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From suppressed to dominant: 3D crown shapes explain the "to grow or wait" growth behavior in close-to-nature forests

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ABSTRACT

Crown plasticity enables trees to acclimate to competition and environmental stress, but how social strata and species-specific behavior modulate crown structure–secondary growth relationships remains poorly understood. We, therefore, tested three hypotheses in close-to-nature forests across wet (Germany) and dry (Spain) sites using terrestrial laser scanning and tree-ring width data of Norway spruce (*Picea abies* (L.) H. Karst.) and Silver fir (*Abies alba* Mill.) in Germany, and Stone pine (*Pinus pinea* L.) in Spain. We examined (HI) crown structure and radial growth are positively correlated and modulated by social strata and species-specific behavior; (HII) local competition and canopy space filling modulate the relationships across sites, (HIII) space-use efficiency varies across social strata and species behavior across sites. We observed that crown shape metrics and ring width variability were significantly correlated ($p < 0.05$), modulated by species and social identity. Dominant and codominant trees showed stronger relationships, while suppressed trees exhibited greater crown plasticity, allowing adaptive responses to canopy gaps. Spruce and fir adjusted crown structure under suppression, while pines maintained static crowns, decoupling structure from growth. Crown-growth relationships were influenced by neighborhood competition and canopy space filling ($p < 0.05$). Site-specific patterns emerged: wet sites had greater light competition, increasing canopy space filling and growth irregularity; dry sites were dominated by competition for water. Crown space- use efficiency also varied by species and social stratum. Dominant trees occupied more canopy space, but suppressed trees showed higher space-use efficiency especially by spruce and fir, by maintaining plastic crowns and waiting for more favorable light conditions. Despite similar biomass investment, dominant spruce and fir had higher space-use but lower biomass-use efficiency, while suppressed trees invested biomass more efficiently, signaling growth potential. These results show that asymmetric crown plasticity drives a grow or wait strategy across strata, informing precision forestry interventions for climate-adaptive forest management.

1. Introduction

Forests are dynamic ecosystems characterized by intricate interactions among trees and the surrounding environment. A critical aspect of this interaction relates to crown plasticity, which can be explained as the ability to adjust crown shape and structure to light availability, impacted by competition. Crown plasticity enables trees to balance structural costs with photosynthetic efficiency, which both affect survival and growth strategies (Seidel et al., 2011; Forrester et al., 2018; Seidel et al., 2019; Hess et al., 2024; Owen and Lines, 2024). The crown shape impacts photosynthesis (Grams and Andersen, 2007; Fischer and Jucker, 2023), with the assimilated carbon allocated into woody stem tissue (Lehnebach et al., 2018; Lines et al., 2022), which explains the strong link between crown structure and radial growth patterns (Sharma et al., 2017; Kröner et al., 2024; Ahmed et al., 2025). Therefore, understanding tree growth dynamics through 3D crown

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shape and its plasticity is critical in forest growth modeling (Jacobs et al., 2021; Pretzsch, 2021a; Yrttimaa et al., 2022). Despite its strong significance in forest growth modeling, the quantification of the link between crown structure and secondary growth patterns has been largely limited due to traditional measurement methods (Pretzsch et al., 2022). However, terrestrial laser scanning (TLS) offers new opportunities to accurately characterize crown shape and structure (Calders et al., 2020; Lines et al., 2022). Building on this, recent studies have shown that 3D crown shape quantified using TLS can reveal patterns in tree secondary growth (Yrttimaa et al., 2022; Ahmed et al., 2024; Kröner et al., 2024; Ahmed et al., 2025). However, no studies have yet quantified this link in plenter or close-to-nature forests to understand tree growth behavior across social strata.

In recent years, there has been growing pressure to develop more species and structurally diverse forest ecosystems that are resilient to climate change (Spiecker, 2003; Millar et al., 2007; Bauhus et al., 2013; O'Hara, 2016; Kolisnyk et al., 2025). The role of tree crown structure and plasticity has emerged as critical for acclimatization to these environmental shifts (Millet et al., 1999; Jucker et al., 2015) in these ecosystems. In close-to-nature or multi-layered forests, crown plasticity facilitates complex interactions among trees, enhancing resource acquisition under varying conditions and shaping forest structure, function, and canopy stratification into distinct tree social strata (Rouvinen and Kuuluvainen, 1997; Strigul et al., 2008; Norby et al., 2022). Across social strata, dominant trees in the upper canopy develop expansive crowns (to occupy space efficiently) to maximize light capture, with the suppression of neighboring individuals likely being an indirect consequence of this strategy. In contrast, to maximize light capture, trees persisting in the shaded understory adopt narrower, top-heavy crowns, often waiting several decades for growth opportunities (Antos et al., 2005; Seidel et al., 2011; Forrester et al., 2017; Mohan et al., 2017). In these low-light environments, diffuse light becomes relatively more important, shaping crown development strategies (Petriţan et al., 2009; Orman et al., 2021). These divergent behaviors—to grow or to wait—reflect a tradeoff between radial growth, height growth, and structural persistence, mediated by species-specific growth strategies (shade-tolerant vs. light-demanding), local competition, and flexibility to adjust growth during repeated suppression–release cycles before reaching the canopy (Pretzsch and Schütze, 2005; Gao et al., 2023; Pavlin et al., 2024). Such divergent behavior of social strata creates a complex web of interaction within the forest stands and drives tree potential and overall growth (Attis Beltran et al., 2013; Ugarković et al., 2021; Jazbec et al., 2023). While it is recognized that trees adjust their crown shape in response to neighborhood competition (Ahmed et al., 2024), our understanding of how these structural adjustments vary across social strata — from dominant to suppressed individuals — remains limited. In particular, how crown plasticity supports long-term persistence and light capture under varying competitive pressures is still not fully understood.

In close-to-nature forests, trees often grow in dense, multi-layered canopies where intense competition occurs across social strata, especially those in understories. This competition is driven by differences in light availability, and crown architecture, which collectively shape tree growth and structure (Spitters, 1980; Oliver et al., 1996; Pretzsch and Schütze, 2005; Ahmed et al., 2024). Light competition, in particular, plays a pivotal role in determining crown development and radial growth patterns (Pretzsch, 2009; Metz et al., 2013; Ahmed et al., 2024). Therefore, the tradeoff between adjusting crown shape and maintaining secondary growth is influenced by interspecific and intraspecific competition, species behavior, and social position, and thus, critical for crown structure–radial growth relationships (Attis Beltran et al., 2013; Hess et al., 2024; Ahmed et al., 2025). Despite advances in understanding crown plasticity, critical knowledge gaps persist; for example, we have a limited understanding of how transitions in social class (e.g., suppressed trees becoming dominant) combined with neighborhood competition modulate crown-growth relationships, particularly in mixed, unmanaged forests. Moreover, local growing conditions, such as surrounding species, their intermixing, and competition for resources, such as light and water availability, may complicate crown shape and secondary growth relationships across social classes. For example, in dense neighborhoods, trees often exhibit pronounced crown asymmetry as a manifestation of crown plasticity, which enables adaptive responses to light competition (Barbeito et al., 2014; Díaz-Varela et al., 2015; Barbeito et al., 2017), which might induce higher variability in growth patterns (Ahmed et al., 2024; Liu et al., 2025).

