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Tree size inequality as a driver of growth dominance across climatic gradients in managed silver fir forests in Europe

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Abstract: Competition for limited resources is a key driver of forest structure and dynamics. While growth dominance and tree size inequality are widely used to describe competitive interactions, their relationship remains poorly understood in managed forests. This study examines the links between growth dominance, tree size inequality, stocking density, and climatic conditions in silver fir (*Abies alba* Mill.) dominated stands. Using data from circular 109 plots established across four sites in Germany, Italy, and Poland, and increment cores from 386 silver fir and 77 European beech trees, we fitted generalized additive models (GAM) to reconstruct individual tree growth and a piecewise structural equation model (SEM) to disentangle the direct and indirect effects of stand structure and climate aridity on growth dominance.

The fitted GAMs showed moderate to high explanatory power (adjusted R^2 = 0.48–0.77). The SEM explained a substantial proportion of variance in growth dominance (marginal R^2 = 0.57). Growth dominance increased strongly with tree size inequality (standardized estimate = 0.635), while climate aridity reduced it directly (–0.321) and indirectly through negative effects on tree size inequality (–0.324) and stocking density (–0.404). The total effect of climate aridity on growth dominance was substantial (–0.472).

These findings demonstrate that growth dominance is an emergent property shaped by resource competition, disturbance, and management legacies. Recognizing this is crucial for forest science and management, as it helps disentangle competition modes and highlights the need to integrate stand structure and competitive dynamics into silvicultural planning to sustain the stability and productivity of silver fir dominated stands.

Keywords: structural diversity, uneven-aged silviculture, forest growth modelling, mode of competition, growth partitioning

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Introduction

Competition for limited resources is a fundamental driver of ecosystem dynamics, shaping species interactions and structural organization across diverse environments (D'Onofrio et al., 2015; Coomes & Allen, 2007). Forest ecosystems follow these same principles, but their structural complexity makes competitive dynamics challenging to quantify (Pretzsch et al., 2015b; Forrester, 2019). A central mechanism is the partitioning of resources, captured by the mode of competition, ranging from symmetric, where resource acquisition is proportional to size, to asymmetric, where larger trees gain disproportionately more, and inverse-asymmetric, where smaller individuals acquire relatively more (Binkley et al., 2006; Pretzsch & Biber, 2010).

Growth dominance is one of the key metrics used to quantify this dynamic and assess the distribution of resources through the distribution of growth among individual trees in a stand. Positive growth dominance occurs when larger trees contribute disproportionately more to total stand growth (size-asymmetric competition, Fig. 1a – below the 1:1 line), whereas negative or reverse growth dominance arises when smaller trees contribute more (size inverse-asymmetric competition, Fig. 1a – above the 1:1 line) (Binkley et al., 2006).

Besides the interplay of competition and facilitation shaped by species life history strategies and growth-limiting factors, growth dominance and the mode of competition in general are also influenced by forest stand characteristics, including species diversity, structural diversity, and stand density (Baret et al., 2017; Soares et al., 2017; Lemire et al., 2020). Tree size inequality is an integral part of structural diversity and an inherent property of all forested ecosystems (Luu et al., 2013; Forrester, 2019). Tree size inequality is frequently numerically depicted using the Gini inequality coefficient (e.g., Dănescu et al., 2016) (Fig. 1b). Tree size inequality reflects historical and ongoing competitive interactions and is also closely associated with the prevailing mode of competition (Weiner & Solbrig, 1984; Chu et al., 2009; Soares et al., 2016). Tree size inequality may result from differential resource acquisition, with positive feedback loops increasing size and growth disparities over time (Fernández-Tschieder & Binkley, 2018). Similarly to growth dominance, in the absence of self-thinning, perfect size-asymmetric competition tends to increase tree size inequality over time, as larger trees continuously dominate access to resources, leaving smaller trees with fewer opportunities to grow (Weiner, 1990; Forrester, 2019). In contrast, perfect size-symmetric competition results in a more balanced size distribution, where all trees contribute to growth in proportion to their size, maintaining relative stability in tree size inequality over time (Forrester, 2019). Similarly, over time, inverse size-asymmetric competition may reduce tree size inequality by limiting the increment of larger individuals as they approach a growth plateau, thereby promoting a more uniform size distribution in the long-term perspective (Schwinning & Weiner, 1998).

