of the total stand (points below the bisecting line in Fig. 3c). However, there are also plots on which the mortality eliminated trees with stem diameters that were, on average similar to or even larger than the trees of the total stand. This suggests that mortality modifies the size distribution in different ways.

### 3.2. Tree size variation depending on site quality (Q I)

The coefficients of variation and the Gini coefficients of the stem diameter and tree height decreased with increasing site index (Fig. 4); i. e., the structural diversity decreased from poor to rich sites. To consider any additional changes in the structural diversity due to differences in the stand development phase, we also included stand age and quadratic mean stand diameter in the regression models. However, these two variables were not significant.

The decrease of the height diversity reflected by the slopes of the CVh and GINIh coefficients (see $a_1$-values in Table 2, models 1b and 1d) was stronger than the decrease of stem diameter diversity (see $a_1$-values in Table 2, model 1a and 1c). This corroborated the dominance of mono-layered stands on rich sites.

### 3.3. Mode of competition, growth distribution, and mortality depending on site quality (Q II)

The plotwise fit of the model $id = a_0 + a_1 \times d$ to the measured stem diameter growth, $id$, and stem diameter at the beginning of the respective growth periods, $d$, (Fig. 5a) resulted in n = 88 $a_0$ and $a_1$ values. Notice that the status data were available from 90 Scots pine plots, the growth data only from 88 plots. The $a_0$ values (mean, min, max) were $a_0$ = -0.003, −0.293, 0.478, and the $a_1$ values $a_1$ = 0.009, −0.008, 0.028. In this context the intercept and slope of the id-d-relationship were not used for prediction but for characterization of the mode of growth partitioning between the trees in the stands.

Straight lines with $a_0 = 0$, i.e., lines through the origin would indicate size symmetric competition and resource partitioning, whereas lower and higher $a_0$ values indicate overproportional and disproportional increase of growth with increasing size, respectively. The
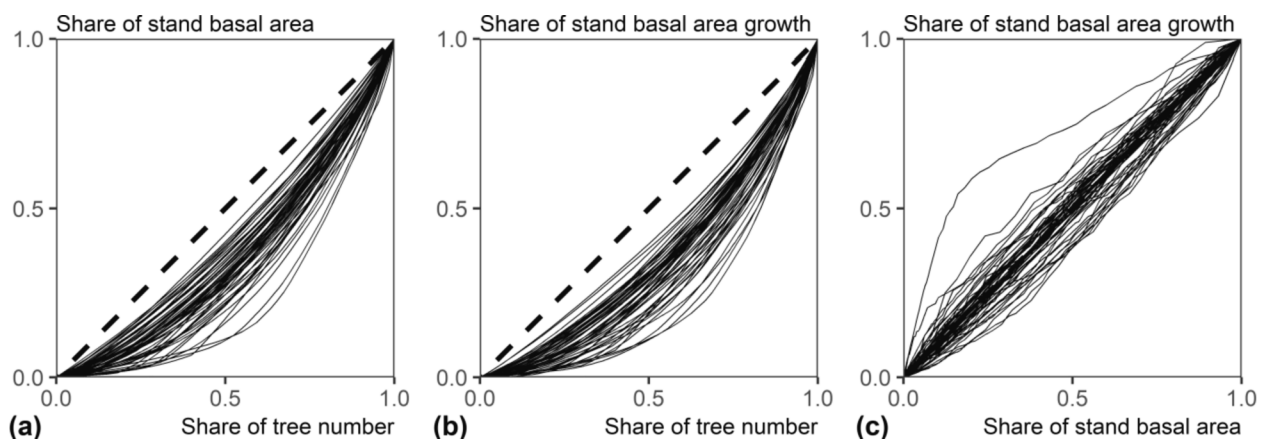


**Fig. 2.** Overview of size distribution and growth partitioning on the 90 Scots pine stands underlying this study. (a) The Gini coefficient of stem basal area distribution, GINIba, indicates the degree of size equality of trees in a forest stand. (b) The Gini coefficient of stem basal area growth distribution, GINIiba, indicates the degree of size growth equality of the trees in a forest stand. (c) the Growth Dominance Coefficient, GDCba, indicates the relative contribution of small compared with big trees to stand growth. In all cases, the bisecting line (dashed) represents equality of size or size growth.
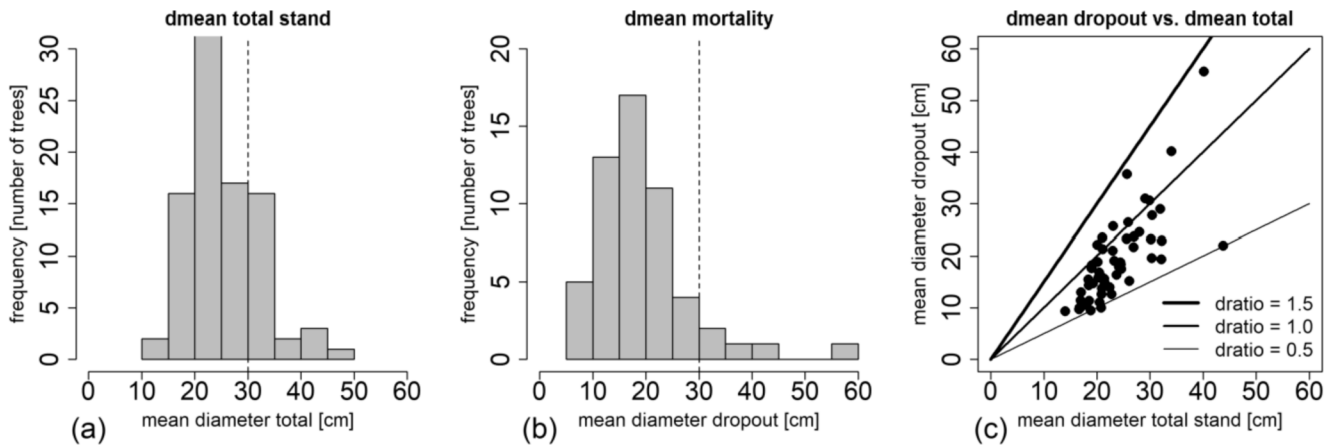
**Fig. 3.** Overview of mortality characteristics of monospecific Scots pine stands underlying this study. (a) Mean stem diameter of the total stand, $d_{total}$. (b) Mean stem diameter of the dropout trees, $d_{mort}$ and (c) $d_{mort}$ plotted over $d_{total}$. Observations below the bisecting line in (c) indicate prevailing mortality of small trees. The vertical lines in (a) and (b) at a stem diameter of 30 cm do not represent the means of the respective distributions. Still, they serve as a reference for better comparing both distributions. The straight lines in (c) represent ratios of 0.5, 1.0, and 1.5 between the mean diameter of the trees dropping out due to mortality and the trees of the total stand.