Competition-driven canopy space filling is another important factor in mixed forests. To escape competition, trees develop highly plastic crowns, adjusting their spatial arrangement to maximize canopy occupation (Ishii and Asano, 2010; Pretzsch, 2014; Ray et al., 2024). Canopy space filling refers to the proportion of space occupied by crown volume relative to unoccupied gaps within the canopy (Pretzsch, 2014; Jucker et al., 2015). Many studies have linked stand-level canopy filling or packing with species richness due to species complementarity and niche differentiation (Fichtner et al., 2013; Pretzsch, 2014; Kunz et al., 2019; Perles-Garcia et al., 2021; Ray et al., 2024), a pattern often observed in close-to-nature forests. However, while research has examined canopy filling and structural complexity at the stand level (Pretzsch, 2014; Jucker et al., 2015; Juchheim et al., 2017), little attention has been given to how local canopy filling influences the link between crown structure and secondary growth, which remains poorly understood. When species with compact crowns (e.g., spruce, *Picea abies* (L.) H. Karst.) mix with those having more transparent crowns (e.g., beech, *Fagus sylvatica* L.), traditional competition indices may suggest strong competition for light (Seidel et al., 2011; Forrester et al., 2018). However, light transmission through transparent crowns can modify growth dynamics, reducing competitive pressures. To fully understand the effects of species mixing, it is crucial to consider how local canopy structure influences light distribution at the tree level. Ehbrecht et al. (2017) and Koller et al. (2025) explained that canopy filling and complexity can be shaped by individual tree characteristics, including their inner and outer crown structures. Therefore, we expect each tree to fill canopy space at different levels, as neighboring species influence how space is shared. These competition-driven local canopy space dynamics could be a key factor shaping crown structure and growth patterns in mixed stands, where light availability is a major driving force.

This study examines how tree crown structure and shape, and secondary growth relate to competition and growing conditions in close-to-nature forests (Fig. 1a), with the idea that suppressed trees maintain static crown form while waiting for better direct light conditions. In contrast, trees in the dominant class may capture more light and grow faster, enabling rapid structural changes. As they age, energy shifts toward reproduction, reducing their focus on structural development (see Fig. 1b). Therefore, the link between crown structure and secondary growth is expected to vary between their social strata, their behavior (light-demanding or shade tolerant), and growing sites (wet or dry) (Fig. 1c, d) with modulation within the neighborhood (Fig. 1e).

Therefore, we tested three specific hypotheses to understand these dynamics. (HI) crown shape and radial growth patterns are positively correlated and modulated by tree social strata (suppressed to dominant) and species-specific behavior (light-demanding vs. shade-tolerant) across sites (Fig. 1b); (HII) Local competition and canopy space filling lead to irregular crown shapes and tree rings, which, in turn, modulate the relationship between crown structure and ring growth across different sites (Fig. 1c), (HIII) canopy space-use efficiency varies across social strata and species behavior (dominant trees may occupy more canopy space, suppressed and shade-tolerant trees often use the available space more efficiently) across sites (Fig. 1d).

To test the hypotheses, we selected three ecologically distinct coniferous species— Norway spruce (*Picea abies* (L.) H. Karst.) (light-demanding, moderately shade-tolerant), Silver fir (*Abies alba* Mill.) (highly shade-tolerant), and Stone pine (*Pinus pinea* L.) (light-demanding and adapted to dry conditions) across social

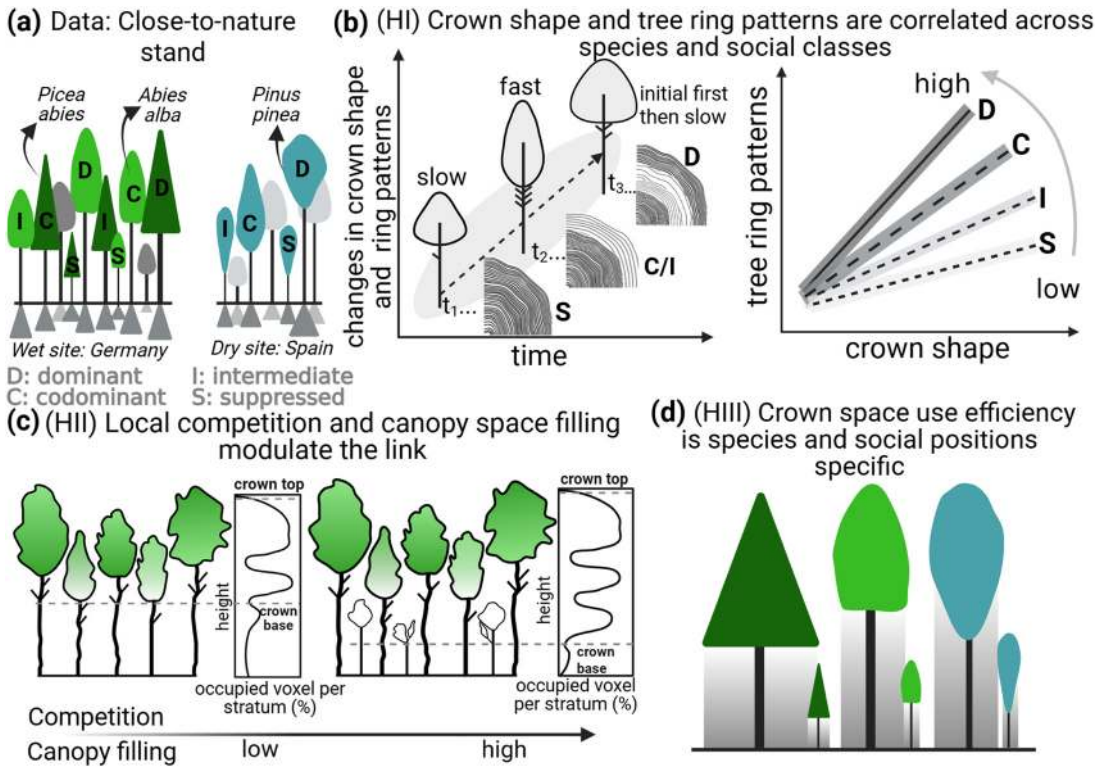


Fig. 1. Conceptualization of the hierarchical structure and development trajectories of trees in close-to-nature forests (panel a), focusing on phenotypic and inner-tree morphological changes (panel b) over time. (b) At t_1, suppressed trees grow slowly, resulting in narrow rings. However, as competition decreases (e.g., due to nearby tree death), growth accelerates, rings become wider, moving them to intermediate→ codominant →dominant status by t_2 and t_3. Crown shape and tree ring pattern relations: expected variations across social strata, with grey-shaded areas indicating potential variation. (c) Competition and canopy filling: effects of local competition and canopy space filling on the link between crown shape and tree ring patterns based on site conditions. (d) Link varies across species; therefore, space occupation, exploitation, and biomass investment efficiency depend on species' behavior and social strata. Tree social strata (suppressed, intermediate, codominant, and dominant) are grouped based on Wertz et al. (2020).

strata—representing a gradient of ecological niches (light demanding and shade tolerant) and site adaptability (dry and wet conditions). These species, widely distributed across European forestry systems, were prioritized for their contrasting resource acquisition strategies and silvicultural resilience, highlighting their potential for future forestry practices.

