



Neighborhood competition modulates the link between crown structure and tree ring variability in monospecific and mixed forest stands

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ARTICLE INFO

Keywords:

Crown shape
Tree ring patterns
Norway Spruce
Silvicultural interventions
Provenances trial and mixing effects
Intra- and inter-specific competition
Terrestrial laser scanner (TLS)

ABSTRACT

3D crown shape and tree ring development are autobiographies of the growth conditions. With advancements in terrestrial laser scanning, modeling growth from 3D crown structure offers insights into trees' structural and functional responses in a non-destructive and repetitive way. However, how the trees in different growing conditions respond in 3D structure and manifest their responses into tree rings remains unexplored, which would help to better explain tree-level growth dynamics and forest management. To enhance this understanding, we tested a set of hypotheses: (HI) that 3D crown shape (CS) and tree ring (width) patterns (TRP) are correlated across different growing conditions or forest stands like monospecific, provenances trials, and mixed forest stands; (HII) that stand types influence the CS-TRP link; and (HIII) local neighborhood competition (LNC) modulates the CS-TRP link. (HIV) 3D crowns manifest local growth conditions; therefore, 3D crown structures can be used to predict tree ring growth. We assessed these hypotheses by employing terrestrial laser scanning-based 3D crown shape and dendrochronology-based tree ring width patterns from Norway spruce (*Picea abies* [L.] Karst.) trees growing in pure spruce (unthinned and thinned), provenances trial, and mixed-species trial (with European Beech, *Fagus sylvatica* [L.] stands covering a large-scale competition gradient. We first show that 3D crown shape and TRP metrics differed significantly across forests ($p < 0.05$) but were correlated ($p < 0.05$). Neighborhood competition among the forest types influences the link between 3D crowns and tree rings. Pathway-based analyses revealed that neighborhood competition indirectly influences ring variability by modifying crown structure ($p < 0.05$), suggesting local growth conditions are mostly manifested into crown shapes, leading to 3D crown shape-based low-error growth predictions (0.44 mm) across forest types. However, incorporating competition legacy information (competition over the last 30 years) in the model slightly improved the prediction performance (error reduced to 0.41 mm), further explaining that the crown likely loses growth information due to growing conditions (competition it faces and species with it is growing). This study reveals how trees in different growing conditions differed structurally and mechanized their responses in tree rings, providing crucial insights into tree-level growth dynamics and management.

1. Introduction

The principle of crown structure and growth patterns relationships is twofold: structural and functional. From a structural perspective, the mechanical support provided by the stems upholds the crown (Esser, 1946). Functionally, the stems facilitate resource sharing by supplying water and nutrients, while the crown reciprocates by depositing photosynthetic carbon to the stem (Lehnebach et al., 2018). Functional

relationships between crown and stem have long been recognized and used to understand tree functional strategy (Shinozaki et al., 1964). In contrast, the quantitative link between crown structure or shape (CS) and tree ring patterns (TRP) once elusive, has now become accountable with the maturation of terrestrial laser scanning based point cloud data (Bayer et al., 2013; Pretzsch et al., 2022; Yrttimaa et al., 2022). Emerging studies suggest that understanding the tree growth dynamics through the CS-TRP link would be a significant advancement in growth

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<https://doi.org/10.1016/j.foreco.2024.121839>

Received 5 January 2024; Received in revised form 8 March 2024; Accepted 11 March 2024

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modeling and management as CS and TRP both manifest historical information of growth development (Jacobs et al., 2021; Lüttge, 2022). Despite recent studies elucidating their interrelationships (Pretzsch, 2021b; Pretzsch et al., 2022; Yrttimaa et al., 2022; Ahmed and Pretzsch, 2023), the correlation between specific crown shapes and inter-annual ring variability remains unexplored across different growth scenarios, limiting our understanding of how trees grow with mechanized responses to growth conditions in the stem and crown structure (Pretzsch, 2021b).

Among others, a forest stands, either managed or unmanaged representing different growth scenarios, is likely to give trees a unique architectural shape, indicating distinct ecological strategies that are reflected in crown structure and stem growth (Assmann, 1961; Rawat et al., 2015). For example, a tree adjusts its crown to light-limited conditions by pushing branches upwards to maximize light interception (Oliver et al., 1996). The dynamics of canopy adjustment, in turn, alter the forest ecosystems, yield, and the canopy itself by influencing microclimates through modulating light regimes (Oliver et al., 1996; Purves et al., 2007; Atkins et al., 2023). In certain scenarios, when wind plays a significant role, trees relocate more carbon to their stems to ensure stability (Donfack et al., 2022). However, the configuration or adjustment of a tree's crown can be influenced by several factors such as species composition of a stand (pure or mixed), genotype or species identity (provenances from different regions or different species) (Li et al., 2014; Barbeito et al., 2017; Uzquiano et al., 2021) and resource availability or competition (Forrester and Albrecht, 2014; Pretzsch et al., 2016; Yrttimaa et al., 2022). All factors listed are intricately linked to the spatial arrangement of trees (Donfack et al., 2022). Thus, competition management may play a critical role by modifying resource availability (e.g., sunlight, water, nutrients, etc.) for retained trees, which may further influence the crown size and stem radial growth (Fichtner et al., 2013; Purahong et al., 2014; Montoro Girona et al., 2017; Donfack et al., 2022). According to Vieilledent et al. (2010), these later elements (species composition and competition) emerge as major determinants of tree growth dynamics and may modulate the CS-TRP link (Pretzsch, 2014; Yrttimaa et al., 2022), which can be varied due to management. To illustrate, inter-specific competition within mixed (either mixed in species or mix in provenances) stands, which is predominantly driven by competition for light (Jucker et al., 2015; Pretzsch, 2022; Condés et al., 2023), can cause changes in crown morphology (Barbeito et al., 2017) and growth rates (Condés et al., 2023; Pretzsch, 2021a; Pretzsch and Schütze, 2009). This phenomenon is supported by numerous studies documenting distinct crown morphologies and growth patterns exhibited by trees within mixed-species stands compared to those in pure stands (Pretzsch and Schütze, 2009b; Barbeito et al., 2017; Pretzsch, 2021a; Condés et al., 2023). These variations in crown structure and growth dynamics might also influence the relationship between crown size and tree ring patterns (CS-TRP link). However, how different species compositions and varying competition within stands modulate the CS-TRP link remains unexplored, but it is critical to understanding the tree growth dynamics in different growth scenarios.

Along with stand types (monospecific or mixed), local growth influences factors such as competition within neighbors, measured by the extent of neighboring tree crowding (Ford et al., 2017), plays a crucial role in influencing the growth and crown structure of individual trees across stand types (Curtis, 1970; Tomé and Burkhart, 1989; Metz et al., 2013; Jucker et al., 2015; Kunz et al., 2019). Competition occurs because trees primarily compete with nearby trees for resources (Bonan, 1993), and this competition can persist throughout the lifespan of the trees (Radtke et al., 2003; Barbeito et al., 2014). By persisting throughout the lifespan, it modifies crown morphology (e.g., crown recession) and reduces tree level wood production through altering light and belowground resource availability (Davies and Pommerening, 2008; Weiskittel et al., 2011; Barbeito et al., 2017).

Besides, competition indices could help better explain differences in

tree radial growth and crown structure across stand types by explaining the crown variation (Owen et al., 2021) and tree growth (Madsen et al., 2021). Therefore, the type (intra vs. inter-specific) and level of competition for a longer period can be a critical factor in defining crown shape and tree ring growth. Hence, few studies have observed that past growth legacies (i.e., competition) strongly define current growth patterns (Pretzsch, 2021c; Schmied et al., 2022), with the effects potentially reaching back as far as five to thirty years (Pretzsch, 2022). Therefore, incorporating past growth history i.e., neighborhood competition legacy may give new perspectives on predicting individual tree level growth (Hanus, 2003; Schmied et al., 2022). Thus, we expect tree-level growth predictions based on a 3D crown structure incorporating legacy information would help better understand forest dynamics.

However, so far, no studies have taken into account neighborhood competition indices and its legacy effects (competition from previous years) in the context of the CS-TRP link and crown shape based tree ring patterns. Understanding this would improve a non-destructive and repetitive growth predictions method based on external tree shape across growth conditions. To address this knowledge gap and explore the relationship between stand type, crown shape variation, and tree ring patterns while also considering the potential influence of neighboring trees, we formulated and tested these four hypotheses:

HI. Crown shape and tree ring patterns will vary across stand types (i.e., pure unthinned, pure thinned, provenance trial, and mixed stands) but remain correlated within stand types (see Fig. 1a).

III. CS-TRP relationships are mediated by stand types (Fig. 1b).

IIII. Neighborhood competition alters the link between CS and TRP. This change can happen directly or indirectly, as via altering the crown shape (shown in Fig. 1c), suggesting two potential mechanisms.

The first mechanism suggests that when there is minimal competition for light, LNC simultaneously impacts CS and TRP or tree adjusts both simultaneously, resulting in no change (i.e., \emptyset impact) in the CS-TRP relationship (Fig. 1c I). The second mechanism indicates that LNC first modifies CS while light competition is significant, followed by TRP alteration, causing a triangular effect (Δ) and subsequently changing the CS-TRP relationship (Fig. 1c II).

HIV. We also anticipated that the current shape of the crown is a result of the growth conditions in recent years, which suggests that the legacy effect of LNC is reflected in CS. Consequently, if we base growth predictions solely on crown shape, we would observe similar growth patterns to those observed across various types of stands.