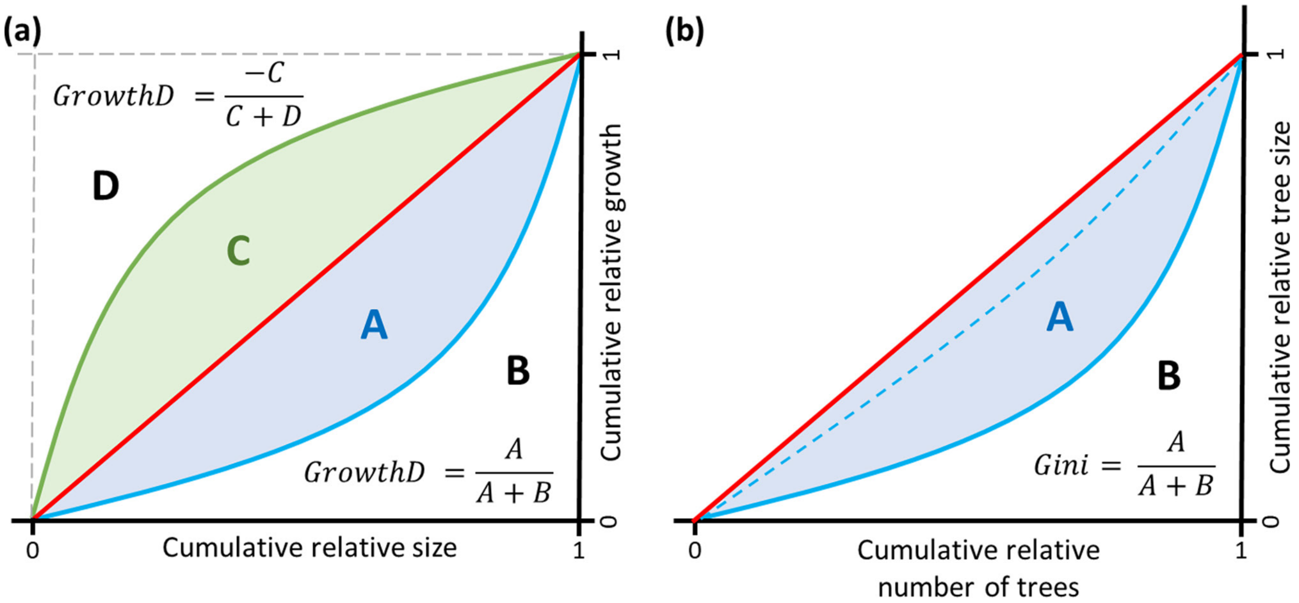

Fig. 1. Schematic framework illustrating (a) growth dominance (GrowthD) and (b) tree size inequality (Gini). In (a), cumulative relative tree size is plotted on the horizontal axis against cumulative relative growth on the vertical axis, with the red 1:1 line representing equal proportional growth. The blue and green shaded areas indicate growth dominance below and above this equality line, respectively. In (b), the cumulative relative number of trees is plotted against the cumulative relative tree size, with solid and dashed blue lines representing high and low size inequality scenarios, respectively

However, the connection between the mode of competition, tree size inequality, and growth dominance holds true primarily in relatively even-aged and undisturbed forest stands, where structural diversification emerges mostly as a result of competition for limited resources (Binkley, 2004; Binkley, 2006; Urgoiti et al., 2023). Tree size inequality, however, is also significantly shaped by past disturbances, both natural (e.g., windthrows, fires) and anthropogenic (e.g., silvicultural interventions) (Forrester, 2019; Kolisnyk et al., 2024). For instance, thinnings targeted at a certain group of size classes (i.e. thinning from below and above) in even-aged stands may temporarily reduce size inequality, while selective harvesting in uneven-aged silviculture tends to increase it (Pretzsch & Hilmers, 2025; Britwum Acquah et al., 2022; Kolisnyk et al., 2025). As such, tree size inequality cannot be interpreted solely as a proxy for the prevailing mode of competition; rather, it also reflects disturbance regimes, successional trajectories, and forest management legacies (Binkley et al., 2006; Forrester, 2019). These disturbance-driven shifts in tree size inequality undoubtedly influence growth dominance, not only from an ecological perspective (i.e. greater growth potential of bigger individuals growing in the conditions of the reduced competition level) but also in terms of the inherent tree size and growth relationships, which directly affect the relative contributions of individual trees to stand-level growth (e.g. Lemire et al., 2020). This raises a critical question: if and how can the mode of competition be meaningfully assessed in managed stands where structural attributes are mostly not the result of natural competitive processes? And does the concept of growth dominance retain ecological relevance in the context of managed stands, or must it be redefined to account for the confounding effects of disturbance history?

In this context, silver fir (*Abies alba* Mill.) serves as a particularly suitable model species to address the formulated questions. Silver fir is economically and one of the most ecologically important species in European mountain forests (Dobrowolska et al., 2017; Bledý et al., 2024). It provides crucial protective functions in Central European mountain landscapes, reducing avalanche risk, preventing soil erosion, and regulating water retention (Dobrowolska et al., 2017; Bledý et al., 2024). This species is classified as C-S (competitive stress-tolerant) according to Grime's CSR theory and is renowned for its plasticity and adaptive capacity to fluctuating light conditions (shade-tolerant strategy) (Brzeziecki & Kienast, 1994). Silver fir is one of the mountain tree species that forms forest stands with varying structural configurations (Pretzsch et al., 2015a; Dobrowolska et al., 2017; Bledý et al., 2024), making it an ideal candidate for uneven-aged silviculture and a suitable model for understanding the interactions between growth-limiting factors, stand structure, and growth dominance. Growth of silver fir within its natural range is often reported to be partially size-asymmetric (Cordonnier & Kunstler, 2015). As such, increasing tree size inequality, whether due to the admixture of other tree species, high competition in dense even-aged stands, or active management in uneven-aged stands, is expected to increase growth dominance in silver fir-dominated stands through the inherently asymmetrically disproportionate growth of larger individuals. Simply put, the larger the individual, the more it grows, regardless of the competitive interactions occurring within the stand (Forrester, 2019). This combination of ecological importance, wide structural variability, and partially asymmetric growth makes silver fir a unique tree species for Central Europe, where it represents both a key species for climate-resilient forestry in mountain areas and an exceptional case to disentangle how competition, disturbance, and management jointly shape growth dominance.

Thus, we aim to understand the relationship between tree size inequality and growth dominance under varying resource availability using data from plots established across four sites with similar eutrophic conditions but very different water availability in managed stands of different structures (even- and uneven-aged). We hypothesize that:

1. Growth dominance inherently increases with tree size inequality.
2. This relationship is mediated by climate aridity.
3. Stocking density influences growth dominance primarily through its effects on tree size inequality.