2. Materials and methods

2.1. Study site descriptions, plot, and tree selection

This study focuses on close-to-nature forest ecosystems in two distinct European sites: Bodenmais, Germany (49° 5′ 12.57" E, 13° 5′ 27.14" N) and Llano de San Marugán, Portillo (Valladolid), Castilla y León, Spain (41° 25′ 37.1″ N, 4° 34′ 15.2″ W). The Bodenmais site, located in the Bavarian forest region of Germany, features mountainous terrain ranging from 500 to 1450 m above sea level. The climate is cool and humid, with a mean annual temperature of 6–8°C and annual precipitation of ~1200 mm, classifying it as a wet site (data collected from two plots divided into four subplots but in the same site). The forests consist of mixed stands dominated by Norway spruce (*Picea abies* (L.) H. Karst.), along with co-occurring Silver fir (*Abies alba* Mill.) and European beech (*Fagus sylvatica L.*). These stands have remained unmanaged since 2011 and minimally managed since at least 1980, allowing for natural structural and compositional development, enabling natural structural and compositional development (Pretzsch, 1985; Pretzsch, 1996). In contrast, the Llano de San Marugán site in Spain represents a Mediterranean woodland ecosystem at 750 to 900 m elevation, characterized by a warmer and drier climate with a mean annual temperature of 12°C and annual precipitation of approximately 500 mm. The region experiences irregular rainfall, with summer precipitation dropping to as low as 64 mm, accompanied by hot, dry summers averaging 30°C. The vegetation is dominated by Stone pine (*Pinus pinea* L.), interspersed with resprouting oaks (*Quercus faginea* Lam. and *Quercus ilex* L.) and naturally regenerating junipers (*Juniperus thurifera* L.). Like the German site, Marugán stands have been minimally managed over the last 30 years, allowing natural structural dynamics (see plot details in Bravo et al. 2021).

A total of 109 trees were sampled across both sites, stratified into four social strata (dominant, codominant, intermediate, suppressed) following Wertz et al. (2020). Trees were classified into different social strata based on their crown positions within the 3D canopy. Sampling focused on individuals growing in different competitive regimes (open canopy to highly dense canopy) to assess growth patterns and adaptive strategies. Data were collected across three permanent monitoring plots (two in the German site, each 0.5 ha, and one in the Spanish site, 1 ha), with comprehensive monitoring records available (Table 1), enabling precise contextualization of environmental and anthropogenic influences.

2.2. Terrestrial (TLS) and mobile laser scanning (MLS) data acquisition and crown structure characterization

Field data collection commenced during the leaf-off season in Spain in March 2023 and in Germany in March 2024. Terrestrial laser scanning (TLS) in Germany was performed using a RIEGL VZ-400i scanner (RIEGL Laser Measurement Systems GmbH, Austria) across permanent experimental plots. To mitigate occlusion effects and optimize crown structure capture, each German plot was scanned from multiple positions spaced approximately 5 m apart, with scan density adjusted according to plot

Table 1
Summary statistics of crown shape and tree ring metrics across sites and species (mean ± SD) with the number of samples. See Sections 2.2 and 2.3 for abbreviated forms. In total, we used data from two plots in Germany and one plot in Spain.

Sites	Species	Trees	DBH (cm)	h (m)	meantrw (mm)	cvtrw	cbh (m)	cl (m)	cvcr	cr (m)	maxcr (m)	hmaxcr (m)	cpa (m^3)
Germany (wet)	spruce	31	39.50 ± 19.77	24.95 ± 8.04	1.28 ± 0.61	0.55 ± 0.15	7.78 ± 4.47	17.17 ± 7.05	0.27 ± 0.04	3.49 ± 1.07	4.02 ± 1.17	11.65 ± 5.83	25.91 ± 15.84
	fir	24	37.71 ± 20.80	21.60 ± 8.72	1.30 ± 0.58	0.52 ± 0.13	4.48 ± 2.04	17.12 ± 7.63	0.27 ± 0.04	3.71 ± 0.98	4.18 ± 1.07	10.49 ± 5.57	29.73 ± 14.35
Spain (dry)	pine	54	28.61 ± 13.06	8.13 ± 1.97	1.42 ± 0.32	0.61 ± 0.12	2.63 ± 1.01	5.50 ± 1.21	0.36 ± 0.09	4.03 ± 1.84	4.90 ± 2.10	2.65 ± 0.82	27.21 ± 19.27

dimensions. Artificial reflectors were deployed as fiducial markers to facilitate the precise alignment of individual scans.

Raw point cloud data were registered or aligned to a local coordinate system and denoised using an octree-based outlier detection algorithm implemented in RiSCAN PRO (v2.10.1, RIEGL GmbH, Austria). This process reduced scatter and noise through octree-based filtering, enhancing post-processing efficiency. The point clouds were voxelized using a 5 cm^3 grid to generate a standardized dataset invariant to scanner type or scan density. A hybrid workflow was implemented to mitigate errors in automated tree isolation: reflector-tagged trees were manually segmented and algorithmically refined to resolve overlaps with adjacent vegetation from TLS data. High-resolution single-tree point clouds enabled crown stratification via polar coordinate classification, which supported the extraction of layered crown structure metrics (Fig. 2, Supplementary Fig.1). The RIEGL VZ-400i TLS, with its higher angular resolution (0.002°), provided enhanced detail for dominant canopy trees in German plots. This workflow ensured compatibility with dendrochronological data derived from increment cores, enabling integrated analysis of structural plasticity and radial growth responses.

In Spain, point cloud data were acquired using a ZEB-Horizon handheld mobile laser scanner (MLS) (GeoSLAM Ltd., Nottingham, UK), following the protocol and the data processing workflow described in Tupinambá-Simões et al. (2024). MLS raw point cloud data were registered and denoised using an octree-based outlier detection algorithm implemented in LIDAR360 software (GreenValley International, v6.0). In MLS data, tree positions were georeferenced with sub-centimeter precision using a Topcon OS-200 total station and SR-series geodetic receivers (Topcon Corporation, Japan) (see Ahmed et al., 2025).

Initial post-processing of MLS data included automated tree isolation in LIDAR360, followed by manual refinement of overlapping crowns in CloudCompare (v2.13.1) (Girardeau-Montaut, 2016). To ensure analytical rigor, trees with incomplete crown tops or excessive occlusion due to adjacent vegetation—severally suppressed individuals in dense understories—were systematically excluded. This curation minimized