In order to assess the hypotheses and predicting crown based tree ring growth, we employed terrestrial laser scanning (TLS) and tree ring data acquired from Norway spruce (*Picea abies* [L.] Karst) trees originating from diverse stands encompassing pure (thinned, unthinned) stands, provenances trials, and mixed (with European beech, *Fagus sylvatica* [L.] stands).

2. Materials and methods

2.1. Study sites

Our study involved the scanning and coring of 122 Norway spruce trees from different long-term experimental plots across four different sites in Germany. (1) Fürstenfeldbruck 612: This site consisted of pure N. spruce stands encompassing differing thinning intensities and initial spacing, with a total of 72 trees included in our study. These series of plots comprised thinned and unthinned plots with different thinning patterns (see SF1a). For more detailed information regarding this site see Pretzsch et al. (2022) and Schmied et al. (2022). (2) Vohenstrauß 622: At this site initial spacing incorporating a buffering zone (gap between plots), we focused on clone-based provenances of N. spruce trees. These N. spruces came from 21 different clones sourced from various regions of Germany, including the Alps, lowlands, and highlands. They were strategically planted with different initial spacing (see SF1b). However, we collected almost similar number of trees our data from five plots

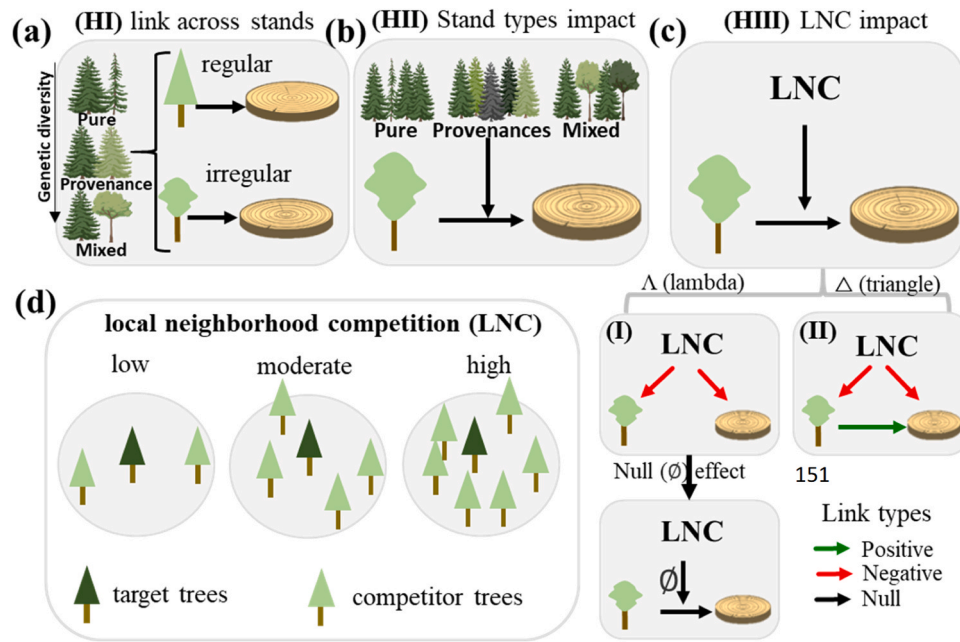


Fig. 1. Hypotheses conceptualization: (a) Crown shape and patterns (variability) define tree ring patterns (variability) in different stands. (b) Stand types or growing conditions strongly influence this link, and (c) competition with neighbors strongly modulates this link. Besides, the impact of the LNC on the link between crown shape and tree ring patterns can take one of two forms: (I) LNC affects both crown shape and tree ring patterns at the same time (i.e., the lambda impact, Δ), resulting in no impact (\emptyset) on the link. (II) LNC first affects the crown shape followed by tree ring patterns and the link between them, forming a triangular (Δ) relationship. (d) Illustration of the LNC (local neighborhood competition index) and its variability: low LNC indicates the target tree is facing low competition, whereas high LNC indicates the target tree is encountering higher competition.

amid nine to cover all provenances. In total, 24 trees from this site were included in our study. Additional information about these clones and the plots can be found in Pretzsch (2021a). (3) Freising and Schongau: These sites featured a mixed stands of N. spruce and E. beech trees (termed as Mixed). Our mixed experiment involved two sets of plots: FRE 813 and SON 814 (see Table 1). These plots contained a mix of trees from different ages (details in SF1c and Pretzsch and Schütze (2009a)). Interestingly, spruce trees grew much faster at SON 814 compared to FRE 813. However, both sites are considered highly productive according to Pretzsch and Schütze (2009a). However, we included 26 trees from these sites in our study encompassing trees from distinct age series. We collected data from a single mixed plot at each location, focusing on trees of different ages. Specific details about the plots and mixing patterns are available in Table 1 and SF1c. Our data collection spanned from November 2021 to February 2022.

Given that crown shape can have manifested past competition effects spanning five to thirty years (as discussed in the introduction), we focused on the most recent 40 years (with 10 buffering years) of growth rings for analysis to cover the whole growth series that might manifested by crowns (as crown response slowly compare to tree growth ring) and to make a consistent comparison across stands. To focus on the past competition legacy specifically, we limited our analysis to the past 30 years, reflecting the constraints imposed by the availability of long-term data.

We used a stratified random selection of trees from various stands to

test our hypotheses. This strategy (based on diameter of breast height) diversified tree sizes and crown shapes from different growth conditions, yielding a variety of crown morphologies and tree ring patterns (Pretzsch et al., 2022). By isolating trees in pure stands subject to varying thinning regimes, as opposed to unmanaged controls, we effectively obtained a diverse array of crown shapes and growth rings due to the structural heterogeneity of density management in mono-specific stands. For precise site details, see Table 1 and the references mentioned above.

2.2. Terrestrial laser scanning (TLS) data acquisition

To characterize crown shape, four permanent experimental plots were scanned using the RIEGL VZ-400i (RIEGL 2019) TLS (see Table 1 for plot details). Each plot underwent multiple scans, with the scanner angled towards the crowns to capture them optimally. The number of scans varied from 102 to 124, based on the plot's accessibility. A consistent distance of approximately 5 m was kept between each scan. This procedure helped to reduce the occlusion effect (Mathes et al., 2023). The scanned raw point clouds were registered and filtered automatically with an octree approach to enable post-processing performance using RiSCAN PRO software (version 2.10.1) (Pretzsch et al., 2022). In order to mitigate potential errors associated with automatic tree isolation, we implemented a multi-step approach that involved the use of a coordinate system and reflector to first identify each tree,

Table 1

Summary of plots and stands demographic and climatic information. (a.s.l-above sea level). Age indicates the age of Spruce trees. Specific sampled tree numbers are presented in Fig. 2. Temperature and precipitation representing the mean yearly rainfall and temperature. Age included seedling age during plantations.

Sites (trial no.)	Stand Types	No. of trees	Location	Altitude (a.s.l)	Precipitation (mm)	Temperature (°C)	Age (yrs.)
Fürstenfeldbruck 612 (FFB 612)	Thinned pure N. Spruce	53	11.05°E, 48.14°N	550	932 mm	8.8	51
	Unthinned pure N. Spruce	19					
Vohenstrauß 622 (VOH 622)	Provenances trial	24	12° 26' E, 49° 41' N	720–740	904 mm	6	47
Freising (FRE 813.5)	N. Spruce with E. Beech	9	11.66 E, 48.42 N	480–515	814 mm	7.7	60
Schongau (SON 814.5)		17	10.77 E, 47.87 N	785–800	1114 mm	6.8	103

followed by manual isolation from the stands. This approach ensured a high degree of accuracy in tree identification, along with minimizing the risk of overlapping errors. In high-density stands, we ensured the quality of our data by examining each tree from all possible angles. Any tree crowns that did not meet our requirements were excluded from the complete dataset.

Individual tree point cloud data processing was done in R (version 4.3.0) (R Core Team, 2023) by using “lidR” (Roussel et al., 2020), “dbscan” (Hahsler et al., 2019), “VoxR” (Lecigne et al., 2018) and the “ITSMe” (Terry et al., 2023) packages. For further details on the scanning procedure and data processing methods used in the analysis (see Fig. 2), refer to Pretzsch et al. (2022). To understand crown shape and tree ring pattern relationships, we used multiple crown shape (CS) and tree ring patterns (TRP) metrics, which are presented in Fig. 2.

2.3. Tree ring data acquisition

The identical set of 122 trees were cored from both north and east cardinal directions at the standard diameter at breast height (130 cm from the ground level) positions, using a 5 mm increment borer (Haglöf, Sweden). The extracted cores amounted to 244 in total and were

subsequently air-dried, affixed to hardwood plates, and meticulously polished to facilitate the measurements. Using Lintab Series 5 software, in tandem with Tsap-Win software, the tree ring widths was measured (Rinntech Heidelberg, Germany) up to the nearest of 0.01 mm. Precise cross-dating was achieved for each core by meticulously matching the patterns of narrow and wide rings. Well-defined drought years, such as 2003, 2015, and 2018, served as reference points in this process, reflecting the trees’ suppressed growth during those periods (Pretzsch et al., 2022).

To statistically verify the accuracy of cross-dating, all tree-ring series underwent detrending. This involved removing low-frequency variations using a 30-year spline function, followed by averaging to create a master dating series. Subsequently, each detrended series was individually compared to the master series, excluding its own influence. By splitting the series into smaller segments and correlating them with corresponding segments in the master series, potential measurement errors were identified. Shifting these segments in different directions allowed for the identification of better fits characterized by higher correlations.

COFECHA, a dedicated software program developed by Holmes (1983), was employed for this statistical cross-dating analysis.