**Fig. 4.** Characteristic of stand structure and their dependency on stand and site conditions. (a and b) The coefficient of variation of stem diameter, CVd, and height, CVh, decreases with site index, SI. (c and d) Gini coefficient of stem diameter and tree height decreases with SI. The curves resulted from models 1, a-d; for statistical characteristics, see Table 2.

$a_0$-values from $-0.293$ to $0.478$ indicate that the plots cover a broad spectrum of different modes of competition, ranging from size-asymmetric competition with growth strongly overproportionally increasing with size ($a_0 < 0$) to size-symmetric competition and partitioning ($a_0 = 0$), and to size-asymmetric competition with growth disproportionally increasing with size ($a_0 > 0$).

Fig. 5b shows how the stem diameter growth depends on the initial individual stem diameter $d$, the developmental state of the stand, represented by $dq$, and on the site index. Latter significantly increases the level of growth and size-asymmetric partitioning in favour of big trees. The effects of d, SI, and dq were significant (see Table 2, model 3). The effect of the site index on the growth partitioning between the trees is

further corroborated by Fig. 5c and d; the site quality decreases the intercept and increases the slope of the individual stands' relationship between stem diameter growth and stem diameter at the beginning of the growth period. This indicates a strong increase in asymmetric growth partitioning favouring big trees on rich sites.

Fig. 6a shows the dependency of dratio on the site index; the better the site conditions, the lower is dratio. This indicates that on poor sites, mortality eliminates more often bigger trees than on rich sites and this tendency increases with stand development state, represented by $dq$.

Interestingly, there seems to be a trade-off between dratio and GDC (Fig. 6b). This finding underpins the observation that size-asymmetric growth partitioning favouring big trees (high GDC values) causes the

**Table 2**
Statistical characteristics of the main models used in this study for answering questions Q I-Q II. The equation numbers refer to the models introduced in statistical models section 2.3 (Statistical models). For reasons of space limitation, the table reports only the fixed effect variables of the respective models. For variable explanation, see section 2.2 and Table 1. All regression coefficients and models that were significant, at least at the level of $p < 0.05$, were set in bold letters.