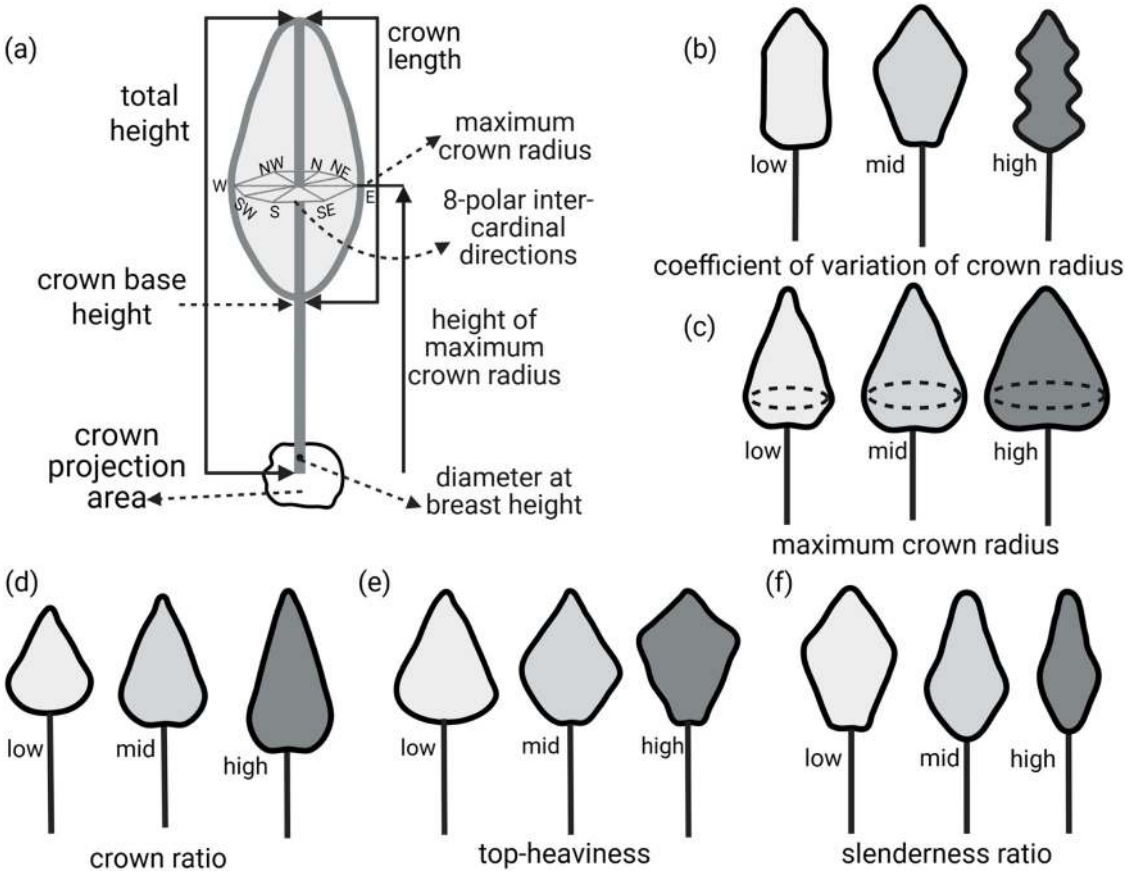


Fig. 2. Characteristics and variability of tree crown structure metrics. (a) Basic crown structure metrics, including total height (h), Diameter at breast height, DBH, crown length, cl, crown base height, cbh, height of maximum crown radius, hmaxcr, crown projection area, cpa, (b) coefficient of variation of crown radius, cvcr, (c) maximum crown radius, maxcr, (d) Crown ratio (cl/h), (e) top-heaviness, th, (h - hmaxcr), (f) slenderness ratio, cslc, (cl/cr).

artifacts in 3D crown reconstruction and growth pattern quantification.

Despite inherent challenges in capturing closed-canopy forests with MLS (Liang et al., 2016), the ZEB-Horizon achieved sufficient point density (>500 pts/m^2) and geometric accuracy for crown metric extraction (Ducey et al., 2013; Ahmed et al., 2025). This performance was attributed to the relatively small stature of sampled trees (<15 m mean height) and the open structure of studied stands (stand density <400 trees/ha).

Post-processed single tree point clouds were analyzed in R (v4.3.0) (R Core Team, 2023) using a multi-package analytical pipeline: the "lidR" (Roussel et al., 2020) was used for voxel-based crown estimation and convex hull delineation. The "dbscan" (Hahsler et al., 2019) was used for density-based clustering and branch hierarchy identification, and the "VoxR" (Lecigne et al., 2018) was used for voxel occupancy profiles and 3D fractal dimension calculations.

2.2.1. Information on metrics for crown structure and shape

All metrics were conceptualized to ensure understanding and biological interpretability (Fig. 2). To characterize the crown shape and test the hypotheses, we used 3D crowns and calculated the following tree and crown metrics: total tree height (h), the height of the crown base (cbh), and crown length (cl). The h was determined by subtracting the Z-axis minimum from the Z-axis maximum of the isolated tree point cloud. The crown length (cl) was calculated as cl = h−cbh, representing the vertical distance from the crown base to the tree top. The cbh was defined as the height of the lowest primary branch, manually identified in the point clouds as the first branch with needles (Pretzsch et al., 2022).

The crown structure was analyzed by dividing it into 5 cm vertical height classes. Each height class was split into eight polar coordinate categories to assess crown expansion metrics (Fig. 2 and SF1). This process yielded detailed crown radii for all height classes and directions. The maximum crown radius (maxcr) was the largest radius detected, with larger values indicating trees with wider crowns (Fig. 2c). The height of the maximum crown radius (hmaxcr) was the mean height of the respective class containing maxcr. The crown projection area (cpa), representing the horizontal area the crown covers when projected onto the ground, was also calculated. Additionally, to characterize crown shape better and link to growth patterns, several other shape metrics were defined to quantify crown variability and shape (Fig. 2b-f):

2.2.1.1. Coefficient of variation of crown radius (cvcr). Measures the variability in crown radii (calculated as the standard deviation of crown radii measured in multiple directions around the tree, divided by their mean). Higher cvcr values indicate more irregular and asymmetrical crowns (Fig. 2b).

2.2.1.2. Crown ratio (cratio). The proportion of tree height occupied by the crown, calculated as cl/h. A high cratio suggests a larger crown relative to tree height (Fig. 2d).

2.2.1.3. Top-heaviness (th). The ratio of the maximum crown radius (maxcr) to the distance between its position and the tree tip (th = h - hmaxcr). A higher th value indicates the crown's relative position and width near the top (Fig. 2e).

2.2.1.4. Crown slenderness ratio (cslc). The ratio of crown length to crown radius, cl/cr. Higher cslc values indicate trees with long, narrow crowns (Fig. 2f).

2.3. Tree ring data processing and information on pattern characterizations

A total of 208 tree-ring cores (from 109 trees) were collected from the three studied species. Each tree, scanned and isolated from point clouds, was cored in two directions at 130 cm height: north and east. The cores were dried, glued to wooden boards, and sanded with progressively finer abrasive paper (from 120 to 800 grit) to enhance the visibility of tree-ring boundaries and ensure accurate identification of annual rings.

Measurements were taken from bark to pith in all the cores, with a precision of 0.01 mm, using the Lintab 5 digital positioning table and TsapWin software (Rinntech, Heidelberg). The resulting growth curves were visually cross-dated by comparing growth years across all cores by sites (Ahmed et al., 2025) and statistically verified using the "dplR" package in R (Bunn, 2008). To minimize biases from crown development, we analyzed only the most recent 70 years of growth in trees older than 70 years. Older growth patterns were excluded, as current crown attributes are likely not representative of growth attributes beyond this period. Instead, existing and accumulated crowns primarily manifest growth trajectories from the past 5 to 70 years (Pretzsch, 2021b; Ahmed et al., 2025).

The two ring-width measurements from the north and east cores were averaged for each tree to create a single growth series. The average chronologies were used to characterize the growth patterns. We used a set of measures and metrics to analyze the relationship between the present crown structure and the present and past stem growth regarding the tree ring patterns. The following four variables characterized the course of the stem secondary growth.

The coefficient of variation of the tree ring width (cvtrw) represents the smoothness or variability of the tree ring growth; the higher value indicates higher irregularity. Mean tree ring width (meantrw): represents the average tree ring width over a period, reflecting growth rate. Higher values indicate faster growth; lower values suggest slower growth. Mean basal area increment (meanbai): represents the annual increase in the tree's basal area, reflecting overall growth and health. meanbai was calculated using the "bai.out" function from the "dplR" package in R, applying the analysis from the bark inward to the pith (Bunn, 2008). Higher values signify robust growth. Basal area (ba): describes the cross-sectional area of the tree trunk at breast height, indicating tree size, and is often used for estimating forest timber volume.