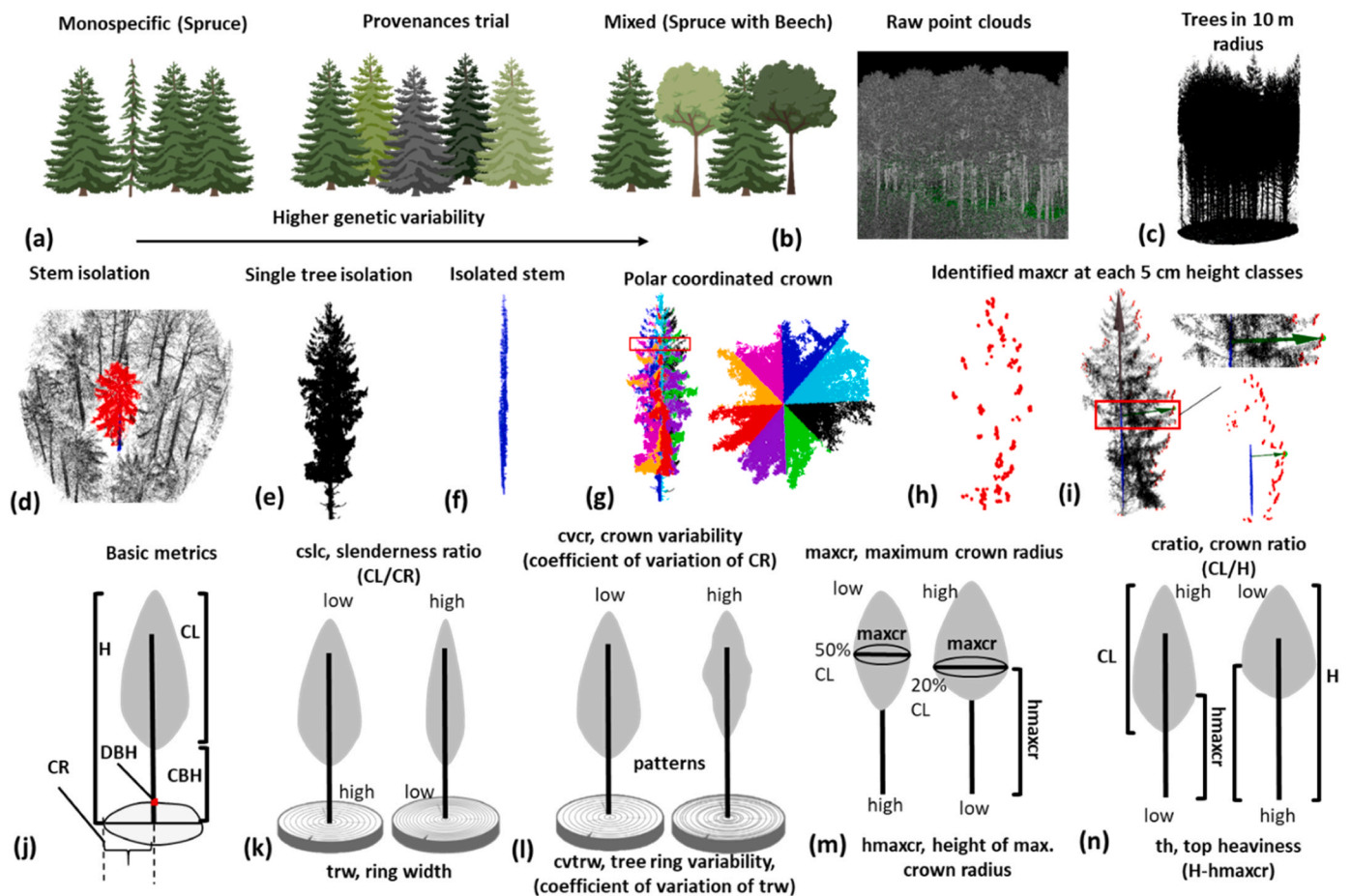


Fig. 2. presents schematic visualizations of the data utilized from various stands and the processes involved. The steps are illustrated: (a) Data from different stands. (b) Raw point clouds are displayed in Riscan Pro software after registration and filtering using (octree). (c) trees showing in small cluster of cropped point clouds with a 10 m radius in R. (d) Manually identified and isolated single tree from stands in Riscan Pro. (e) Isolated single tree in R. (f) Isolated stem (from crown base to top). (g) Division of crowns into eight polar coordinate classes at 5 cm height intervals from the crown base to the top to determine the maximum crown radius (maxcr) at each class. (h) (red dots) Identification of maxcr at each 5 cm height classes. (i) Identification of tree maxcr shown with a green arrow. The subsequent schematic presentations (j-n) demonstrate evaluated TLidar-based crown shape and tree ring metrics. Crown metrics: (j) Diameter at breast height (cm) – DBH, Tree height (m) – H, Crown base height (m) – CBH, Crown length (m) – CL, Crown radius (m) – CR, Crown ratio (CL/H) – cratio, (k) Crown slenderness ratio (CL/CR)–cslc and mean tree ring width (mm) – trw, (l) Coefficient of variation of crown radius – cvcr and coefficient of variation of tree ring widths – cvtrw. (m) Maximum crown radius (m) – maxcr, Height of maximum crown radius (m) – hmaxcr, (n) Top heaviness (H-hmaxcr) (m) – th. See supplementary table ST1 for a detailed explanation of the variables and all variables considered in this study.

Additional basal area increment (BAI) analyses were conducted using the “dplr” package within the R statistical environment (Bunn, 2008).

2.4. Local neighborhood competition index (LNC) evaluation

Local neighborhood competition index (LNC) is mainly attributed to the distance of neighborhood trees, which therefore the use of distance-dependent competition indices is widely assumed to improve the accuracy of single-tree level growth predictions (see Metz et al. (2013); Weiskittel et al. (2011), p 33)). However, to assess how local neighboring trees affects the target tree growth dynamics, we employed a local neighborhood competition index, which later combined with competition legacy (competition from the past 30 years). To understand how competition among trees has changed over time or considering past competition, we calculated competition by analyzing conventional data (tree positions and sizes) collected every five years from 1992 to 2021. We assumed that competition increased linearly within each five-year interval as described in Schmied et al. (2022). Following Pretzsch and Schütze (2021), we used a search radius of rd (rd = 60% of the target tree height) and considered the trees within the circle as neighbors to calculate the LNC. We then applied the distance-dependent Hegyi competition equation to calculate the LNC (mean LNC and LNC₃₀ for latest 30 years) for each target tree by following Eq. 1 (Hegyi, 1974).

$$LNC = \sum_{i=1}^n \frac{DBHi}{DBH \times DIST_i} \quad (1)$$

Where LNC, DBH_i, DBH, and DIST_i represent the distance-dependent neighborhood competition index, the DBH of the *i*th neighbor tree (cm), the DBH of the target tree (cm), and the distance between the target tree and *i*th neighbor tree (m), respectively (see example in SF1a).

Moreover, when dealing with mixed stands (either provenances or mixed with E. beech), we employed a method of segregating the LNC within a specified search radius (rd) based on the species present to understand intra and inter-specific LNC. This separation and calculation involves distinguishing competition with the same species (here Spruce or a specific provenance), which was later converted into percentage (% of intraspecific LNC). Instead of using absolute LNC values, we expressed them as percentages. This provided a more interpretable metric that reflects the relative contribution of intraspecific competition to the overall LNC (de Sauvage et al., 2023). Additional methodological details and graphical representation can be found in Supplementary Figure SF2.

2.5. Statistical analyses

All statistical analyses and visualizations were done in R (version 4.3.0) (R Core Team, 2023).

Statistics for HI: Prior to linking crown shape and tree ring patterns, we first compared their variability and structure across stand types. This involved fitting a beta (β) distribution to the crown profile (Barbeito et al., 2017). In addition, we employed different other crown and tree ring metrics to compare shapes and patterns across stand types, including pure unthinned, pure thinned, provenances trials, and mixed stands. This involved applying a one-way ANOVA followed by a Tukey post-hoc test, after verifying the assumptions of normality and homogeneity. In cases where required, log-transformed data was used.

After comparing crown structure and tree ring width variability across stands, we linked them by developing a correlation matrix, where we checked individual variable-level relationships.

We selected some crown variables that were related to variability, such as the coefficient of crown radius and the crown slenderness ratio, and used them to model the coefficient of variation of tree ring width. This was to understand how trees adapt to their growth conditions, as tree ring variability reflects the environmental and physiological factors affecting tree growth patterns (Rathgeber, 2017). Besides, past inter-annual variability also explains present growth rates (Pretzsch,

2021c). We avoided using crown variables that were correlated with each other, to prevent multicollinearity problems.

Before modeling, we first standardized and scaled (0–1) our selected variables (with the formula $f(x) = (x_i - x_{\min}) / (x_{\max} - x_{\min})$, where x_i represents the variables of interest with their respective maximum (x_{\max}) and minimum (x_{\min}) values. This process allowed us to compare the effect sizes, enabling a better understanding of their contributions. Subsequently, we fit a multiple linear mixed-effect model by employing “lme4” and “lmerTest” packages in R (Bates, 2010; Kuznetsova et al., 2017), taking data from four different sites (see Table 1) into account (sites as random factors). However, the random factor showed no impact on the model; therefore, we excluded it from the model and fitted a multiple linear model (see Eq. 3). Later, we again statistically cross-checked multicollinearity by evaluating the variance inflation factor higher than two ($VIF < 2$) to avoid potential issues of multicollinearity. We calculated VIF using the “car” package (Fox et al., 2012).

$$cvtrw = \beta_0 + \beta_1 cvcr + \beta_2 cscl + \epsilon \quad (2)$$

where β_0 and $\beta_{1..n}$ indicate the intercept and slope or regression coefficients for independent variables, respectively.