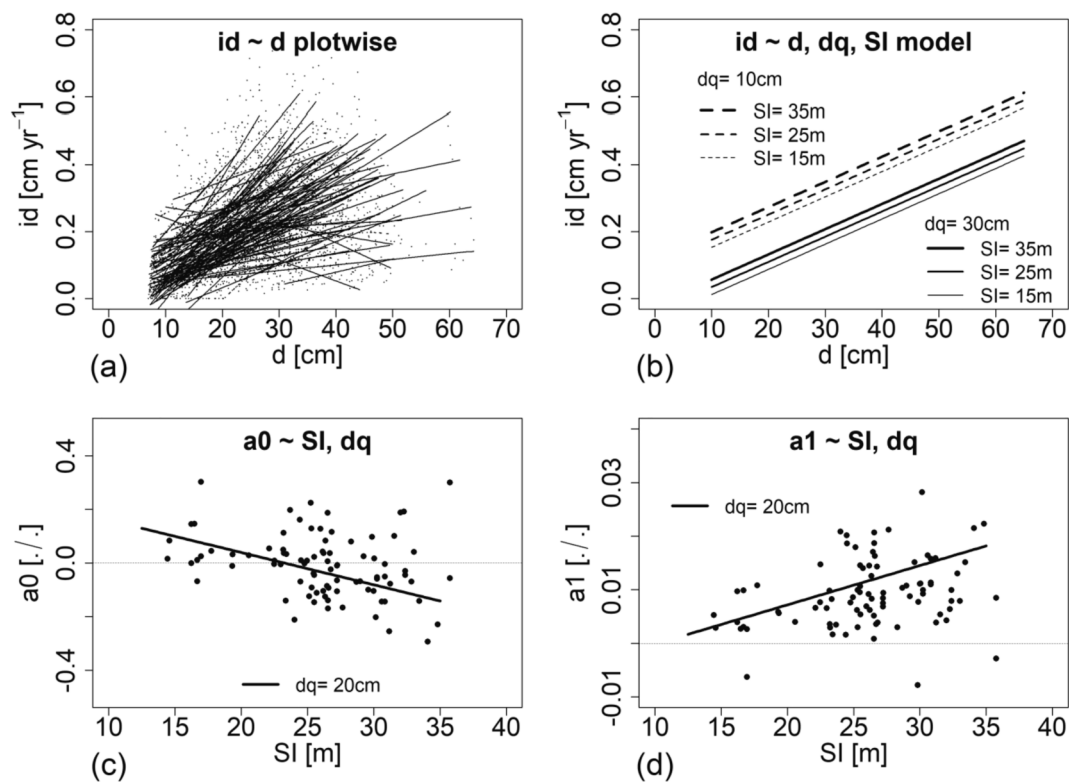| model | variables | n | $a_0$ | std $(a_0)$ | *p*-value | $a_1$ | std $(a_1)$ | *p*-value | $a_2$ | std $(a_2)$ | *p*-value | $a_3$ | std $(a_3)$ | *p*-value |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| *Q I:* | | | | | | | | | | | | | | |
| 1a | ln(CVd) ~ ln(SI) | 90 | 0.98 | 0.49 | **0.048** | −0.69 | 0.15 | **<0.001** | | | | | | |
| 1b | ln(CVh) ~ ln(SI) | 90 | 2.19 | 0.84 | **0.011** | −1.22 | 0.26 | **<0.001** | | | | | | |
| 1c | ln(GINId) ~ ln(SI) | 90 | 0.46 | 0.50 | 0.272 | −0.71 | 0.15 | **<0.001** | | | | | | |
| 1d | ln(GINIh) ~ ln(SI) | 90 | 1.80 | 0.83 | **0.033** | −1.29 | 0.26 | **<0.001** | | | | | | |
| *Q II:* | | | | | | | | | | | | | | |
| 2 | id ~ d | see section 3.3 | | | | | | | | | | | | |
| 3 | id ~ d, SI, dq | 88 | 0.11 | 0.01 | **<0.001** | 0.01 | 0.0001 | **<0.001** | 0.002 | 0.0002 | **<0.001** | −0.007 | 0.0003 | **<0.001** |
| 4 | a0 ~ SI, dq, SI × dq | 88 | 0.97 | 0.36 | **0.008** | −0.04 | 0.01 | **0.002** | −0.03 | 0.02 | **0.03** | 0.002 | 0.0006 | **0.009** |
| 5 | a1 ~ SI, dq, SI × dq | 88 | −0.003 | 0.015 | **0.047** | 0.0002 | 0.0005 | **<0.001** | 0.001 | 0.0005 | 0.09 | −0.00007 | −0.00007 | **0.007** |
| 6 | dratio ~ SI, dq | 34 | 0.76 | 0.18 | **<0.001** | −0.02 | 0.005 | **0.003** | 0.02 | 0.005 | **<0.001** | | | |
| 7 | dratio ~ GDC | 34 | 0.85 | 0.03 | **<0.001** | −0.54 | 0.16 | **0.002** | | | | | | |



**Fig. 5.** Visualization of the relationship between annual stem diameter growth, *id*, initial stem diameter, *d*, and covariables site index, *SI*, and quadratic mean stem diameter of the stand, *dq*. (a) Individual tree measurements of *id* and *d* (black points) and plotwise relationships $id = a_0 + a_1 \times d$ fitted by linear regression (see model 2 and model coefficients $a_0$ and $a_1$ reported at the beginning of section 3.3). (b) Overall model 3 for the stem diameter growth depending on *d*, *dq*, and *SI* (model 3, coefficients see Table 2). (c and d) Dependency of the model coefficients $a_0$ and $a_1$ of the plotwise relationships between *id* and *SI* and *dq* (models 4 and 5, coefficients see Table 2).

mortality of mainly small trees (low dratios). In contrast, more equal growth partitioning (low GDC values) is coupled with a more uniformly distributed mortality (higher dratios) that eliminates trees throughout the whole stem diameter range.

*3.4. Effect of the growth and mortality of trees on the size variation at the stand level revealed by scenario simulations (Q III)*

Among the many scenario runs, we selected the ones shown in Fig. 7 as they convey the main results. Scenarios 1–3 reflect the net effect of the overlay of partitioning of growth and mortality for poor (black curves),