Methods

Study sites and study design

In this study, we used circular plots (0.05 ha) from an experimental network established to investigate growth patterns along climatic gradients and forest structural diversity (Kolisnyk et al., 2025), under comparable eutrophic site conditions according to the Polish national site classification (Kliczkowska, 2004). The network covers a substantial part of the natural range of silver fir, with sites spanning contrasting climates (Table 1): water-limited marginal populations in the Holy Cross Mountains (PL1, classified as Dfb according to Köppen–Geiger), optimal habitats in the Low Beskid Mountains (PL2, Dfb), South Tyrol, Italy (IT1, Dfb approaching Dfc at higher elevations), and water-rich conditions in the Bavarian Alps, Germany (GE1, Dfb) (Beck et al., 2023). Altogether, 109 plots were established between 2021 and 2024, representing silver fir-dominated stands with at most 20% basal area of European beech (*Fagus sylvatica* L.) (Fig. 2). The plots encompass a wide gradient of tree size inequality, from structurally simple, even-aged stands to structurally complex, uneven-aged forests (Fig. 3).

Data collection

Within each plot, all trees ≥ 7 cm DBH were recorded, including species identity, DBH, and visible signs of damage (e.g. windbreaks). Increment cores were collected from 386 healthy silver fir and 77 European beech individuals, with samples extracted from the side of the stem oriented perpendicular to the slope to minimize the influence of reaction wood using the Haglof increment borer bits of 5 mm. In even-aged stands, 3–4 silver fir and, where present, 2 European beech trees closest to the plot center were cored; in uneven-aged and transition stands, 4–6 trees of both species were sampled across different strata. Tree-ring width (TRW) was measured with a precision of 0.01 mm and cross-dated using the CooRecorder and CDendro software (Maxwell & Larsson, 2021). Further methodological details, including detailed site descriptions and cross-dating protocols, are available in Kolisnyk et al. (2025).

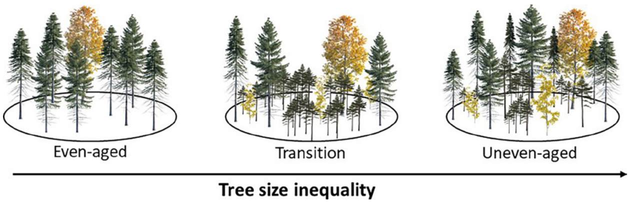

Fig. 3. Conceptual figure illustrating how tree size inequality increases along a silvicultural gradient, from even-aged, clear-cut based systems to structurally complex, uneven-aged forests approaching the steady state

Table 1. The general characteristics of the study sites (adapted from Kolisnyk et al., 2025)

Site	Elevation	Average annual temp. (C)	Sum of annual precipitation (mm)	Total basal area (m^2 ha^{-1})	Admixture of broadleaf species (%)
Tissens-Laurein, Italy (IT1)	1060–1750 (1330)	3.1–8.8 (6.8)	642–1336 (894)	30.3–90.5 (55.3)	0 –19.1 (5.2)
Inzell, Germany (GE1)	820–1140 (920)	6.2–8.5 (7.6)	1471–2081 (1805)	40.7–70.1 (54.2)	0 –18.9 (9.0)
Zagnansk, Poland (PL1)	340–400 (360)	6.7–9.1 (8.1)	608–1003 (749)	24.2–46.9 (35.3)	0–18.4 (5.8)
Nawojowa, Poland (PL2)	600–810 (670)	5.9–8.4 (7.0)	731–1522 (989)	34.4–62.9 (48.4)	0–18.5 (6.6)