We also fitted the model (2) by separating the data across stand types to compare magnitude of crown shape and tree ring patterns link within stand.

Statistics for HII: To test the second hypothesis, i.e., the impact of stand types on the link between CS-TRP, we incorporate stand types as interaction to the Eq. (2) and checked all possible interactions before selecting the best model (see Eq. 3). The best parsimonious model was selected based on the lowest AIC values after comparing between different fitted models, as explained in Burnham and Anderson (2004).

$$cvtrw = \beta_0 + \beta_1 cvcr + \beta_2 cscl + \beta_3 stand_types + \beta_4 cscl \times stand_types + \epsilon \quad (3)$$

Statistics for HIII: To evaluate how the local neighborhood competition (LNC) influences the relationship between crown shape (CS) and tree ring patterns (TRP), we first incorporated the 30 years mean LNC index into our model as an interactive term. We then selected Eq. (4) to elucidate the effects of LNC on the connection between CS and TRP. We used a similar method to identify the most parsimonious model, which is the model with the lowest Akaike Information Criterion (AIC) value after comparing multiple models.

$$cvtrw = \beta_0 + \beta_1 cvcr + \beta_2 cscl + \beta_3 LNC + \beta_4 cvcr \times LNC + \beta_5 cscl \times LNC + \epsilon \quad (4)$$

In order to comprehend the impact of both intra- and inter-specific competition on the CS-TRP link, we examined the interactive effect of intraspecific LNC percentage (% of intraspecific LNC) by incorporating it into the model (Model 4).

Next, we assessed the relative contributions (direct and indirect effects) of LNC by the structural equation model (SEM) (Fan et al., 2016). The “lavaan” package was used for our SEM analysis (Rosseel, 2012). The best-fit model was assessed by fit indices, including the comparative fit index (CFI) ($CFI > 0.95$), the chi-square (χ^2) test ($0 \leq \chi^2/df \leq 2$), non-significant paths ($p > 0.05$), and the standardized root mean square residual (SRMR) ($SRMR < 0.05$) (Schermelele-Engel et al., 2003).

Statistics for HIV: Finally, to predict temporal changes (calendar year) in tree ring widths (i.e., trw) using crown shape parameters (i.e., cvcr and cscl), we applied a linear mixed model represented by Eq. (5):

$$trw_i = \beta_0 + \beta_1 cvcr_i + \beta_2 cscl_i + \beta_3 year_i + \beta_4 cvcr_i \times year_i + \beta_5 cscl_i \times year_i + b_i + \epsilon_i \quad (5)$$

Here, b_i and ϵ_i represent random effect (i.e., tree id) and residuals [$\epsilon_i \sim N(0, \sigma^2)$, σ^2 is the standard deviation], respectively. Besides, the

indices i represent the individual trees on a plot.

Furthermore, we also projected temporal changes in tree ring widths (trw) by incorporating the interaction with LNC₃₀ to understand LNC₃₀ legacy effect on growth ring, and assessed the model performance by comparing goodness-of-fit indices and plotting observed versus predicted values from both models.

However, we evaluated the final prediction model by plotting the values that were actually observed on the Y-axis and the values that the models predicted on the X-axis, as suggested in Piñeiro et al. (2008).

3. Results

3.1. Variability in crown shape and tree ring patterns across stand types

Our sampling strategy encompassed a wide range of variability in both crown shape and tree ring patterns, as illustrated in Figs. 3 and 4.

In Fig. 4A, beta distribution indicates that averaged over all trees from pure thinned and provenances trial stands, ~80% of the larger crown radius is distributed around in the lower 50% of the crown (that means lower-reaching crown). In contrast, pure unthinned and mixed stands showed upper-reaching crown profiles.

Our further comparisons using multiple crown and tree ring metrics affirmed that stand types contributed significantly to the observed variability ($p < 0.05$) (Fig. 4B-I). The result revealed that trees with higher crown variability (higher cvcr in pure thinned stands) were characterized by low ring variability (lower cvtrw), while provenances remained comparatively more stable (low cvcr and cvtrw) (depicted in Fig. 4B-C). Conversely, mixed stands exhibited distinct patterns, showcasing elevated growth rates paired with moderate crown and ring irregularities, thus presenting asymmetric growth response across different stands (see crown and tree ring patterns in Fig. 4).

3.2. Linking crown shape and its variability to tree ring patterns across stand types (HI)

Although the crown shape and tree ring patterns varied strongly across stand types, Pearson correlation revealed that multiple crown shape metrics, e.g., cvcr, maxcr, hmaxcr, th, and cratio were significantly correlated to several tree ring pattern metrics (Fig. 5; see correlation coefficients for all relationships). More specifically, crown variability (cvcr) and tree ring variability showed strong correlation

(cvtrw). Besides, a significant correlation was observed between trw, and cvtrw with respect to cratio, maxcr, hmaxcr, CR, CL, and cvcr ($p < 0.05$), which supports our first hypothesis HI.

Moreover, we observed similar results in multiple linear model. For example, in fitted multiple linear model explained crown variability (cvcr) was significantly associated with tree ring variability (cvtrw) ($b = -0.2$, $p < 0.001$) and slenderness ($b = -0.28$) (ST2).

3.3. Impact of stand types on crown shape and tree ring patterns link (HII)

Fig. 6 presents the interaction between crown shape and tree ring patterns and influence of stand types, thereby corroborating our hypothesis HII. We found tree ring variability, cvtrw, decreased with crown slenderness, cscl, in all stand types except provenances trial (Fig. 6a). Importantly, model predictions supported the interactive effect between crown shape and stand types on tree ring patterns (Fig. 6b).

3.4. Impact of local neighborhood competition on crown shape and tree ring patterns (HIII)

The LNC-dependent model revealed that the incorporation of LNC strongly altered the crown shape and tree ring patterns (CS-TRP) relationship (effect size = -1.58 , $p < 0.05$) (Fig. 7a) and enhanced the predictive ability of the CS-TRP model by reducing the AIC and increased the R^2 value for ring variability (cvtrw) (see ST3 and compare with ST2). We found that the interplay between LNC and cvcr reduced cvtrw, which is shown by the model predictions (Fig. 7b, c), and supports the hypothesis HIII.

However, the percentage of intraspecific competition had a non-significant influence on the CS-TRP link ($p < 0.05$) but effect sizes are comparable with total LNC (compare the effect sizes in SF3).

The structural equation model (SEM) further specified how competition associated with crown variability and tree ring variability through multiple pathways (Fig. 8). The final SEM showed a good fit ($\chi^2 = 0.521$, $p = 0.47$, SRMR = 0.01) and a high proportion of tree ring patterns variability (see R^2 values), indicating multivariate pathways linking neighborhood competition to tree ring patterns. The SEM model explained 26% and 25% of the variation in cvcr and cvtrw, respectively. Local neighborhood competition (LNC) showed direct positive effects on cvtrw ($\beta = 0.11$, $p < 0.1$), as well as indirect stronger effects mediated

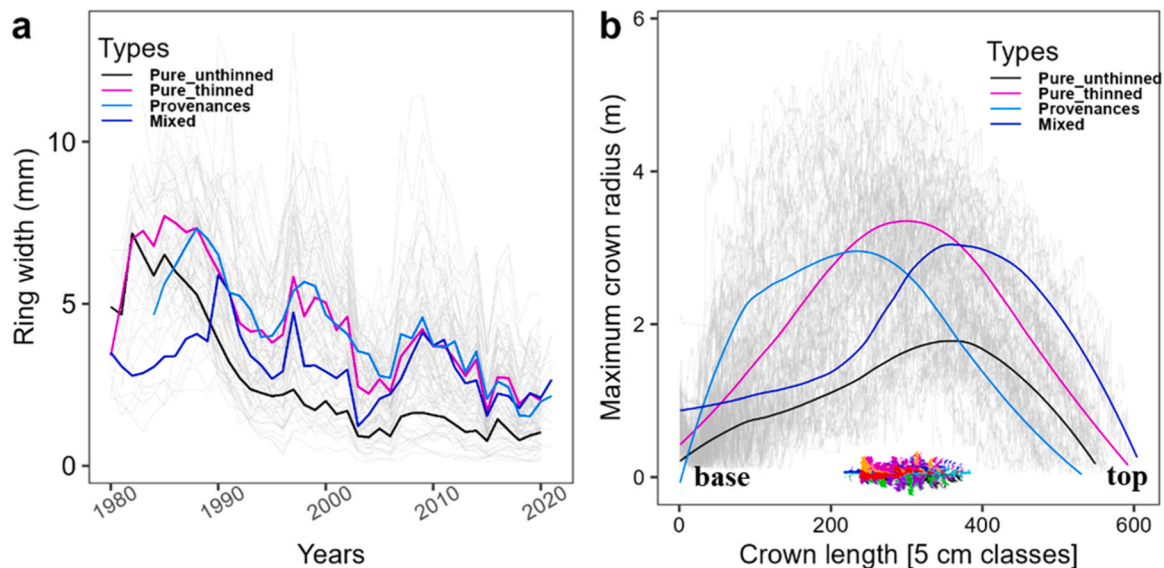


Fig. 3. Visualizing (a) raw tree ring width (trw) and (b) crown profiles for each tree. Each line indicates individual tree-level data (grey shaded). In sub fig (b), mean lines across stand types were drawn by using “loess” functions. Inset shows polarized crown to understand the distribution from the crown base to top.