medium (red curves), and rich site conditions (green curves) (SI = 15, 25, 35 m height at age 100). To reproduce and demonstrate the effects of both partitioning of growth and mortality on the stand structure, we assumed a characteristic initial diameter distribution and modes of growth and mortality for poor, medium, and rich sites. Then, using the model introduced in section 2.4, we simulated the stand development in terms of SDI, GDC, dratio, CVd and other variables. The model functions were based on the 90 Scots pine stands that were middle aged but did not include really old stands. The diameter growth function (see model 3, Table 2) reflects that the level of the id ~ d relationship decreases with progressing stand development. However, it does not reflect that the
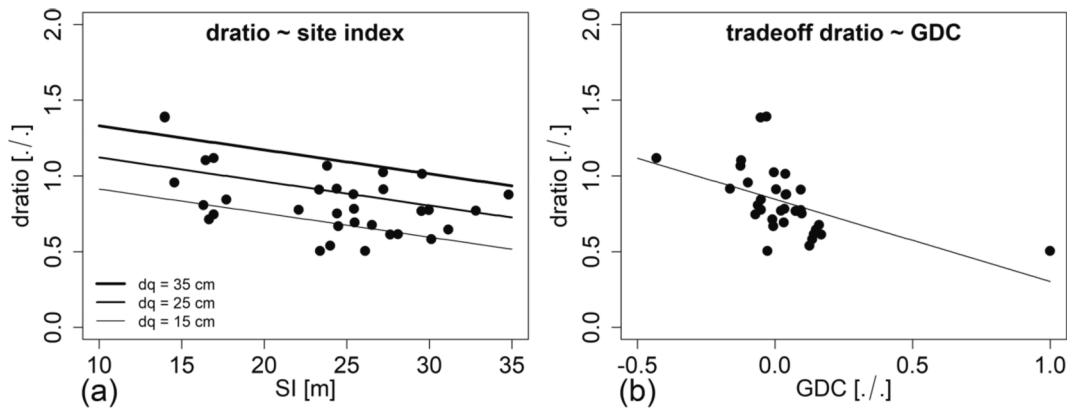
**Fig. 6.** Mode of mortality in terms of the ratio $d_{ratio} = \overline{d}_{mort}/\overline{d}_{total}$ depending on (a) site index, SI, and (b) the Growth Dominance Coefficient, GDC. For underlying models and statistical characteristics, see Table 1.
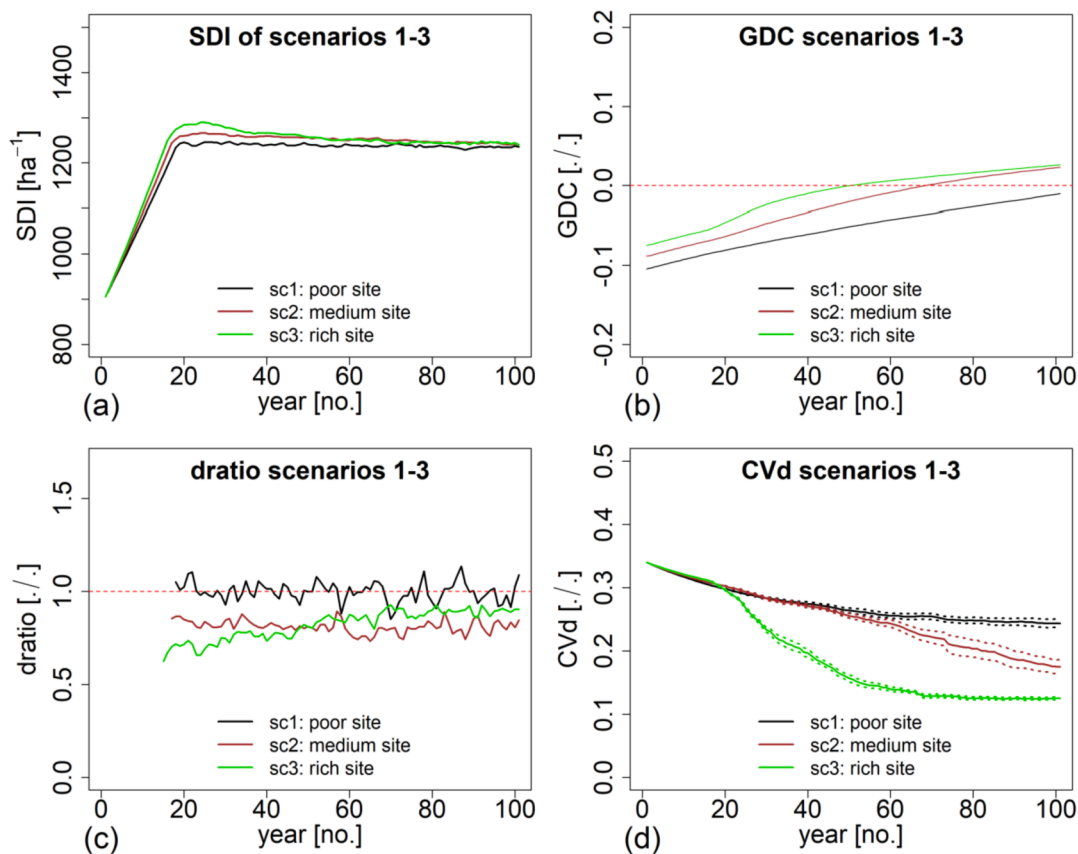


**Fig. 7.** Results of three scenario runs (means $\pm SE$ of 10 replications each) assuming the site-specific growth and mortality partitioning on poor, medium, and rich sites (underlying assumptions see Fig. 6. Development of (a) SDI, (b) GDC, (c) dratio, and (d) CVd.

slope of the id ~ d relationship can flatten continuously or even become negative in old stands. The age (mean $\pm$ standard deviation) of the underlying stands was 66.5 $\pm$ 22.6 years (see Table 1); thus the trajectories beyond stand age 90 represent extrapolations and should be interpreted cautiously.