2.4. Local neighborhood competition index and canopy space-filling calculation

We employed two complementary metrics to quantify these competitive interactions at the individual tree level: the KKL (Kronenkonkurrenz um Licht) competition index and competition-driven local canopy space-filling (LCSF).

To assess light-driven competition among neighboring trees, we used the distance-dependent KKL competition index (see Fig. 3a, b, and Pretzsch 2009). This index accounts for competitors' spatial proximity and size asymmetry relative to a target tree, making it particularly effective for modeling competition in dense stands. Calculations were performed using the "TreeCompR" R package (Rieder et al., 2024), which integrates tree coordinates, crown dimensions, and competitive status (see Fig. 3a, b). Distance-dependent indices like KKL are widely recognized for improving single-tree growth prediction accuracy by capturing fine-scale neighborhood effects (Weiskittel et al., 2011).

To evaluate the competition-driven interspecific competition and species mixing effects on crown plasticity and growth, specifically how they occupy the canopy at the local level, we calculated local canopy space-filling (LCSF). This metric quantifies the proportion of available 3D canopy space occupied by tree crowns within a defined area, reflecting resource-use efficiency and canopy complementarity (Pretzsch and Schütze, 2005; Ray et al., 2024). LCSF is strongly correlated with species diversity, as mixed stands often exhibit canopy stratification, though the specific arrangement of shade-tolerant and light-demanding species varies by forest type and region (Ehbrecht et al., 2017; Juchheim et al., 2017; Ray et al., 2024). To calculate LCSF,

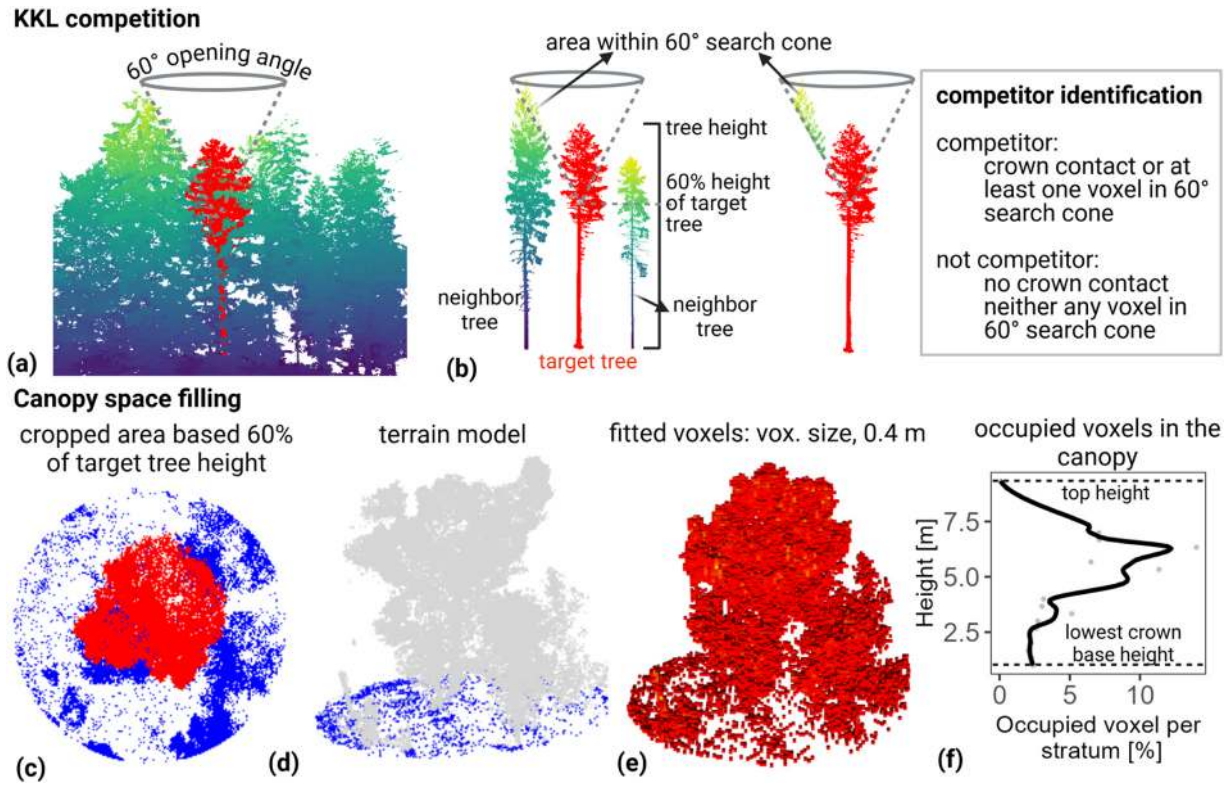


Fig. 3. Steps in calculating KKL competition and local canopy space-filling (LCSF). (a) Identifying the parts of neighboring tree crowns that fall within a 60° search cone, positioned at 60 % of the target tree's height. (b) Displaying the identified competitor trees separately. From Figs. (c)~(f) Showing local canopy space filling calculation steps. (c) Point clouds of a subplot with a target tree in red color. (d) Canopy height model, separating the soil surface from the above-ground point cloud. (e) voxelized point clouds using a voxel size of 0.4 m edge length. (f) Occupied voxels per strata: occupied voxels between the lowest crown base height and the highest tree height within the subplot.

we followed three crucial steps as follows:

2.4.1. Subplot delineation

We defined a circular subplot with a radius equal to 60 % of the tree's height for each target tree to standardize the analysis scale (Fig. 3c). The center of the subplot is positioned at the stem of the target tree.

2.4.2. Voxelization

The vertical canopy space (from the highest treetop to the lowest crown base) within each subplot was divided into 0.4 m^3 voxels using LAStools (Béland et al., 2011; Ray et al., 2024). This resolution balances occlusion mitigation and computational efficiency (Fig. 3e).

2.4.3. Occupancy analysis

LCSF was derived as the percentage of voxels occupied by crowns relative to the total voxelized space (Seidel et al., 2013) (see Fig. 3e-f).

In dense understory conditions, accurately identifying the lowest crown base posed challenges due to overlapping vegetation (e.g., shrubs, regeneration). To prevent overestimation of LCSF, crown bases were manually verified and adjusted through 3D point clouds visualizations. This step ensured a robust spatial representation of canopy occupancy.

2.5. Statistical analyses

All statistical analyses were conducted in R (version 4.3.3; R Core Team 2023).

2.5.1. Hypothesis I (HI)

We initially combined the data to test the first hypothesis, HI, i.e., the relationships between crown shape and tree ring metrics across species and social classes. We developed a correlation matrix and principal components analysis (PCA). The correlation matrix and PCA further helped to address the redundancy and collinearity among variables, summarizing crown variables and facilitating growth pattern modeling. It also allowed us to explore groupings across species and social classes to find similar characteristics.

Before PCA, all numerical variables were normalized and scaled using R's "scale()" function. PCA was performed with the "prcomp()" function, where tree ring metrics were treated as response variables, crown shape variables as predictors, and species and social classes as replicates. To standardize, the mean value of each variable across species was subtracted and divided by its standard deviation.