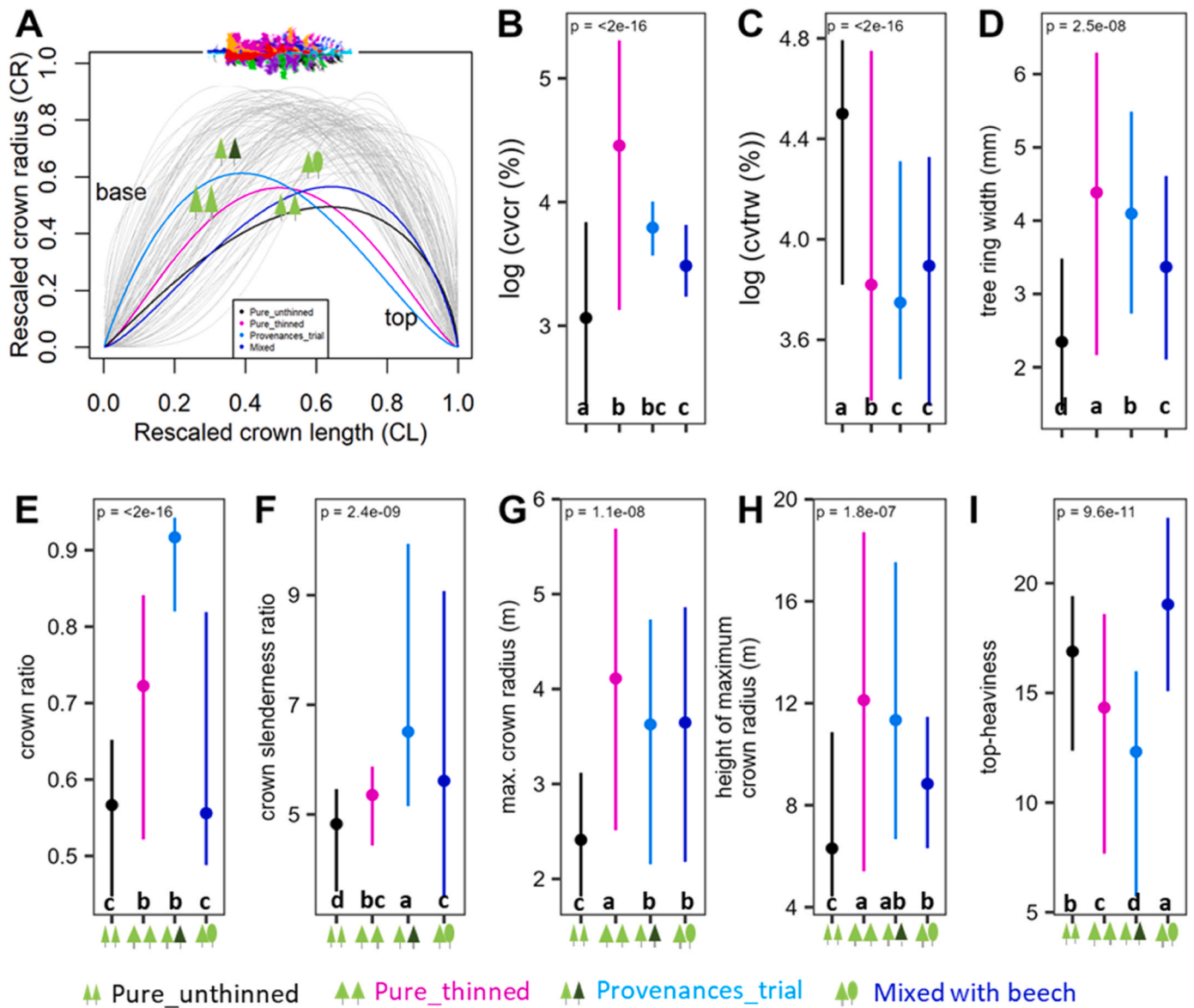


Fig. 4. Variations in crown shape and tree ring patterns among different stand types. These variations are depicted through the following metrics: (A) β -distribution fitted to crown profiles (CR-crown radius and CL-crown length); (B) coefficient of variation of crown radius (cvcr); (C) coefficient of variation of tree ring width (cvtrw); (D) mean tree ring width (trw); (E) crown ratio (CL/H); (F) crown slenderness coefficient (CL/CR); (G) maximum crown radius (maxcr); and (H) height of maxcr; (I) top-heaviness (H-maxcr). The vertical lines represent a 95% confidence interval, and the solid, larger circles indicate the median values. The p-value reflects the level of significance, derived from the one-way ANOVA. The letters used are from the Tukey post-hoc test, where similar letters indicate no significant difference among the groups.

through crown morphology (cvcr and cscl). Specifically, higher LNC was associated with reduced irregularity in crown (cvcr) ($\beta=-0.50$, $p=0.001$). These competition-induced crown changes (cvcr), in turn, correlated with decreased variability in the tree ring (cvtrw) ($\beta=-0.30$, $p=0.001$).

3.5. Growth curve predictions from crown shape by incorporating neighborhood competition legacy (LNC_{30}) (HIV)

Our projected growth curve, utilizing crown shape parameters as inputs, yielded comparable results with observed growth curve while discerning different stand types (make a visual comparison between Fig. 9a and b). An evaluation of the accuracy of our crown-based model, achieved through a comparison of observed and predicted values, demonstrated that crown shape closely approximated tree ring growth, resulting in a root mean square error (RMSE) of 0.44 mm, as depicted in

Fig. 9c. Moreover, integrating the local neighborhood competition legacy (LNC_{30}) into our model clarifies the decrease in tree ring width as LNC_{30} increases across stands (see Fig. 9d). This addition also resulted in a slight improvement in model accuracy, as evidenced by the reduction in RMSE from 0.44 to 0.41 (compare Fig. 9c and e). This implies that using crown shape parameters alone can effectively predict internal growth patterns and validate the findings of the structural equation model (refer to Fig. 9). However, it's worth noting that there is some underestimation, particularly in pure unthinned and mixed stands, which is evident in the point distributions as shown in Fig. 9c and the shaded grey areas as depicted in Fig. 10.

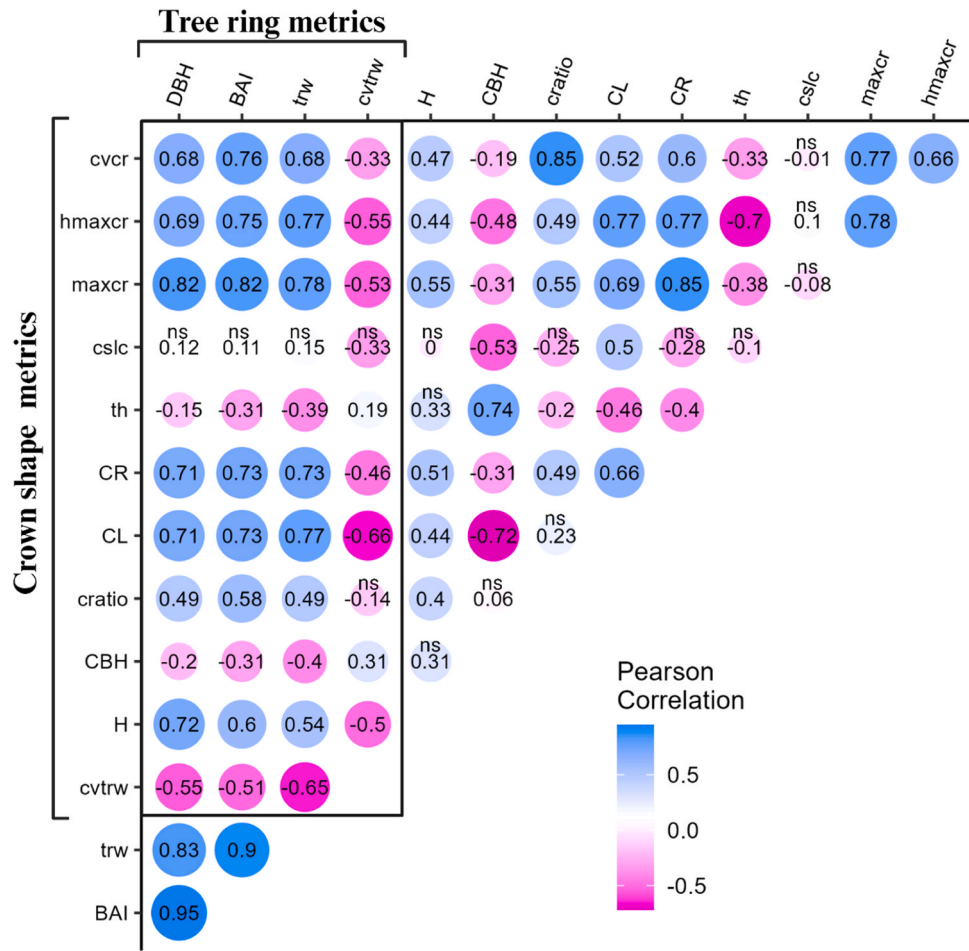


Fig. 5. Pairwise correlation between crown shape and tree ring pattern metrics. Non-significant relationships are indicated by ns ($p > 0.05$). Abbreviated forms are explained in ST1.