Fig. 7 shows the mean course of 10 replications for each scenario (in the case of CVd means $\pm SE$). To keep the scenario results simple, we added the confidence bands ($\pm SE$) only in the case of the most interesting output variable CVd (see Supplement Fig. 2 for analogous representations of variables SDI, GDC, and dratio).

All three scenarios start with the same diameter distribution (2000 trees ha$^{-1}$, mean diameter 15 cm, standard deviation 5 cm). After about

20 years, the stand approached the assigned maximum stand density of SDI = 1200 trees ha$^{-1}$ at dq = 25 cm and followed this line until advanced age (Fig. 7a). The default id-d relationships for poor, medium, and rich sites result in the GDC developments shown in Fig. 7b. The growth dominance (the inequality of growth partitioning indicated by the GDC) continuously increased in all three scenarios. However, the growth dominance was permanently higher on richer sites than on poorer ones. The GDC remained below the 0-line into advanced age on poor sites, indicating an always relatively equal growth distribution (Fig. 7b). The scenarios of dratio reveal that on poor sites, the diameter of the dropout trees is similar to the mean diameter of the total stand. In contrast, the mortality eliminates smaller trees on medium and rich sites

and thus reduced dratio (Fig. 7c). The interaction between growth partitioning and mortality results in more heterogeneous structures on poor sites and homogeneous structures indicated by low CVd values on rich sites (Fig. 7d). Interestingly, although the GDC indicates higher inequality in terms of growth distribution, the structural inequality is lower on rich sites.

The richer the sites, the more important the mortality becomes at the smaller end of the size distribution. Due to the elimination of small trees at rich sites, the effect of the asymmetric growth partitioning in terms of structering at such sites is cancelled.

Based on the three scenarios (with 10 replications each) for poor, medium, and rich sites (black, brown, and green dots), we visualize four basic relationships between metrics for growth and mortality partitioning, growth dominance and stand structure (Fig. 8). The GDC, i.e., the concentration of growth partitioning on dominant trees and thus the asymmetry of partitioning increases with the slope of the id-d relationship (Fig. 8a).

The Growth Dominance Coefficient and GINI coefficient of the stem diameter distribution are closely correlated with each other and convey similar information about growth partitioning (Fig. 8b).

Fig. 8c shows that the scenario runs indicate the same trade-off between dratio and GDC as the empirical part of this study (see Fig. 6).

Fig. 8d reveals that the GINI coefficient of the stem diameter distribution and the coefficient of variation of the stem diameter distribution are closely correlated and convey similar biological information about the stand structure.

Fig. 9 is also based on scenarios 1–3 and shows that the density curve of the stem diameter distribution becomes more left-skewed with improving site conditions (Fig. 9, a-c). On poorer sites, the peak of the density function at age 50 is close to 25 cm (Fig. 9a), whereas it is found between 30 and 40 cm on better sites (Fig. 9b and c). The density curve of the dropout trees and the remaining trees are rather similar on poor sites (Fig. 9a vs Fig. 9d). In contrast, the dropout of trees reduced rather the left side of the stem diameter distribution on better sites. This is reflected by smaller dratios on rich than on poor sites. Thus on rich sites, the extension of the diameter distribution (by growth) at the right side is coupled with a reduction (by mortality) at the left side (Fig. 9, c and f). On poor sites, the extension at the right side is slower but also the reduction at the left side of the diameter distribution (Fig. 9, a and d). So, the size variation finally results from the interaction between growth and mortality and both are modulated by the site conditions.

## 4. Discussion

### 4.1. Site-dependent partitioning of growth and mortality

The analyzed Scots pine stands covered a wide range of site conditions across Europe and revealed an increasing inequality of growth partitioning favouring big trees with increasing site index. The id-d relationship, the Gini coefficient of growth, and the GDC indicated that the growth partitioning changes in favour of big trees with increasing site index. On poor sites, the growth partitioning between small and big trees was more similar, whereas the gain of big trees increased continuously with the site quality. This is in line with many theoretical considerations (Schwinning and Weiner 1998, Hara 1993, 1988) and empirical findings (Pretzsch et al. 2012, Pretzsch and Biber 2010), after which on rich sites, big trees benefit overproportionally from their size. If light is the limiting resource, big trees benefit from privileged access to light and the pre-emption of light to slow down competitors (Körner 2014). On poor sites, where water and nutrients rather than light are the limiting factors, tree size and better access to light are less advantageous or even detrimental as big trees may be exposed to heat and drought and shade smaller ones (Carl et al. 2018, Grime 1987). An analogous dependency of the growth partitioning from site conditions was found in wet versus dry years (Pretzsch et al. 2022, 2018, Wichmann 2002); ample water supply promotes big trees, whereas drought stress equalizes the growth partitioning or even promotes small subdominant trees (Pretzsch et al. 2020b). The unequal growth partitioning may suggest a higher structural heterogeneity on rich sites, as the higher growth rates may accelerate the extension of the size distribution at the larger end, the inequality between predominant and subdominant trees, and thereby the heterogeneity of tree sizes and stand structure (Binkley et al., 2006). Accordingly, in the long term, moist years may contribute to enhancing size structural heterogeneity, whereas dry years may cause structural homogenization.