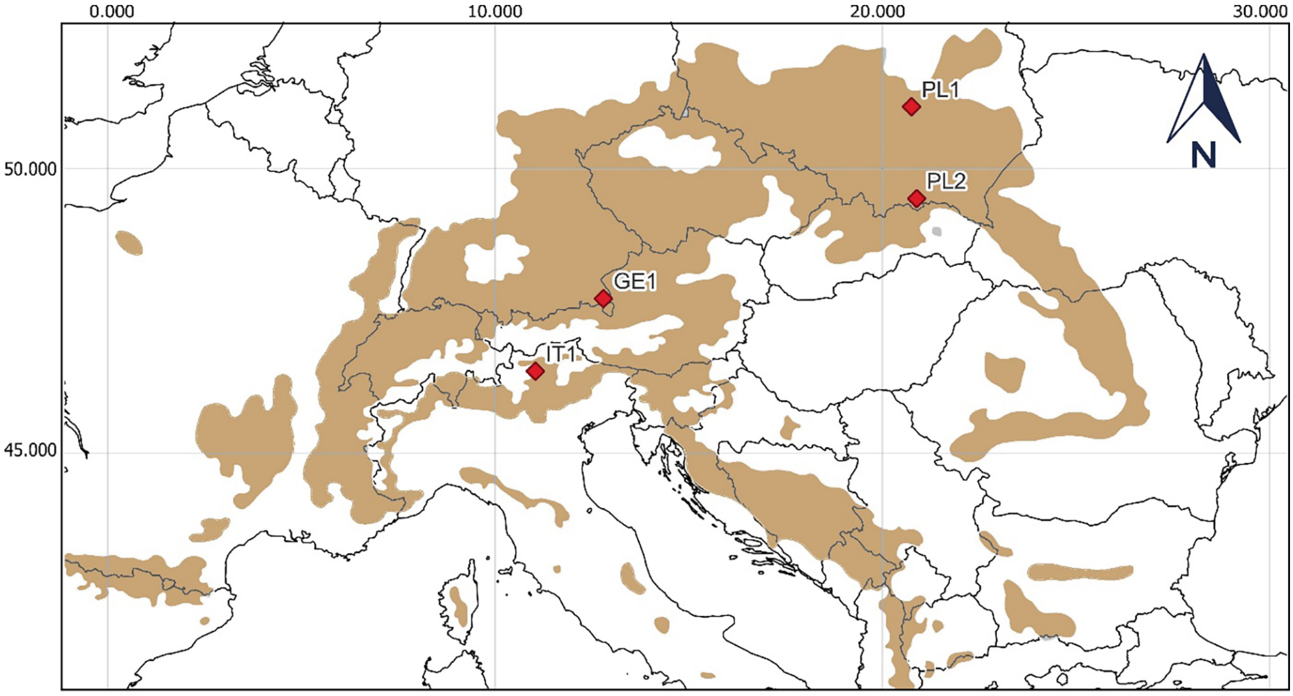

Fig. 2. The location of study sites (red rhombi) and distribution of *Abies alba* Mill. (brown shaded area), source: European Forest Genetic Resources Programme (EUFORGEN, https://www.euforgen.org/species)

Evaluation of long-term climatic conditions using the forest aridity index

To quantitatively characterize climate humidity, we used the Forest Aridity Index (FAI) as proposed by Führer et al. (2011) (Eq. 1).

$$FAI = 100 \times \frac{T_{VII-VIII}}{P_{V-VII} + P_{VII-VIII}} \tag{1}$$

where $T_{VII-VIII}$ is the mean temperature in July and August, P_{V-VII} and $P_{VII-VIII}$ are the precipitation sums from May to July and July to August, respectively. The FAI is based on the identification of growth-limiting seasonal periods and was originally developed for broadleaved species under Hungarian climatic conditions. It was selected over alternative indices (De Martonne aridity index) as central assumption, that the months from May to August represent a critical phase for radial growth, is also applicable to silver fir across the regions included in this study (Kolisnyk et al., 2025).

For the IT1 and GE1 sites, daily temperature and precipitation data were obtained from the ensembled E-OBS dataset (Cornes et al., 2018) at a spatial resolution of 0.1 degrees. For PL1 and PL2, the G2DC-PL+ gridded dataset at a 2 km resolution (Piniewski et al., 2021) was used due to the known tendency of E-OBS to underestimate precipitation in central Poland. The climatic characterization was based on a 10-year period comprising the year of coring and the preceding nine years, in order to capture longer-term average site conditions.

Competition-dependent individual tree growth reconstruction

The growth of individual trees that were not cored was reconstructed using a separate Generalized Additive Models (GAM) for each site. These models were fitted employing a stepwise backward approach, where insignificant variables were progressively excluded from the full model (Eq. 2).

$$Increment = \beta_0 + \beta_1 DBH + \beta_2 Species + \beta_3 Competition + f_1(\mathrm{DBH}|\mathrm{Species}) + f_2(Competition|Species) \tag{2}$$

where *Increment* represents the square root of cumulative basal area increment (BAI) over the last three years,; β_0 is the model intercept, and β_1, β_2, β_3 are the fixed parameters for the DBH, species (coniferous, broadleaf) and competition respectively; f_1 and f_2 are smooth functions that account for nonlinear relationships between DBH, competition, and increment, as influenced by species.

The distance-independent competition index was calculated as the sum of the ratio of the focal tree's basal area to the basal area of the remaining trees in the plot (Corona & Ferrara, 1989) (Eq. 3). This index was selected, because it captures the biosocial position of the focal tree as well as the stocking density. The lower the value, the higher the competitive pressure on the focal tree.

$$Competition = \sum_{j=1}^{n} \frac{DBH_i}{DBH_j} \tag{3}$$

where DBH_i is the DBH of the focal tree, DBH_j is the DBH of the j^{th} competitor tree.

The smoothing penalty (sp) and the number of knots (k) for DBH and competition index were selected based on the goodness of fit (AIC) for all the fitted GAM models. The predictive performance of the GAMs was evaluated with 10-fold cross-validation and residual diagnostics. In each fold, 90% of the data were used for fitting and 10% for testing. Since models were fitted on the square-root scale, predictions were back-transformed to the original BAI scale before calculating error metrics. Model assumptions were further checked with the DHARMa package (Hartig, 2024), testing residuals for uniformity, dispersion, zero-inflation, outliers, and heteroskedasticity.

Quantification of growth dominance, tree size inequality, and stocking density

The growth dominance coefficient (GrowthD) was calculated by subtracting the area beneath the growth dominance curve, representing BAI as a function of cumulative tree size, from the area under the 1:1 line, which illustrates a state of perfect symmetry where trees contribute to growth in direct proportion to their size (Fig. 1a).

$$GrowthD = 1 - \sum_{i=1}^{n} (s_i - s_{i-1})(\varphi_i - \varphi_{i-1}) \tag{4}$$

where i is the order of the trees in each stand; s_i and s_{i-1} are the cumulative proportional BA, φ_i and φ_{i-1} are the cumulative proportional BAI of tree i and tree $i-1$, respectively.