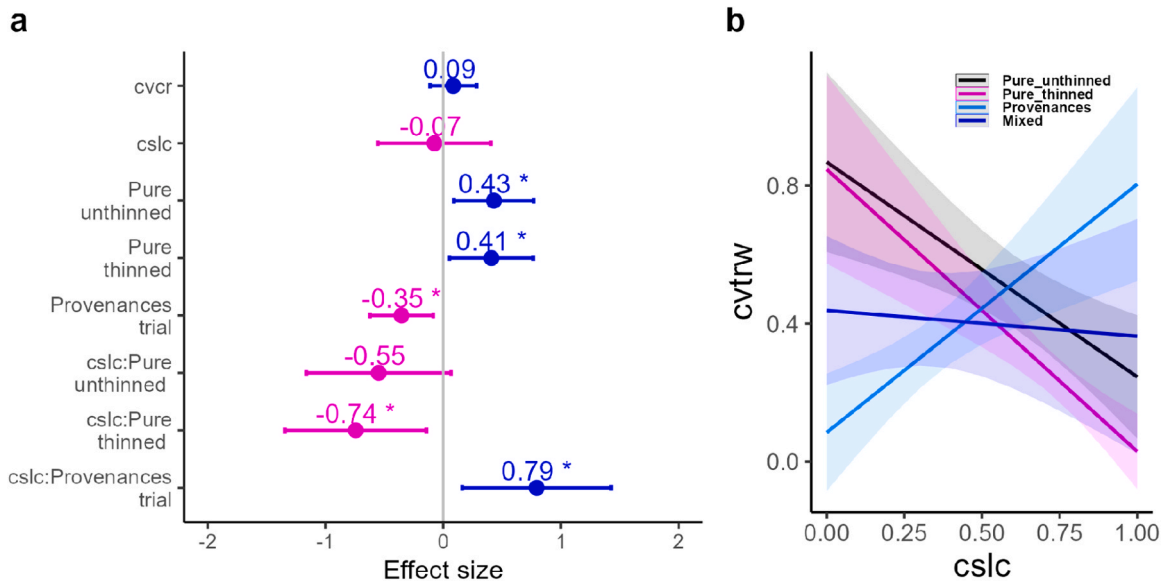


Fig. 6. Showing impact of stand types on CS-TR link. (a) the standardized estimates of parameter with level of significance ($*p < 0.05$). Horizontal lines indicate 95% confidence interval (CI). (b) model predictions for tree ring variability (cvtrw). Shaded lines denote 95% CI. Model details summary are presented in ST2. Note that mixed stands used as reference stand.

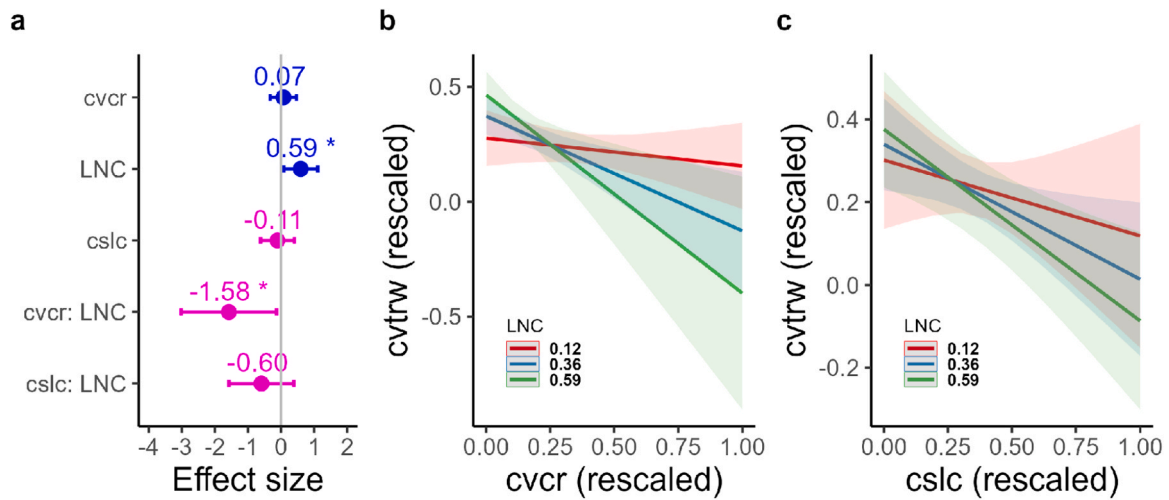


Fig. 7. Showing impact of LNC on CS-TR link. (a) the standardized estimates of parameter with level of significance (*<0.05, **<0.01, ***<0.001). Horizontal lines indicate 95% confidence interval (CI). (b and c) model predictions for tree ring variability (cvtrw) in relation to crown shape variability (cvcr) and crown slenderness (cslc) and LNC. Shaded ribbons denote 95% CI. Model details are presented in ST3.

4. Discussion

4.1. Relationships between crown shape and tree ring patterns in different stands types

4.1.1. Variability of crown shape and tree ring patterns across stand types

Our results suggest that crown shape and tree ring patterns strongly vary due to silvicultural interventions (see Figs. 3–5). Beta distributions and crown metrics (e.g., cratio, top-heaviness) further indicate that trees from pure thinned and provenance stands had lower reaching crowns. In contrast, trees in mixed and pure unthinned stands had more upper reaching crowns (Fig. 4). This phenomenon may be attributed to competition for light, which is intensified by a high stand density. For example, when sunlight is scarce, trees compete for it by extending their upper branches towards the canopy, which (competition) leads to a higher ratio of upper crown to lower crown (Oliver et al., 1996). However, in mixed stands, slower growth (low trw) could be attributed to higher tree age as we only considered last 40 years’ tree ring growth (see stand age in Table 1). However, trees from mixed stands faced competition and had shorter crowns, but showed higher growth than trees in pure unthinned stands (Figs. 3 and 4). This phenomenon could potentially be attributed to reduced competition for resources within the inter-neighborhood context, accompanied by facilitation advantages, indicating similar competition produced different consequences based on growing conditions (Aussenac et al., 2019; Pretzsch, 2021a; Yrttimaa et al., 2022). Furthermore, it could also be happened due to age of the stands.

However, thinning caused crowns to become more asymmetric, but tree ring growth to become more symmetric or regular (high cvcr but low cvtrw). This could be due to thinning and spacing, which increases the growing space by reducing competition, resulting irregular branch extension towards light (Ahmed and Pretzsch, 2023). Besides, trees tend to translocate more carbon to the stem as a resistance mechanism against winds to maintain stem stability (Donfack et al., 2022), ultimately increasing stem growth by increasing crown shape and tree ring (see Figs. 3, 4). Moreover, trees from the provenance trial exhibited relatively more symmetrical crowns and stable growth patterns. This could be attributed to reduced competition among different provenances, as detailed in Pretzsch (2021a). These findings underscore the idea that the same species can exhibit varied responses under different growing conditions and suggest that lowering the competition (by mixing or thinning) would benefit trees and promote higher growth by maintaining larger crowns.

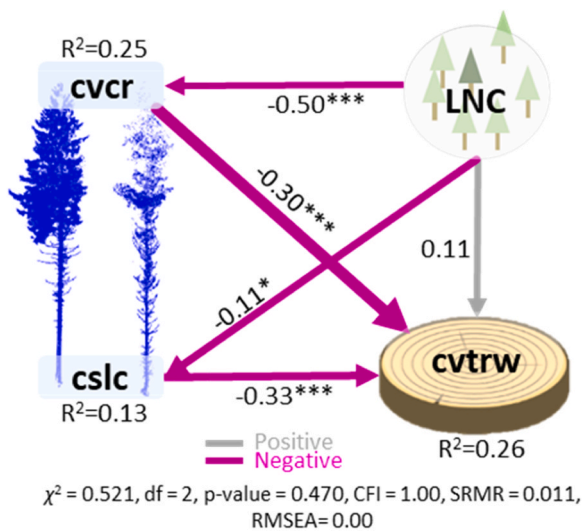


Fig. 8. Structural Equation Model (SEM) illustrating the complex relationships and pathways involving crown shape (cslc, cvcr), tree ring variability (cvtrw), and the influence of LNC. The model’s goodness of fit tests yielded the following results: $\chi^2 = 0.52$, $p = 0.47$, indicating a good fit to the data. Additionally, the Comparative Fit Index (CFI) was 1.00, and the Root Mean Square Error of Approximation (RMSEA) and Standardized Root Mean Square Residual (SRMR) were 0.00 and 0.011, respectively, both indicating no significant deviation from the model’s dataset. These results were obtained with 2 degrees of freedom. In the diagram, gray arrows represent positive effects between covariates, while pink arrows indicate negative effects. Numbers on the arrows indicate the standardized strength of the associations between predictors and dependent variables. The numbers beside the variables indicate the amount of explained variance (expressed as the coefficient of determination, R^2) by all the predictors. Furthermore, the adjacent path values represent standardized path coefficients and include significance levels denoted by asterisk signs (*** $p < 0.001$; ** $p < 0.01$; * $p < 0.05$). Line thickness indicates the magnitude or strength of the relationships.