Our results show that both the partitioning of growth and mortality shape the size distribution, that both are site-dependent, and that their interaction may result in the counterintuitive decrease of stand heterogeneity with increasing site quality, despite the increase of inequality growth distribution. We found that the partitioning of mortality (the pattern of dropout of small compared to tall trees) changed with increasing site quality. We used the variable dratio, defined as the ratio between the mean diameter of the dropout trees and that of the whole stand, as an indicator for the partitioning of mortality and found that it decreased with increasing site quality. This means that we found that mortality was distributed over the whole stem diameter range on poor sites. In contrast, mortality was more restricted to the smaller diameter
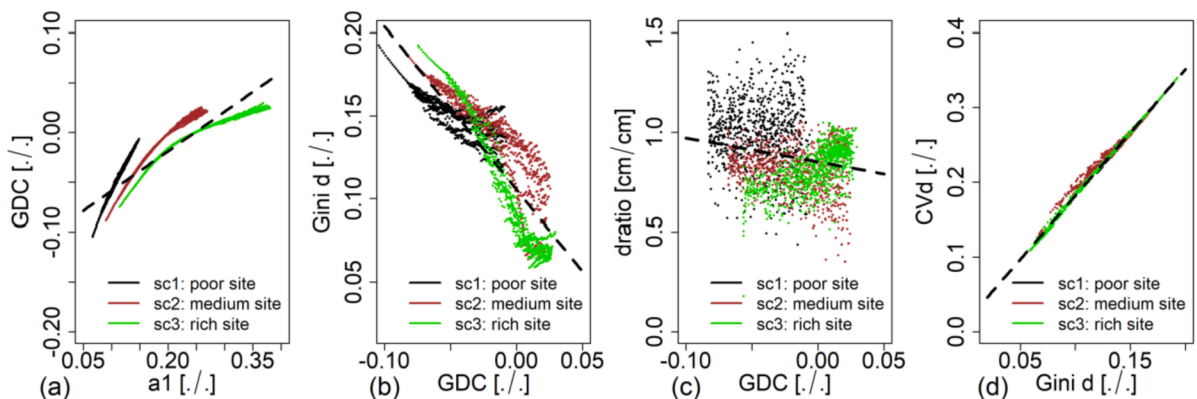
**Fig. 8.** Basic relationships between variables for partitioning and structure generated by scenario runs 1–3 with subproportional ($a_0 > 0$, $a_1$ shallow slope, black), proportional ($a_0 = 0$, $a_1$ medium steep slope, brown), and overproportional ($a_0 < 0$, $a_1$ steep slope, green) id-d relationship (see section 2.4). Simulated values (dots) and fitted trends (broken lines). Relationship between (a) slope $a_1$ of the id-d line and Growth Dominance Coefficient, GDC, (b) GDC and Gini coefficient of the stem diameter distribution, GINId, (c) GDC and dratio, and (d) GINId and the Coefficient of variation of the stem diameter distribution, CVd. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)
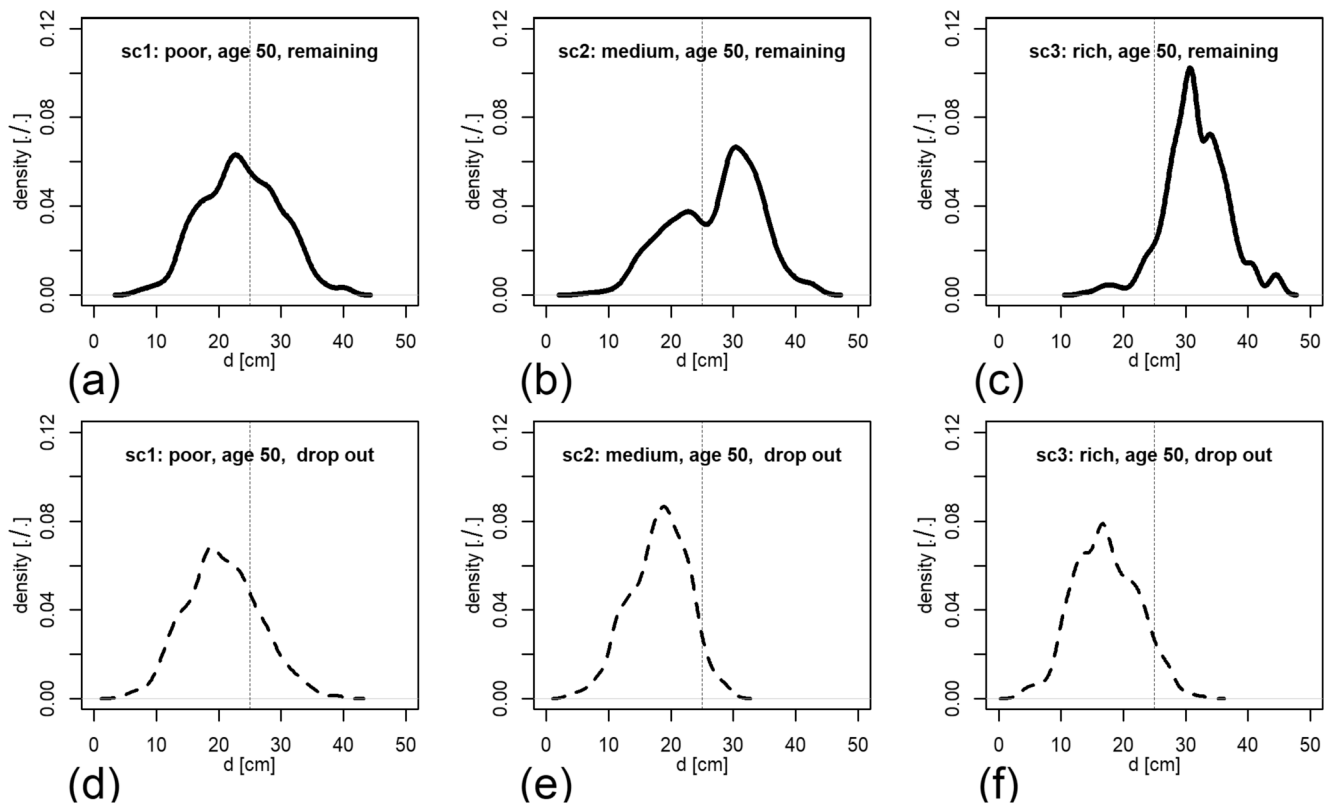
**Fig. 9.** Density curve of the stem diameter distribution at age 50 according to scenarios 1–3 for all trees (a-c) and for the trees that dropped out until age 50 (d-f). The vertical lines in (a)-(f) at a stem diameter of 25 cm do not represent the means of the respective distributions. Still, they serve as a reference for better comparing the shown size distributions.