The Gini coefficient (Gini, 1936) was used to quantify the inequality in tree size distribution within the stand. It measures the degree to which tree sizes deviate from an equal distribution among individuals. The coefficient ranges from 0 to 1, where higher values signify greater tree size inequality (Cordonnier & Kunstler, 2015). To calculate the Gini coefficient, tree data were ordered based on increasing tree basal area (BA) (Eq. 5), following the methodology outlined by Sen (1973).

$$Gini = \frac{\sum_{l=1}^{n}(2 \times l - n - 1) \times x_l}{\sum_{l=1}^{n}(n - 1) \times x_l} \quad (5)$$

where l is the rank of the tree from larger to smaller, x_l is the BA of the l^{th} ranked tree.

Stocking density was calculated as the total stand basal area per hectare (TBA) by summing the BA of all trees within the plot and multiplying by 20 to adjust for the plot size.

Modeling growth dominance drivers and their pathways

To statistically evaluate the complex ecological phenomena and quantify the impact of tree size inequality, as well as the direct and indirect impact of climate aridity and stocking density on growth dominance, we used the Structural Equation Model (SEM) approach and piecewiseSEM R package (Lefcheck et al., 2024). In piecewiseSEM, the SEM can be constructed as a set of individual models for each dependent variable (Fig. 4) using linear mixed effect models, thus accounting for different data distributions and sampling design.

Growth dominance coefficient (GrowthD) is expected to change with tree size inequality (Gini), stocking density (TBA), and climate aridity (FAI) (Fig 4a; Eq. 6). However, Gini can also be modified by TBA and FAI (Fig 4b; Eq. 7); and TBA can, in turn, be modified by FAI (Fig 4c; Eq. 8).

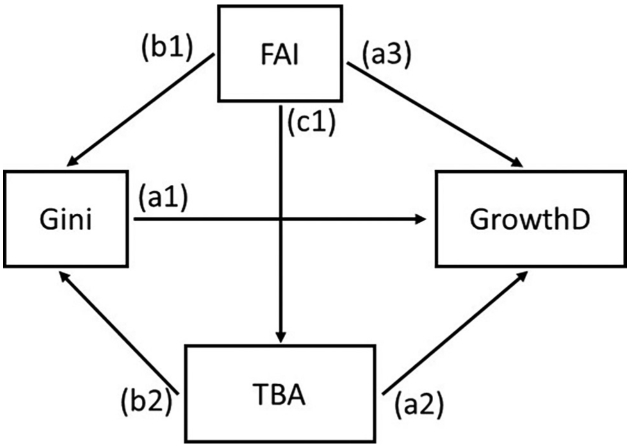

Fig. 4. Theoretical design of the structural equation model (SEM). Arrows indicate the direction of influence among variables. Letters and numbers denote specific pathways: for example, a1, a2, a3 represent direct effects on growth dominance (GrowthD) from tree size inequality (Gini), forest aridity index (FAI), and total basal area (TBA), respectively; b1, b2 represent direct effects on Gini from TBA and FAI; and c1 indicates the direct effect of FAI on TBA

$$GrowthD = \beta_0 + \beta_1 Gini + \beta_2 TBA + \beta_3 FAI + u_{1j} Gini + u_{2j} + \epsilon_j \quad (6)$$

$$Gini = \beta_0 + \beta_1 TBA + \beta_2 FAI + u_{2j} + \epsilon_j \quad (7)$$

$$\mathrm{TBA} = \beta_0 + \beta_1 FAI + u_{2j} + \epsilon_j \quad (8)$$

where β_0 is the model intercept, and β_n are the fixed parameters and their interaction coefficients. *Gini* stands for the Gini tree size inequality index u_{1j} is the random slope for Gini index and u_{2j} is the random intercept at site j, respectively.

To calculate the indirect effects within the structural equation model, we used the product of path coefficients (standardized estimates) along the causal pathways. Specifically, the indirect effect of a predictor on the outcome variable is the result of one or more mediated relationships. In our model, for example, the indirect effect of the FAI on GrowthD through Gini was calculated by multiplying the standardized coefficients along the path (Fig. 4. b1×a1). This was done for each of the indirect pathways identified in the SEM. For the multi-step mediation pathway (i.e., FAI → TBA → GrowthD), the indirect effect was computed by multiplying the coefficients for each link in the chain (Fig. 4. c1×b2). The total indirect effect was the sum of these individual indirect effects, providing a comprehensive view of how variables influenced growth dominance through multiple mediators. Finally, the total effect of a predictor on the outcome variable is the sum of the direct effect and all indirect effects.

Results

Individual tree growth reconstruction

The performance of the four fitted GAMs for BAI over the last 3 years varied across sites, with adjusted R^2 values ranging from 0.475 to 0.765 (Table 2), indicating a moderate to high proportion of explained variance. The smooth effect of DBH by species group was statistically significant in all models, demonstrating that nonlinear growth patterns differ between coniferous and broadleaf species across all sites. For the PL1 and PL2 sites, the inclusion of a competition index enhanced model performance, with the smooth term for competition being significant in both models ($p < 0.05$). Cross-validation confirmed stable predictive performance of the GAM reconstructions across sites. The root mean squared error (RMSE) was 0.0079 ± 0.0033 (GE1), 0.0044 ± 0.0009 (IT1), 0.0041 ± 0.0012 (PL1), and 0.0037 ± 0.0015 (PL2). Model diagnostics revealed no significant deviations from assumptions, as tests for residual uniformity, dispersion, zero inflation,

Table 2. Summary of generalized additive models (GAMs) fitted to reconstruct individual tree growth. The models account for species group-specific nonlinear relationships between DBH, competition, and BAI over the last three years. The table reports parametric coefficients, degrees of freedom (edf and Ref.df), t/F values, p-values, and significance codes for each model term. Model performance is reflected in adjusted R^2, deviance explained, and the number of observations (n)