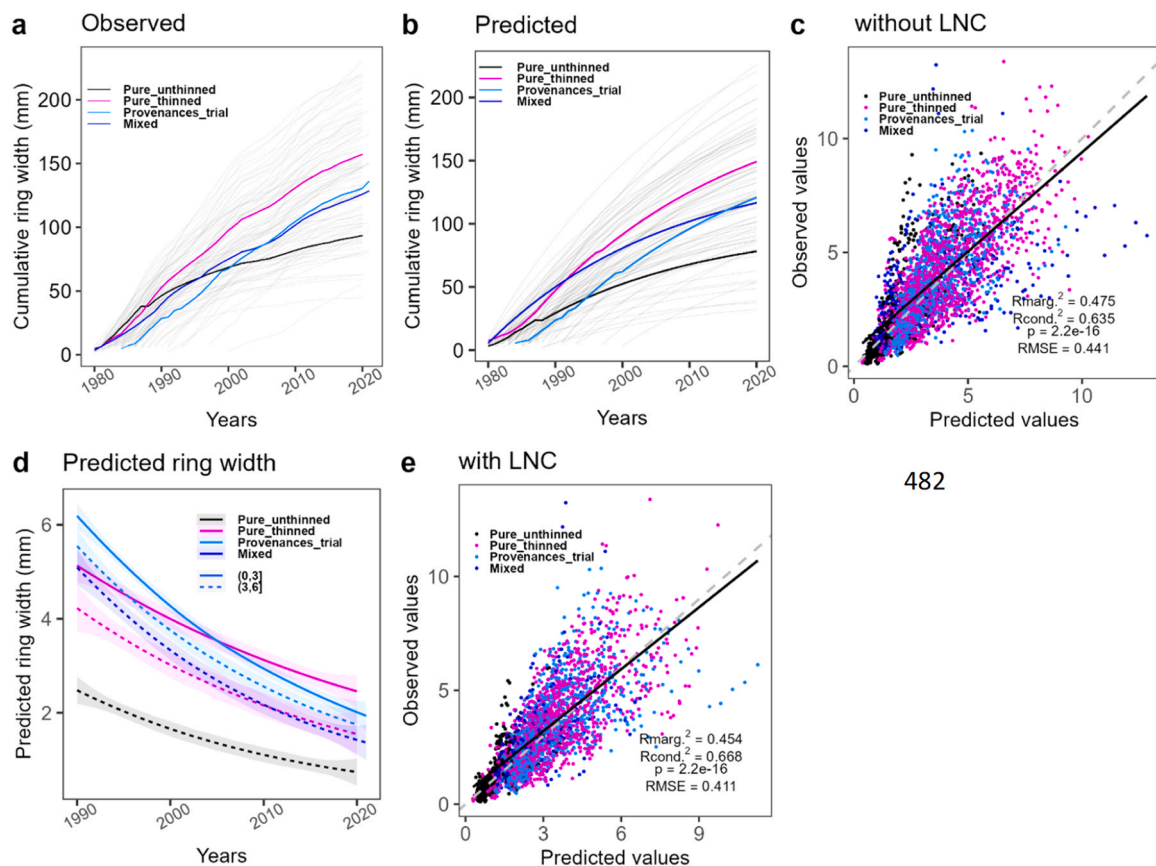


Fig. 9. Visualizing the growth curve prediction as some function of crown shape parameters (cvcr and cratio) and LNC₃₀. (a) Observed and (b) predicted cumulative tree ring width across stand types (interrogated from ring width). (c) the actual vs. predicted plot for tree ring width (trw). (d) ring width predictions across LNC₃₀ (e) the actual vs. predicted plot for tree ring width (trw) while with LNC considered. Shaded lines denote 95% CI. The black solid and grey dashed lines denote the predicted and 1:1 lines, respectively. R_{marg}^2 and R_{cond}^2 and RMSE denotes marginal, conditional R^2 , and root mean standard error, respectively, which are directly adopted from the model summary. The model summary is presented in ST4 and ST5. Note: tree ring width is incorporated into cumulative ring width for easy comparison.

4.1.2. Relationships between crown shape and tree ring patterns (HI)

We found a strong link between crown shape and tree ring patterns metrics across stand types (Fig. 5), suggesting competitive environment drives differences in morphology and growth while their association persists regardless of stand conditions. Interestingly, we found strong correlations between crown shape measurements (like crown radius, maximum crown radius - maxcr, and the height of maxcr) (that represent exposed crown parts to sunlight) and the patterns in tree ring growth (cvtrw) (Fig. 5). This observation aligns with findings from previous studies (Pretzsch, 2021b; Yrttimaa et al., 2022).

Our study found overall a negative correlation between coefficient of variation of crown radius (cvcr) and tree ring width (cvtrw), indicating irregular crowns produced more stable ring growth (Fig. 5). But, separating the observational data across stand types showed positive correlation between cvcr and cvtrw (albeit negative in provenances trial), which partly supports our first hypothesis (HI). Additionally, the crown shape metric such as cscl contributions was much higher than crown variability (cvcr) metrics across stand types (compare effect sizes in SF4), indicating overall crown size (wider or narrower) may be more important than crown variability to explain tree ring as crown size defines leaf area, photosynthesis and thereafter growth (Liu et al., 2021).

4.2. Stand types modulate CS-TRP relationships (HII)

Significant variations in crown morphology, ring patterns and CS-TRP link across different stand types underscore the potential impacts of stand types on the relationship between crown shape and tree ring

patterns. Our results suggest that stand types strongly modulate CS-TRP relationships and support our second hypothesis (HII). Similar results were also discussed in previous research, for example, species mixing modifies the allometry between crown structure and stem growth (Guisasola et al., 2015; Barbeito et al., 2017). More specifically, our investigation reveals that stand types (pure unthinned, pure thinned, mixed-provenances and mixed-species) interact uniquely and differently (crown and tree ring variability are in all stands except provenances trial) with crown shapes, exerting discernible influences on tree ring variability (cvtrw). These interactions with stand types emphasize the contextual nature of the effects (Fig. 6). For instance, the connection between crown shape and tree ring patterns shows its strongest manifestation in thinned stands (see the effect size -0.74 , and strong slope in prediction model), surpassing the influence observed in pure unthinned and mixed stands (compare effect sizes and slopes) (Fig. 6). This could have occurred due to management interventions or uneven data distribution. For example, different thinning-spacing trials result in a diverse range of crown shapes (Pretzsch et al., 2022), positively influencing tree ring patterns. Additionally, the interaction effect suggests that crown changes in unmanaged or minimally managed mixed stands might be less pronounced. This could be due to two factors: limited competition from a similar lack of management, or the trees simply benefiting from consistent local growing conditions over recent years. This lack of pronounced change contributes to the lowest levels of CS-TRP relationships, as indicated by interactions and the slope of predicted line in Fig. 6 and ST2. This observation highlights how manipulating competition through thinning for several years can have a lasting impact on growth

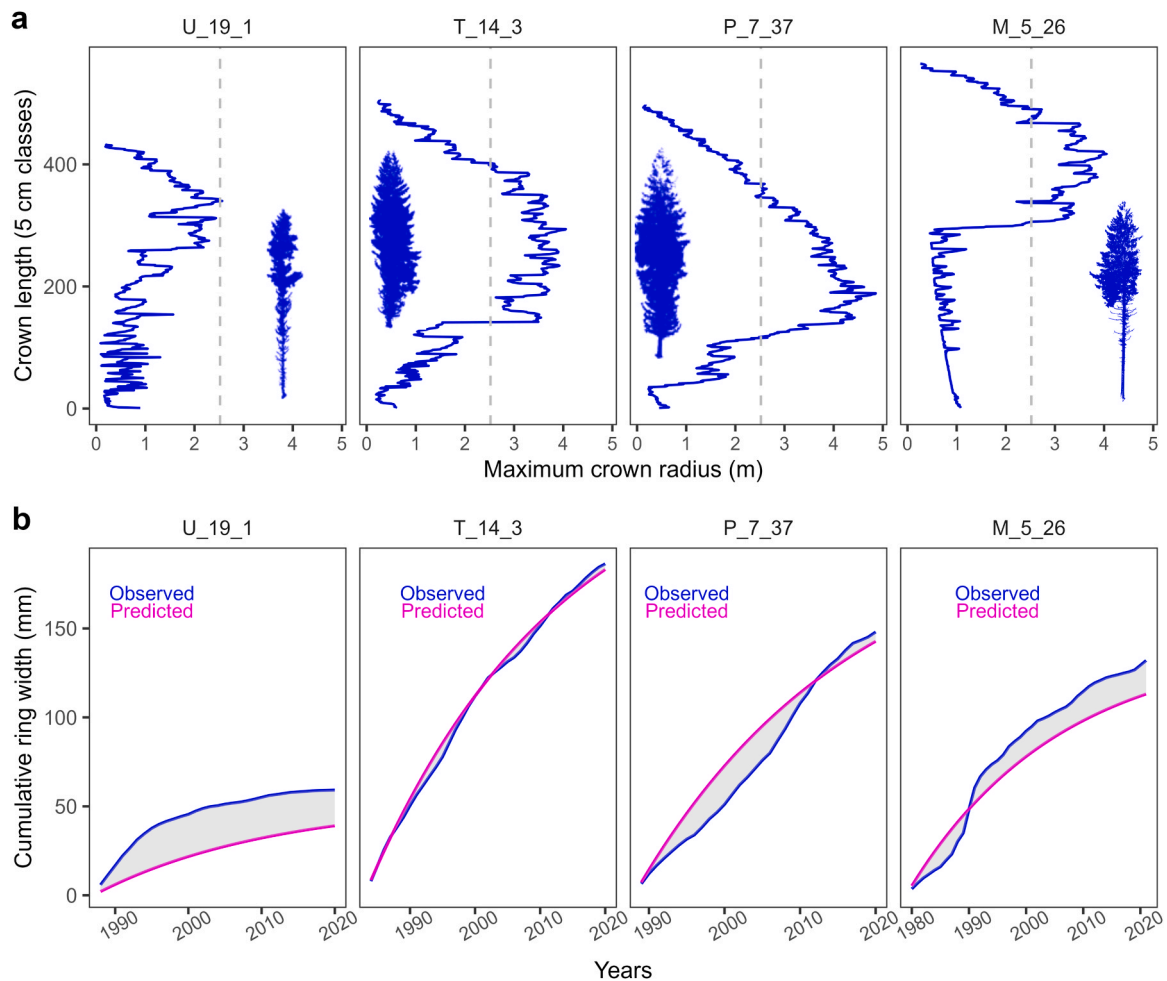


Fig. 10. Visualizing the different crown shapes (top row) and growth patterns of *N. Spruce* with management status (i.e., T, U, P, and M indicate pure unthinned, pure thinned, provenances trial, and mixed stands, respectively) and its comparative predictions (bottom row) for four individuals. Grey shaded area indicates the comparative area (i.e., the difference between observed vs. predicted lines).

conditions, significantly affecting crown shape and the resulting patterns in tree rings.