trees on rich sites. Our findings regarding the dependency of stand structure on site conditions are in line with works by Gracia and Retana (1996) and Aber et al. (1982) about broadleaved forests. However, to our knowledge, our study is the first that found a distinct decrease in structural heterogeneity with increasing site quality in Scots pine stands.

We hypothesize that the higher stand and canopy density on rich sites result in a stronger shading of understory trees. Mortality mainly eliminates small subdominant trees on such sites due to their higher light limitation. On poor sites, stand densities are lower, the small trees are less light limited, and the water limitation affects all stem diameter classes. Biotic and abiotic disturbances may further increase mortality on poor sites. Canopy openings close more slowly on poor sites due to slower growth compared to rich sites. In contrast, at rich sites, canopy gaps can close faster and do not provide sufficient light for the survival of smaller trees. On rich sites, size asymmetric competition and growth distribution may create an extension on the right, but truncation on the left side of the size distribution by self-thinning (Looney et al. 2021) and lead to lower size variability and stand structure. On poor sites, disproportional growth partitioning may slow down the growth of tall trees but keep alive the small trees and thus extend the size distribution and size variability compared to rich sites.

By empirical evaluations and scenario analyses, we could show why the size structure of stands on rich sites may be homogeneous despite the inequality of the growth distribution and on poor sites vice versa. We showed that on rich sites, the mortality eliminated predominantly small trees, thereby reducing the size variation and thus reversing the impact of size-asymmetric growth partitioning on stand structure. Finally, the reverse effects of mode of growth partitioning and mortality on the stand structure resulted in the highest size variation on poor sites and a decrease of structural heterogeneity with site quality.

Taking into account mortality may resolve the contradiction of why the competition and growth distribution can be asymmetric and unequal, but the resulting structure can be more equal than on poor sites. Despite the more unequal competition and growth distribution, the size structure may be more equal on rich and unequal on poor sites due to mortality at the smaller and taller end of the size distribution, respectively. In essence, we can show that both the partitioning of growth and mortality are site-dependent.

Our findings apply primarily to stands in the early and middle developmental stages; in older stands that fall below the maximum stand density line due to tree mortality caused by senescence, stand disintegration may deviate from this behaviour and create other structural patterns: At higher ages, when forest stands begin to disintegrate, the consequences of size variation on poor sites versus size-equality on rich sites may become essential for the growth stability and regeneration. The low vertical layering on rich sites may be promoted in this phase by density reduction due to senescence, open gaps and growth losses due to open space.

Similarly, our findings are based on a shade-intolerant species and even-aged stands, but they could differ for shade-tolerant species. Pothier (2017) found a negative correlation between GDC and site index for two shade-tolerant species, likely related to negative relationships between GDC and size heterogeneity. However, in line with our findings, he found a similar relationship between GDC and the mode of competition to the one observed, which points to the relevance of mode of mortality on size heterogeneity. Finally, initial stand structural complexity can also modify the effect of growth partitioning on size heterogeneity relationships. Looney et al. (2021) found a pattern similar to that in our study for even-aged stands but the opposite for complex stands (multi-aged mixed forest stands).

### 4.2. Relevance for tree and stand modelling

Neglecting site-dependent partitioning of growth and mortality in

models may result in false predictions of the stand structure and growth, especially when models are applied for poorer or richer sites than the sites used for model parameterization. In the case of Scots pine, the structural heterogeneity may be underestimated on poorer and over-estimated on richer sites. The finding that the interplay between growth and mortality partitioning extended the size distribution on poor sites and restricted it on rich sites certainly affects many other structure-dependent stand characteristics (see Introduction section). Models are increasingly used for predicting tree and stand growth under deteriorating growing conditions (e. g., drought events or more extended drought periods). This means an extrapolation beyond their range of parameterization and requires better consideration of the revealed site-dependent partitioning of growth and mortality.

One may ask how tree and stand modelling can consider the dependence of growth and mortality partitioning on site conditions mechanistically? This is only possible with process-based ecophysiological models that depend on environmental conditions and explicitly consider individual trees or at least differently sized social classes (e.g. Grote and Pretzsch 2002, Deckmyn et al. 2008, Grote et al. 2020, Jonard et al. 2020). Only then carbon assimilation and stand development can be dynamically represented based on regionally different or temporally shifting light and/or water limitations (Pretzsch et al. 2011, 2008). The range between size-asymmetric competition and resource partitioning (promotion of big trees) under ample water or nutrient supply to size symmetric competition (growth proportional to size) or even over-proportioned growth and survival of small trees under harsh conditions is then inherently integrated.