Site	Term	edf	Ref.df	Estimate	Std. Error	t/F value	p-value	Signif.	Adj. R^2	Deviance Explained (%)	REML	n
GE1	Intercept			0.106	0.0032	32.88	<2e-16	***	0.727	73.6	−191.26	97
GE1	s(DBH): Coniferous	1.926	2.387			92.59	<2e-16	***				
GE1	s(DBH): Broadleaf	1.133	1.253			24.1	1.78E-06	***				
IT1	Intercept			0.075	0.0021	35.77	<2e-16	***	0.635	64.3	−292	131
IT1	s(DBH): Coniferous	1.785	2.176			88.09	<2e-16	***				
IT1	s(DBH): Broadleaf	1.211	1.384			22.68	8.33E-07	***				
PL1	Intercept			0.08	0.002	39.09	<2e-16	***	0.475	49.2	−269.92	121
PL1	s(DBH): Coniferous	1.797	2.238			7.719	0.000591	***				
PL1	s(DBH): Broadleaf	1.047	1.092			2.136	0.054821	.				
PL1	s(Competition index)	1.047	1.083			6.158	0.011314	*				
PL2	Intercept			0.0777	0.0019	41.93	<2e-16	***	0.765	77.2	−269.52	114
PL2	s(DBH): Coniferous	1.223	1.385			50.55	<2e-16	***				
PL2	s(DBH): Broadleaf	1.035	1.069			8.33	0.0037	**				
PL2	s(Competition index)	1.152	1.271			6.87	0.00747	**				

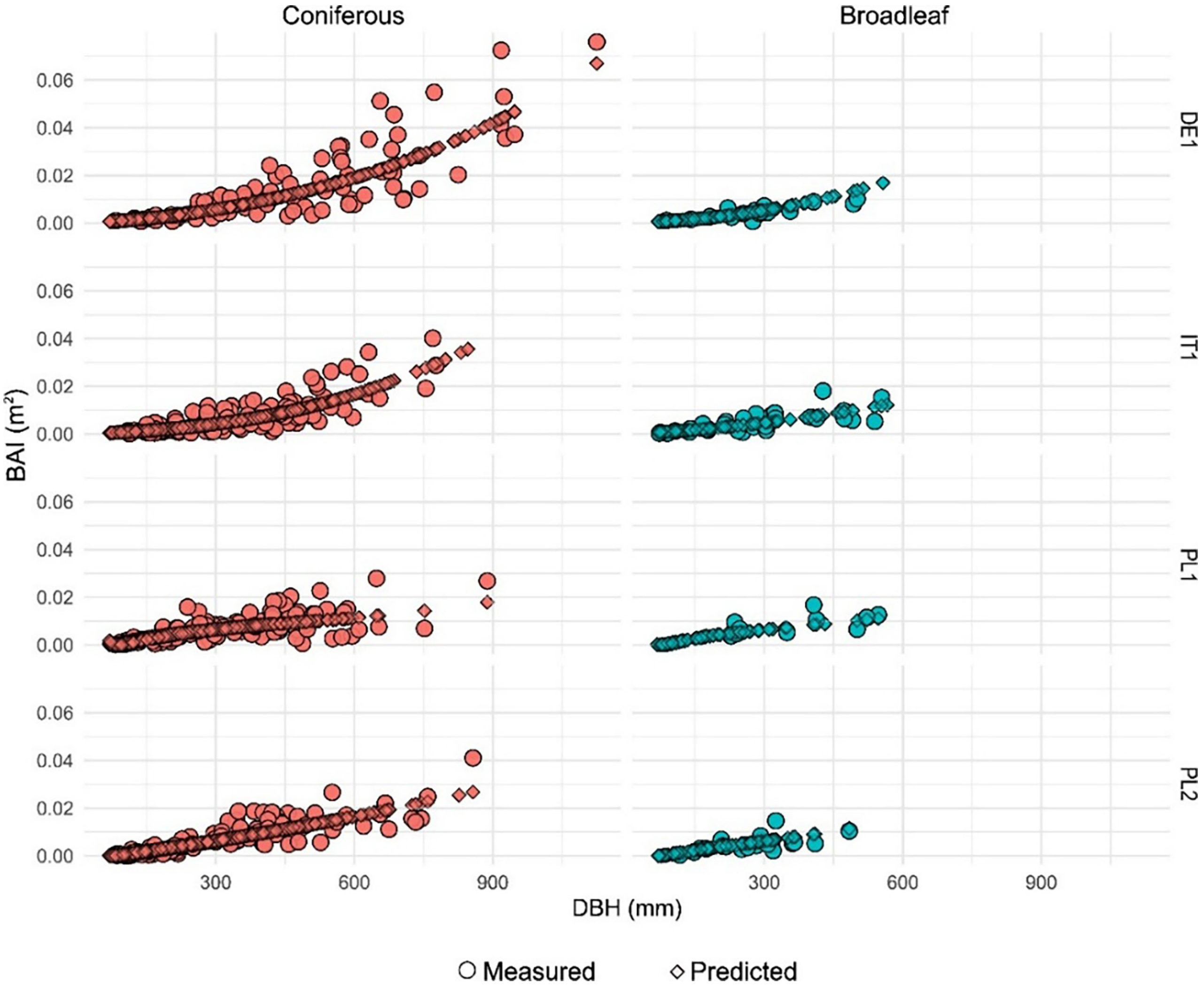

Fig. 5. Measured and predicted basal area increment (BAI) as a function of diameter at breast height (DBH) for coniferous and broadleaf species across four sites (GE1, IT1, PL1, PL2). Circles show measured BAI; diamonds show predictions from site-specific generalized additive models (GAMs)

and outliers showed no issues. Therefore, the fitted models were used to reconstruct the increment of the remaining trees (Fig. 5) and subsequently to calculate growth dominance.