To investigate how the relationship between crown shape metrics and tree ring patterns varies across species and social classes, we also analyzed the link between tree ring patterns and specific crown shape metrics by treating species and social class as factors. The coefficient of variation in tree ring width (cvtrw) was evaluated concerning crown shape metrics, including crown ratio (cratio), top-heaviness (th), crown slenderness (cslc), and coefficient of variation in crown radius (cvcr). For biological interpretability, we fitted log-log bivariate relationships between cvtrw and crown shape metrics, following the approach explained by Tian et al. (2024). This approach allowed us to better understand growth variability and the influence of crown shape across species and social classes.

2.5.2. Hypothesis II (HII)

To test hypothesis HII, i.e., to understand the combined effect of crown variables and how competition and canopy space filling modulate the crown-tree ring patterns link, we applied a linear mixed model using the "lmer()" function from the "lme4" package (Bates, 2010), by combining all data. In the global models, local neighborhood

competition (KKL) and local canopy space-filling (LCSF) were included as interacting variables with crown metrics. The most parsimonious model was selected and presented across sites (Eqn. 1). Social strata within sites were included as a random effect. In the second stage, we fitted two separate models for both sites (Germany and Spain), relating the observed variations in PCA. In Germany, or wet site, spruce and fir overlap in characteristics compared to pine from Spain (see the PCA); therefore, we grouped them and fitted a linear mixed model by putting social class and species as a random effect. Besides, Spanish data come from a single site and are based on a single species; thus, we fitted another mixed effect model with LCSF and KKL as an interaction and social class as random effects and the best parsimonious model is selected (Eqn. 3). However, we did not fit separate models to check combined effects for each social class group due to limited data availability for particular social groups.

$$\ln(cvtrw_i) = a_0 + a_1 \ln(cvcr_i) + a_2 \ln(cpa_i) + a_3 \ln(LCSF_i) + a_4 \ln(cpa_i)\cdot \ln(LCSF_i) + b_j + \varepsilon_i \text{(Eqn. 1)}$$

$$\ln(cvtrw_i) = a_0 + a_1 \ln(maxcr_i) + a_2 \ln(cpa_i) + a_3 \ln(LCSF_i) + a_4 \ln(maxcr_i)\cdot\ln(LCSF_i) + a_5 \ln(cpa_i)\cdot\ln(LCSF_i) + s_k + \varepsilon_i \text{(Eqn. 2)}$$

$$\ln(cvtrw_i) = a_0 + a_1 \ln(cpa_i) + a_2 \ln(cvcr_i) + a_3 \ln(KKL_{i+}1) + a_4 \ln(cpa_i)\cdot\ln(KKL_{i+}1) + a_5 \ln(cvcr_i)\cdot \ln(KKL_{i+}1) + l_m + \varepsilon_i \text{(Eqn. 3)}$$

$a_0,\ldots,a_5$ are fixed regression coefficients. b_j, s_k, and l_m are the random effects for site, species k, and social strata l_m are assumed to be normally distributed with mean zero and variance $\sigma^2_{\alpha j}$. ε_i is the residual error, assumed to follow $b_j \sim N(0, \sigma^2_b)$, $s_k \sim N(0, \sigma^2_s)$, and $l_m \sim N(0, \sigma^2_m)$. The random effects b_j, s_k, and l_m are independent across sites, species, and social classes, respectively, and the residual errors ε_i are independent across observations. In Eqn. 3, KKL_i (e.g., some additional scaling or correction factor), is transformed as ln(KKL+1) to avoid issues with zero values.

Model selection was guided by multimodel inference, identifying the best model to explain tree ring growth variability (cvtrw) through crown variables. Predictor variables with a variance inflation factor (VIF) above 3 (VIF>3) were removed to reduce multicollinearity, calculated using the "vif()" function from the "car" package (Fox et al., 2012). This process was repeated until all variables had VIF < 3 (Akinwande et al., 2015).

The final model selection procedure based on Akaike's information criterion (AIC) was used to select the best models. Those models with the lowest AIC were considered final models (Burnham and Anderson, 2004). These final models' marginal R^2 (R^2_m) was reported in subsequent analyses. This procedure was performed by the dredge function in the "MuMIn" package (Barton, 2010). Marginal R^2 values quantified the variation in tree ring growth explained by each crown fixed effect. The final model was validated using the "performance" function from the performance package (Lüdecke et al., 2021), comparing predicted and observed values while assessing AIC, R^2, and RMSE (root mean squared error). Residual diagnostics were conducted by checking residuals against fitted values to determine fit and bias, and Q-Q plots were used to evaluate residual normality (Piñeiro et al., 2008; Ahmed et al., 2025).

2.5.3. Hypothesis III (HIII)

For hypothesis HIII, we investigated how species with differing growth behavior and canopy positions efficiently occupied space, exploited it, and invested biomass in stems. We calculated three growth space occupancy metrics, followed by Pretzsch and Schütze (2005):

Efficiency in Growth Space Occupation (ESOC): basal area (ba) / crown projection area (cpa)

Efficiency in Growth Exploitation (EEX): basal area increment (bai)/ cpa

Efficiency in Biomass Investment (EBI): bai/ba (ESOC/EEX).

We fitted log-log models by using the reduced major axis (RMA) regressions with the "lmodel2" package (Legendre and Oksanen, 2018) for species and social classes. RMA is often recommended for analyses where measurement errors exist in both the x and y variables and produce better results than OLS regression (Niklas, 1994; Pretzsch, 2006).

3. Results

3.1. Descriptive statistics

Summary statistics are presented in Table 1. A total of 109 spruce, fir, and pine trees across four social classes revealed substantial interspecific and hierarchical variations in crown structure (e.g., crown radius), size (DBH), and growth (ring width) across species and sites, highlighting strong site-specific growth patterns and age variations among sample trees (Table 1, Supplementary Fig. 2).

Overall, spruce and fir in the dominant and intermediate classes produced more conical-shaped crowns. In contrast, codominant and suppressed trees developed upper-reaching or top-heavy crowns. Pine trees are significantly shorter and consistently maintain a broader and shorter crown across all social classes (Supplementary Fig. 2).

3.2. Crown structure and growth patterns relationships across species, growth behavior, and social classes (HI)

We found significant correlations between crown shape and tree ring pattern metrics (Fig. 4a, b). The relationship between crown structure and tree ring patterns varied significantly across species and social classes (Fig. 4c, d). Principal Component Analysis (PCA) revealed that 38.2 % of the variance was explained by the first principal component (PCA1), with crown projection area (cpa) and crown ratio (cratio) contributing positively. In contrast, crown radius variability (cvcr) and tree ring width variability (cvtrw) contributed negatively (Fig. 4b).

Besides, the bivariate analyses showed crown shape metrics such as crown ratio (cratio), top-heaviness (th), crown slenderness (cslc), and crown variability (cvcr), strongly correlated with tree ring variability (cvtrw). Still, variations were observed across species and social groups (Fig. 5), which supports our hypothesis HI. To illustrate, th was positively correlated with cvtrw in the fir and spruce across different social classes like dominant, codominant, and suppressed trees ($p < 0.05$) (Fig. 5).