4.3. Neighborhood competition modulates CS-TRP relationships (HIII)

The interplay of competition and spatial distribution among neighbors significantly influences the intricate structure of the surrounding environment (Vieilledent et al., 2010; Pretzsch, 2014; Yrttimaa et al., 2022). Incorporating mean LNC into the CS-TRP model significantly modulated the CS-TRP link (which supports our hypothesis HIII) and enhanced model performance, as evident from AIC and RMSE values (Fig. 7, ST3). Building on previous research, our findings suggest that crown structure and competition have an even greater impact on stem growth when this additional factor is considered (Yrttimaa et al., 2022). Our findings indicate that LNC led to a reduction in tree ring variability when interacting with crown shape (Fig. 7a). This could be attributed to LNC causing a decrease in both crown size and tree ring width, ultimately resulting in consistently lower ring width growth. Consequently, growth reduction diminishes the width variability by reducing the likelihood of mixing high- and low-ring width growth combinations.

However, the competition-tree growth relationship is intricate. Notably, the CS-TRP linkage displayed significant differences between varying competition levels (Fig. 7b). For instance, when lower competition, the cvcr-cvtrw relationship slope remains relatively flat. This underscores the potential significance of competition in shaping tree growth patterns in specific levels competition.

Similarly, our structural equation model (SEM) also explained the similar things i.e., negative relationships between cvcr and cvtrw. SEM revealed that the local neighborhood competition (LNC) primarily modulates tree ring patterns in a triangular way (directly and indirectly) via modifying crown shape and variability (Fig. 8). More particularly, the indirect impact of LNC on cvtrw through modifying cvcr, csclw were stronger (cvcr = -30 and csclw = -0.33, $p < 0.001$) than direct LNC impact (LNC = 0.11, $p > 0.05$), which indicate LNC impacts mostly mechanized into crown. This aligns with Yrttimaa et al. (2022) explanation that growing conditions lead to initial crown structure changes, subsequently influencing stem growth. This could happen due to the light interception strategy, where trees with upper-reaching crowns try to maximize light interception before directing growth toward the stem (Oliver et al., 1996). This is evident from the beta distributions, as seen in pure unthinned stands where upper-reaching crowns coexist with limited stem growth (see Figs. 3, 4). Therefore, our finding suggests that competition's impact on tree growth goes beyond direct resource competition and encompasses indirect effects mediated by crown shape. However, unexplained variance (SEM explained 26% ring patterns) highlights that additional environmental factors (such as tree age, growing conditions for example climate, mixing proportion) also might influence tree ring development. Therefore, future research including these factors will most likely explain the missing information.

Besides, our study observed that the mixing proportion's impact was insignificant on the CS-TRP link (SF3). This lack of strong influence might be attributed to a couple of factors. Firstly, the uneven

distribution of our data sampling could play a role, as the dataset consisted of only around 20% from mixed-species stands and 80% from monospecific stands. Secondly, the effects of species mixing might predominantly manifest in the structural aspects and shape of the trees (see above discussion) rather than directly influencing the link between CS and TRP, as structural diversity might provide a more explanatory factor than species diversity alone, as suggested by Ali et al. (2016). Moreover, the manifestation and optimization of these effects might be closely tied to stand types. Another interesting factor could be that mixed-species neighborhoods might not significantly influence ring growth during normal (drought free) years. However, it is plausible that their influence becomes more apparent during periods of stress (i.e., drought), as indicated by Vitali et al. (2018). In comparison, the stress can also be minimized by mixing and facilitation phenomenon (Dănescu et al., 2018; Pardos et al., 2021).

This finding gives a foundational mechanistic understanding of how external tree appearances can be used to model and explain internal tree ring patterns by taking neighborhood competition into account. These results also indicate how silvicultural treatments can be applied in these relationships, as LNC can be managed by silvicultural treatments (Metz et al., 2013).

4.4. Growth curve based on crown shapes and competition legacy (HIV)

As SEM model explained, neighborhood competition (LNC) impacts is mostly mechanized into crown shape and variability therefore, by using cvcr and cslc, we predicted tree ring width (trw) to compare the growth curves across stand types. The primary objective of this analysis was to discern the extent to which the crown dimensions elucidate the tree ring growth. In this pursuit, we deliberately omitted the influences of LNC₃₀ legacy from the model despite our observation that their inclusion enhances the model's overall performance. However, our comparable results indicate that crown shape likely integrates the stand's growth conditions and environmental factors over the ages, while imprinting on the tree rings. Thus, crown shape can be considered as a proxy for ecological factors which drive tree ring growth. Although crown shape alone demonstrates the potential to predict internal growth patterns (as evidenced by evaluated models with an RMSE of 0.44 mm), incorporating growth conditions (for example LNC₃₀ legacy effect) enhanced predictive capabilities (as RMSE reduced to 0.41 mm) (Fig. 9). However, the interplay of these factors may lead to limitations in predicting growth patterns, as competition effects could be mechanized by crown shape and tree rings, indicating their mutual exclusivity.

Moreover, it should be noted that variability in crown width and crown length strongly changes with the growth conditions and produce heterogeneous growth patterns which may cause the underestimation of the whole growth (Júnior et al., 2020) as we have seen higher variability in growth rings in the mixed and pure unthinned stands (Fig. 9c). This underestimation is likely due to crown recession and loss of leaf area over time due to competition in these trees (compare sample trees from different stand types of Fig. 10a). Crown recession often occurs from historical maxima due to factors like competition and aging (Havreljuk et al., 2013). In contrast, predictions align more closely with observations for thinned and provenance stands, which have undergone less crown recession (with mostly intact crowns) and competition (Fig. 10). Therefore, including the LNC₃₀ legacy will likely cover that crown recession for particular trees that faced more competition and lost the part of crown. However, the limited crown recession in the cases of pure thinned and provenances trial may be attributed to lower density or genetic diversity. Reduced historical competition is often linked to genetic diversity and inter-provenance complementarity of tree allometry (see Pretzsch (2021a)). This observation further suggests that trees from thinned and provenance stands intercept and utilize more light, contributing to greater photosynthesis and wood growth rates (Rom, 1991). On the contrary, lower-reaching crowns (i.e., in pure unthinned stands) result in increased shading within the canopy, subsequently

limiting light interception and growth (Petrișan et al., 2009).

This result has strong implications for growth prediction incorporating crown changes caused by external influential factors (e.g., drought, wind damage, insect attack, topography and so on). However, studying past competition between trees along with different factors like rainfall, temperature, topography and species can further improve forest growth modeling from crown. This could help us manage forests more sustainably by letting us know how well we can swap traditional tree ring data with newer 3D crown measurements.

5. Conclusions

This study highlights how trees in different growth scenarios respond differently and adjust into crown and growth rings. Specifically, we found that high variability within crowns is associated with lower variability in tree ring width patterns, likely reflecting crown plasticity to optimize light capture under competition. Stand composition and management interventions like thinning and intermixing individuals of several provenances strongly modulate crown-ring linkages by altering resource availability and competition. Local neighborhood crowding influenced the crown shape and tree ring pattern relationships by directly influencing tree ring patterns and mostly indirectly via crown morphological adjustments. Therefore, crown shape can predict tree ring growth closely and promote a non-destructive and repeatable growth modeling approach. More precisely, leveraging these connections could improve tree- and stand-level growth predictions, better detect impacts from disturbances like drought or disease, and help to manage forests sustainably. However, further research should explore a broader range of species, growing conditions, and competitive environments. Furthermore, we measured crown structure at only one point, and future studies that include past measurements of crown structure would be useful.

Funding

This work is funded by European Union's Horizon 2020 research and innovation program under Marie Skłodowska-Curie Grant Agreement No. H2020-MSCA-ITN-2020-956355.

CRedit authorship contribution statement

Hans Pretzsch: Writing – review & editing, Supervision, Resources, Methodology, Funding acquisition, Conceptualization. **Bohdan Kolisnyk:** Writing – review & editing. **Miren del Río:** Writing – review & editing. **Martin Jacobs:** Writing – review & editing, Methodology, Data curation. **Luke Bohnhorst:** Writing – review & editing, Data curation. **Torben Hilmers:** Writing – review & editing, Supervision, Methodology, Conceptualization. **Enno Uhl:** Writing – review & editing, Supervision, Project administration, Conceptualization. **Shamim Ahmed:** Writing – review & editing, Writing – original draft, Visualization, Validation, Resources, Methodology, Investigation, Formal analysis, Data curation, Conceptualization.

Declaration of Competing Interest

The authors declare no competing interest.

Data availability

Link shared

Acknowledgements

The authors want to thank their colleagues from TUM for their assistance in collecting TLS and dendrochronological data. Special thanks goes to Mr. Gerhard Schmied for sharing the tree ring data for

pure stands. We also would like to thank Dr. Peter Biber, Julia Schmucker, and Chien Chen, Chair of Forest Growth and Yield Science, TUM School of Life Sciences, Technical University of Munich (TUM), who helped us during data analysis in R.

Appendix A. Supporting information

Supplementary data associated with this article can be found in the online version at doi:10.1016/j.foreco.2024.121839.

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