Direct and indirect drivers of growth dominance

The structural equation model showed a good fit to the observed data (Fisher's C = 2.257; $\chi^2 = 0.974$). GrowthD was significantly and positively influenced by Gini (Table 3, Fig. 6; standardized effect = 0.635), indicating that an increase in tree size inequality is inherently linked to higher growth dominance in managed stands. This effect was by far the strongest among all predictors, confirming tree size inequality as the main driver of asymmetry in growth distribution. In addition, GrowthD was negatively affected by FAI (Table 3, Fig. 6; −0.321), demonstrating a direct influence of water availability on the growth distribution between individuals. Gini was negatively affected by both FAI (−0.324) and TBA (−0.215) (Table 3, Fig. 6), showing that increasing aridity and higher stand density inherently reduce tree size inequality. In turn, TBA was negatively influenced by FAI (−0.404) (Table 3, Fig. 6), meaning that more arid conditions were associated with lower stocking density.

Table 3. Direct, indirect, and total effects of tree size inequality (Gini), forest aridity index (FAI), and stocking density (TBA) on growth dominance (GrowthD) based on the structural equation model (SEM). Standardized estimates are shown for each effect type

Effect Type	Path	Standardized Estimate
Direct/Total	Gini → GrowthD	0.635
Direct	FAI → GrowthD	−0.321
Direct	FAI → TBA	−0.404
Direct	FAI → Gini	−0.324
Indirect	FAI → Gini → GrowthD	−0.206
Indirect	FAI → TBA → Gini → GrowthD	0.055
Total Effect	FAI → GrowthD	−0.472
Direct	TBA → Gini	−0.215
Direct	TBA → GrowthD	n.s.
Indirect	TBA → Gini→ GrowthD	−0.137
Total Effect	TBA → GrowthD	−0.137

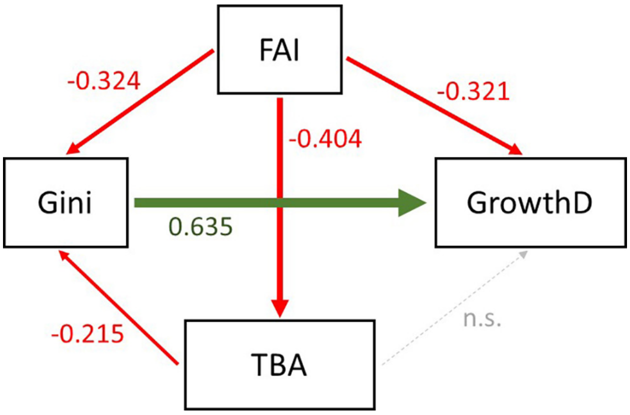

Fig. 6. Standardized estimates of direct effects in the structural equation model (SEM). The figure illustrates the relationships between tree size inequality (Gini), forest aridity index (FAI), and stocking density (TBA) on growth dominance (GrowthD)

Several significant indirect pathways to GrowthD were also identified. FAI exerted an indirect negative effect (−0.206) on GrowthD through its influence on Gini (Table 3, Fig. 6). Another indirect effect of FAI on GrowthD (0.055) occurred through its impact on TBA and subsequent effects on Gini. The total standardized indirect effect of FAI on GrowthD, combining both pathways, was substantial and negative (−0.472), underscoring the central role of aridity in shaping competitive asymmetry via stand structure. TBA also exhibited a negative indirect effect (−0.137) on GrowthD via changes in Gini (Table 3, Fig. 6), even though the direct pathway TBA to GrowthD was not significant.

The model explained a substantial proportion of variance in growth dominance, with a marginal R^2 of 0.57 and a conditional R^2 of 0.60 (Supplementary 1). The explained variance was lower for tree size inequality (marginal $R^2 = 0.09$; conditional $R^2 = 0.11$) and for stocking density (marginal $R^2 = 0.17$; conditional $R^2 = 0.27$) (Supplementary 1), suggesting that while these variables mediate the effect of climate, they are less directly predictable. Overall, the SEM results highlight a robust and consistent link between structural heterogeneity and growth dominance, modulated by the climate aridity gradient across sites.

Discussion

Tree size inequality as a structural driver of growth dominance in managed stands

Our study demonstrated that climate aridity, as captured by FAI, had a negative influence on both tree size inequality and growth dominance. Beyond its direct effect on growth dominance, FAI also exerted an indirect influence through its impact on stocking density. In turn, stocking density had no significant direct impact on growth dominance, acting only indirectly through its influence on tree size inequality. Tree size inequality consistently emerged as the strongest predictor of growth dominance across all sites, showing the highest direct and total effects in the structural equation model. This finding suggests that the relationship between tree size inequality and growth dominance in silver fir–dominated stands is inherent and robust, persisting regardless of site-level differences in resource availability and stocking density.