3.3. Relationships between crown shape and tree ring patterns modulated by neighborhood competition and local canopy filling (HII)

The analysis demonstrated significant site-specific differences in how crown traits and competition modulated tree ring patterns. Across all sites, crown projection area (cpa) positively correlated with growth variability (*β=1.65* *), while interactions with local canopy space-filling (LCSF) increased growth irregularity (*β=1.05* *), indicating resource limitation in dense canopies. In the wet site, LCSF interactions with crown projection area (cpa: LCSF, *β=3.45* **) and maximum crown size (maxcr: LCSF, β=−6.24 **) suppressed growth irregularity, with cpa itself reflecting stress (β=5.58 **) in moisture-rich forests. Conversely, in dry site, competition (KKL) interacted positively with crown traits: cpa: *KKL (β=0.11* **)* and cvcr: KKL (*β=0.21***; ST1, Fig. 6) enhanced growth irregularity.

3.4. Efficiency in space occupation (ESOC), exploitation (EEX), and biomass investment (EBI) across social classes and species (HIII)

Spruce and fir exhibited higher space occupation efficiency (ESOC) values as crown size increased (β ranging from 0.6 to 1.6), reflecting their superior ability to occupy space efficiently despite having lower or similar biomass investment efficiency (EBI) across social classes (β ranging from −0.9 to −3.9) (Fig. 7). In contrast, space exploitation efficiency (EEX) declined with increasing crown size in spruce, indicating that smaller crowns exploit space more effectively (Fig. 7b). However,

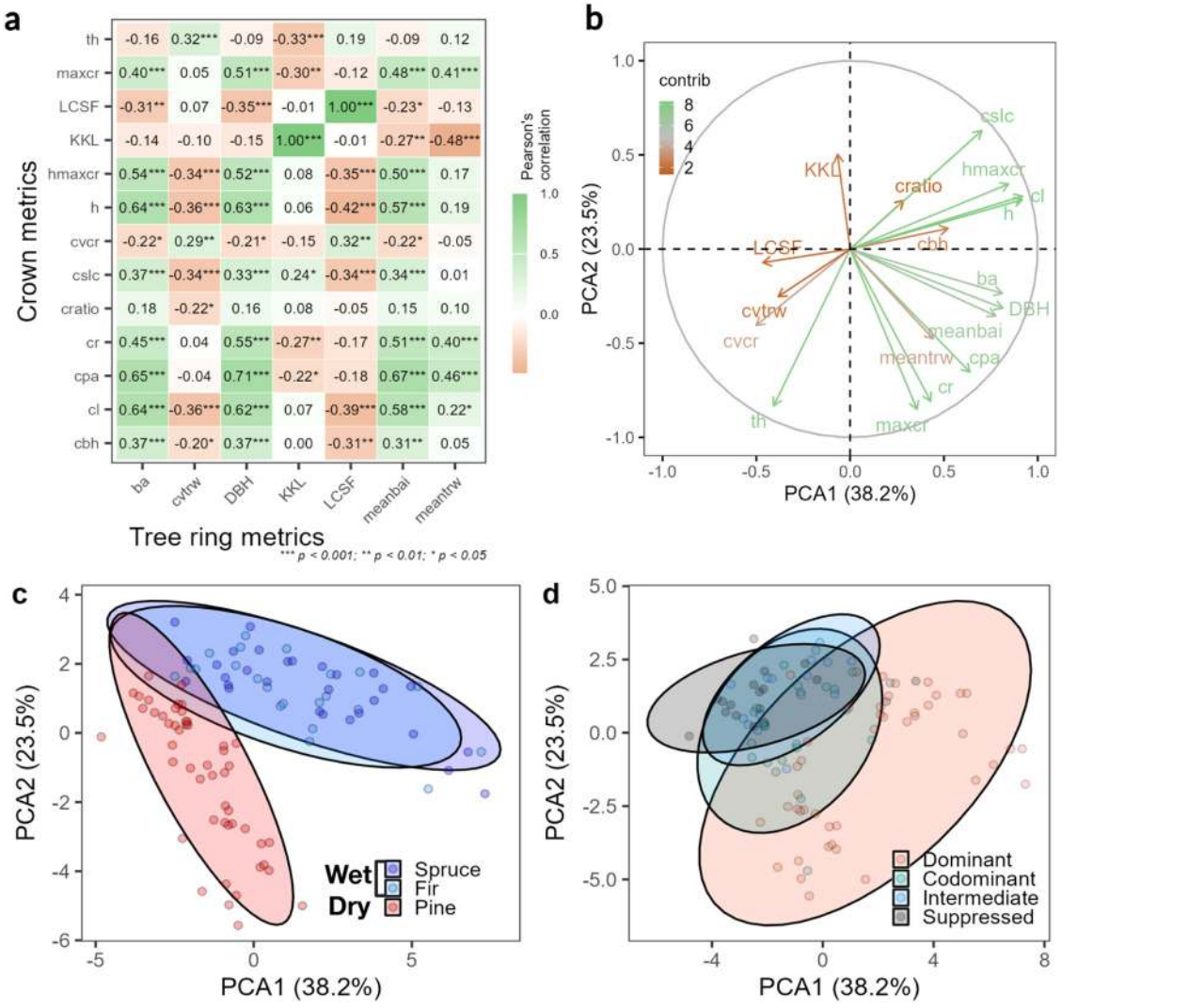


Fig. 4. Multivariate analysis of tree growth patterns and crown characteristics across different conifer species and social classes. (a) Correlation matrix displaying the relationships between crown metrics (vertical axis) and tree ring metrics (horizontal axis), with correlation coefficients and p-values. (b) PCA biplot shows variable loadings and their contributions to the first two principal components, which explain nearly 62 % of the total variance (PCA1: 38.2 %, PCA2: 23.5 %). (c) Distribution of individual trees in PCA space, grouped by species, with 95 % confidence ellipses showing distinct clustering patterns. (d) The same PCA space shows trees classified by their crown social positions.

fir exhibited the opposite trend across most social classes (dominant, intermediate, and suppressed), indicating that larger crowns in fir are more efficient in space use, likely due to their denser branching and shade-tolerant architecture. A similar pattern was observed in intermediate and suppressed pine trees, possibly reflecting their adaptive strategy to maximize light capture in lower canopy positions (Fig. 7b).

Pine showed higher variability across space efficiency metrics, suggesting species-specific trade-offs or ecological behavior. Due to space limitations, suppressed trees, particularly in pine, exhibited weaker growth responses. EEX declined with crown size across all species and social classes, with suppressed trees experiencing the steepest declines, especially in spruce and fir (Fig. 7b). Similarly, EBI decreased with basal area across all species, with suppressed trees showing the lowest or similar biomass investment efficiency due to competition and resource stress (Fig. 7c).