Dendrometric models that estimate tree growth and mortality depending on competition indices and additional tree covariables such as stem size or crown dimension (e.g. Bravo-Oviedo et al. 2006, Pretzsch et al. 2002, Le Moguedec et al. 2012, Thurnher et al. 2017) assume ceteris paribus a strong exponential decrease of growth and survival with increasing competition index. Our results suggest that this may apply in regions with ample water supply and years without drought stress, i. e., when light is the growth limiting factor and competition is asymmetric. Under such conditions, the likelihood of growth and survival may strongly decrease with decreasing social position and competitive status. However, in dry regions or years, being big and predominant may become less advantageous, the slope of the growth-competition relation becomes less steep, and the growth and survival difference between small and big trees smaller. This pattern agrees with the findings reported by Condés & del Río (2015) for Scots pine, who found a greater effect of size-asymmetric competition on tree growth and mortality at more humid sites and highlights the importance of including site conditions interacting with the competition status or tree social position in mortality models. Nevertheless, when mortality models include site indexes, they predict greater mortality rates at better sites (Weiskittel et al. 2011). The greater mortality frequently predicted for suppressed trees might result in size homogeneization at better but still lacking realism at poorer sites.

Most size-class and diameter distribution models predict tree growth and survival depending on size. Our results showed that the site conditions represented by the site index strongly modify the growth partitioning between the trees of a stand; rich site conditions increased size-asymmetric growth partitioning and poor sites reduced the size-asymmetry. In this study, the climate variables T, P, and MA did not significantly contribute to explaining the variation of the stand structure along the transect across Europe; the rather unspecific site index was a better predictor. However, future studies should consider the site effects by including resource supply and environmental factors as predictors.

Many fertilization experiments (e.g. Foerster 1990) and studies of site-growth relationships (e.g. Prietzel et al. 2020) suggest that the nutrient supply is a key factor for the site index and growth of Scots pine; this may explain why the site index but not the climate variables T, P, and MA significantly contributed to explaining the variation of the stand structure along the transect across Europe.

## 4.3. Silvicultural implications

On poor sites, the partitioning of mortality was extended to the bigger trees in favour of smaller ones and allowed the survival of smaller trees due to water and nutrient limitations and naturally lower stand density. This means that structurally rich stands or even selection forests of Scots pine, as proposed by Gallo et al. (2020) and Andrzejczyk (2003), may be easier to be created and maintained on poor compared to rich sites (Guldin et al. 2017, Ciancio et al. 2006. Yamahata 1965). There may be a stronger natural tendency towards equality of tree size and mono-layering on rich sites. Thus, creating structured or selectively managed forests may require more silviculture interventions on rich sites such as density reductions by eliminating bigger trees to keep or promote smaller ones (Schutz, 2002, Meyer 2000). Such stand density reductions may create structures at the expense of stand productivity, whereas on poor sites, stand structures seem to be more heterogeneously per se. Alonso et al. (2016) found greater differences in stand size heterogeneity among silvicultural systems (from uniform to irregular shelterwood systems) at rich than at poor sites, suggesting the need to promote irregular structures by silviculture at better sites when the objective is to increase structuring.

On sites where the ongoing climate changes reduce water supply and create drought stress, more structured stands of Scots pine will develop, which may be an attractive silvicultural option (Czacharowski and Drozdowski 2021). It will allow a continuous forest cover, natural regeneration, and structural diversification (Bílek et al. 2016) with many advantageous forest functions and services mentioned in the introduction section. Intense drought and heat stress may reduce the growth of big trees more than subdominant trees, which may benefit from being shaded (Pretzsch et al. 2022). Small and medium-sized trees in structured stands may suffer less from drought and stabilize stand growth. Ehbrecht et al. (2019) showed that the diurnal temperature range was much lower in a structurally heterogeneous stand with high tree size diversity and vertical stratification.

On rich sites, the growth partitioning favours the big trees over-proportionally. This is indicated by the steeper id-d relationships and higher GINI and GDC coefficients compared with poor sites. It means that future crop trees when selected and released on rich sites, benefit more from their superior size in terms of resource and growth allocation. On poor sites, the partitioning is more equal between the trees, and future crop trees benefit less from their size when water and nutrient, rather than light are the growth limiting factors. After the release of crop trees by thinning, the available resources and the growth may be distributed more equally between neighbouring trees of all sizes and is less concentrated on the big crop trees. Both the comparably low promotion of the diameter growth of crop trees by thinning and the slow gap closure, which can cause considerable losses of stand growth, may call heavy crop tree thinning on poor sites into question.

## 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.

### Author contributions statement

H.P. designed the study with contributions from M.d.R., T.H., R.R.-R., Ll.C., and A.B-O. H.P., M.d.R., R.R.-R., M.S., and M.H. compiled and elaborated the database. H.P., M.d.R., and T.H. performed the analyses. H.P. lead the writing with inputs from M.d.R. and A.B-O. All authors contributed data, contributed critically to the drafts and gave final approval for publication.

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