This interpretation supports previous simulation studies. For example, Pommerening et al. (2016) showed that even when growth is uniformly distributed across tree sizes, reverse growth dominance can emerge as a function of a skewed size distribution, such as the negative exponential shape typical of steady-state, uneven-aged forests. Forrester (2019) also demonstrated that stand growth rates and distribution are strongly influenced by the shape of the size distribution and the nature of the size–growth relationship, even at a constant stand density. For instance, forests with normal or reverse-J-shaped tree size distributions can result in negative or positive growth dominance depending on the underlying size–growth relationships. Moreover, numerous empirical studies have shown that silvicultural interventions, such as thinnings, often affect both growth dominance and tree size inequality in similar directions (e.g., Bradford et al., 2010; Moreau et al., 2020).

Thus, there is a need for a re-evaluation of how growth dominance is interpreted. Rather than viewing growth dominance purely as a proxy for the prevailing competition mode, it is crucial to first consider whether underlying tree size inequality, often a legacy of past disturbance or management, may be exerting a dominant influence on growth distribution. Therefore, to disentangle these relationships and understand competitive dynamics, temporal analyses can be especially valuable. For instance, Britwum Acquah et al. (2022) traced the development of tree size inequality and growth dominance over time in uneven-aged Douglas-fir stands subjected to different thinning intensities, analyzing the temporal interactions between structure, competition, and growth, thus accounting for potential initial structural and competitive differences. A similar approach was used in managed Eucalyptus plantations in Brazil to understand the dynamics of stand heterogeneity and growth dominance across thinning intensities and stages of stand development (Soares et al., 2017).

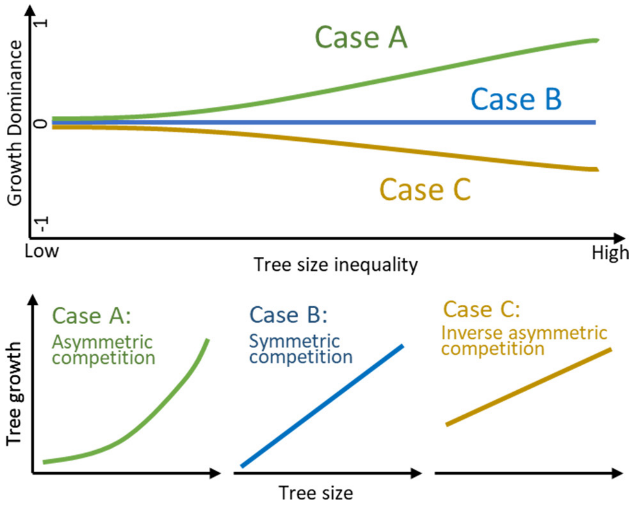

Fig. 7. Conceptual framework illustrating how the mode of competition and the resulting size–growth relationship influence the link between growth dominance (GrowthD) and tree size inequality (Gini)

Since such a temporal approach does not explicitly depict the structure–competition mode relationship, as it tracks changes over time without directly quantifying resource partitioning, another perspective is to analyze multiple stands within each site to explore the link between tree size inequality and growth dominance. In this conceptual framework, under size-asymmetric competition, growth dominance is expected to increase with tree size inequality (Fig. 7, Case A). Under symmetric competition, growth dominance remains stable (Fig. 7, Case B). Under inverse-asymmetric competition, growth dominance may slightly decline as tree size inequality increases (Fig. 7, Case C).

Our findings underline the importance of explicitly considering stand structure and mode of competition when planning silvicultural interventions. For instance, we believe that adapting harvesting strategies to promote stand structures that perform better under given site conditions, for example, reducing q factor in uneven-aged stands managed using BDq method where high growth dominance of large trees limits the contribution of smaller trees, or maintaining higher q factor where smaller trees contribute disproportionately to stand growth. Similarly, in even-aged stands, thinning intensity and timing can be adjusted to either reduce competitive pressure from dominant cohorts or to promote structural diversity, depending on site-specific resilience and productivity goals.

Limitations of the study

The key limitation of this study is its reliance on reconstructed growth data. While this approach enabled us to address the formulated questions with the available dataset, it cannot fully capture the complexity, variability, and stochasticity inherent in continuous, long-term observational data (Nehrbass-Ahles et al., 2014). Tree-ring based reconstructions are inevitably affected by sampling design and coverage, and may underrepresent certain size classes or competitive positions, thereby introducing uncertainty in stand-level growth estimates. As a result, the conceptual framework proposed here, although supported by empirical evidence, is constrained by the limited availability of suitable long-term datasets (Pretzsch et al., 2019). The relationship between tree size inequality and growth dominance is further shaped by the intensity of competition and by structural differences among stands, which can modify how resources are partitioned across tree size classes (Dănescu, 2016; Forrester, 2019). Thus, broader testing of the hypothesized relationships, particularly the role of stand structure, require additional long-term studies across diverse climatic conditions and forest types. Therefore, we encourage further exploration of the proposed framework.

Conclusions

This study demonstrates that tree size inequality is a key driver of growth dominance in managed forest stands. Across multiple sites, greater disparities in tree size consistently corresponded with increased growth dominance. Climate aridity also influenced negatively, directly and indirectly, the growth dominance, as well as stocking density, and tree size inequality. While stocking density did affect growth dominance, its influence was mainly indirect, operating through changes in tree size inequality. These findings highlight the importance of interpreting growth dominance not merely as a reflection of competition mode, but as an emergent property shaped by stand structure and the legacy of past management or disturbances. This has significant implications for forest ecology and management, underscoring the need to integrate structural attributes into silvicultural interventions (e.g., thinning regimes) to ensure the stability, long-term productivity and resilience of silver fir stands under global climate change

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