4. Discussions

4.1. Crown shape and tree ring patterns are correlated but varied across growth behavior and social classes (HI)

Our findings revealed a strong linkage between crown shape metrics (e.g., top-heaviness, slenderness, coefficient of variation of crown radius, etc.) and tree ring variability (coefficient of variation of ring width), underscoring how crown architecture governs secondary growth dynamics in close-to-nature forests (Figs. 4, 5). These results align with studies demonstrating that crown shape directly influences radial growth variability by modulating resource acquisition and allocation strategies (Lines et al., 2012; Pretzsch, 2014; Liu et al., 2025). PCA demonstrated these relationships, with distinct clustering patterns reflecting species-specific growth behavior and social stratification within the canopy (Figs. 4, 5) and supporting our first hypothesis. For example, the light-demanding pine, which acclimates or adjusts its crown shape and growth patterns to drier environments, was clearly separated along a different PCA axis from the shade-tolerant spruce and fir, reflecting the divergence in their ecological niches (Grubb, 1977; Messier et al., 1999). Besides, spruce and fir could also share similar

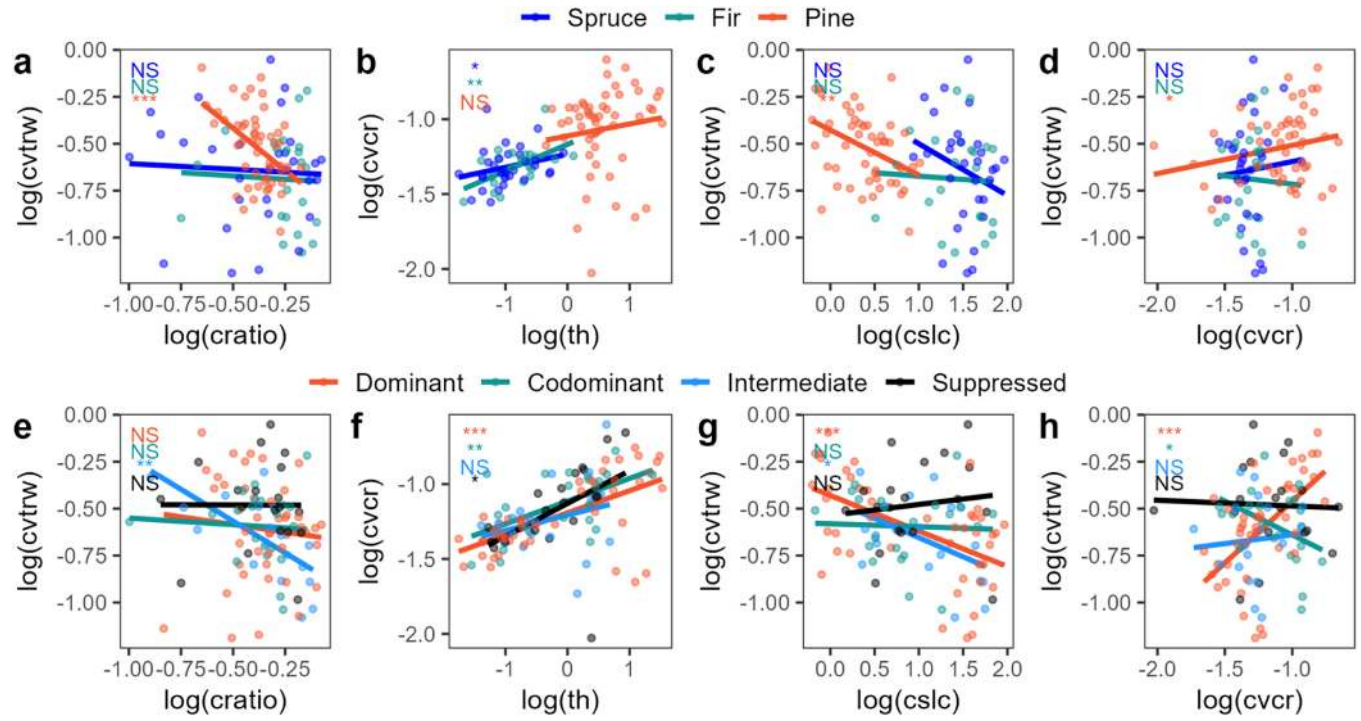


Fig. 5. Relationships between tree ring variability and crown shape metrics across species and social strata. The top row (a-d) compares species, while the bottom row (e-h) displays the same relationships categorized by tree social status. All variables are log-transformed. Trend lines indicate the relationship direction, while 'NS-non-significant' and asterisks denote statistical significance levels (*p < 0.05, **p < 0.01, ***p < 0.001), respectively. Each point represents an individual tree measurement.

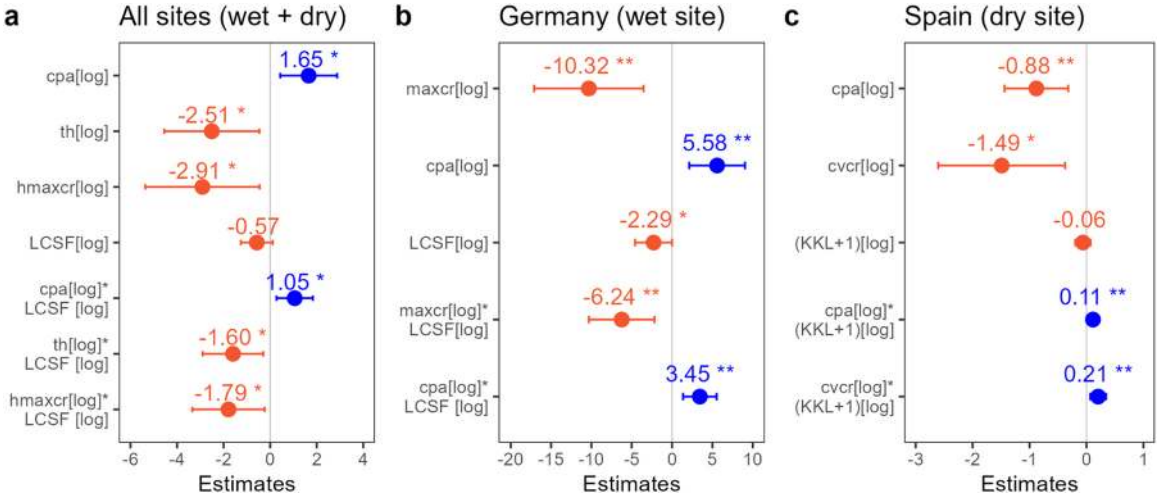


Fig. 6. Relationships between crown shape and tree ring patterns (cvtrw) across different sites. (a) showing results for all data (Eqn. 1), (b) results for wet or German site (Eqn. 2), and (c) relationships in dry site or Spain (Eqn. 3). Horizontal lines indicate a 95 % confidence interval with estimates. Asterisk signs indicate level of significance (*p < 0.05, **p < 0.01). Model summaries are presented in Supplementary Table 1. Blue and orange colors indicate positive and negative values.

structural properties due to their growing conditions (e.g., higher moisture availability and lower light) and wood properties (e.g., lower wood density), which influence their mechanical strategies and crown development (Schattenberg et al., 2024). This dichotomy echoes niche differentiation theory, where light and moisture gradients drive species sorting in mixed forests (Canham et al., 1994). In this context, species acclimate to specific microhabitats along these gradients, reducing direct competition by occupying distinct ecological niches, ultimately promoting coexistence within the forest ecosystem. Moreover, social stratification was equally pronounced: dominant and suppressed trees formed discrete clusters, while intermediate and codominant individuals exhibited overlapping distributions, likely reflecting transitional growth phases (Fig. 5d). Such hierarchical structuring aligns with studies of canopy competition, where asymmetric light partitioning creates distinct growth trajectories (Linares et al., 2010). These results emphasize the necessity of integrating species-specific behavior and social position when analyzing crown-growth interactions (Binkley et al., 2013).

We found that in dominant and suppressed trees (primarily fir and pine), top-heavy crown structures correlated positively with tree ring width variability (Fig. 5). For light-demanding pines, this aligns with their umbrella-shaped crowns—a morphological acclimation and

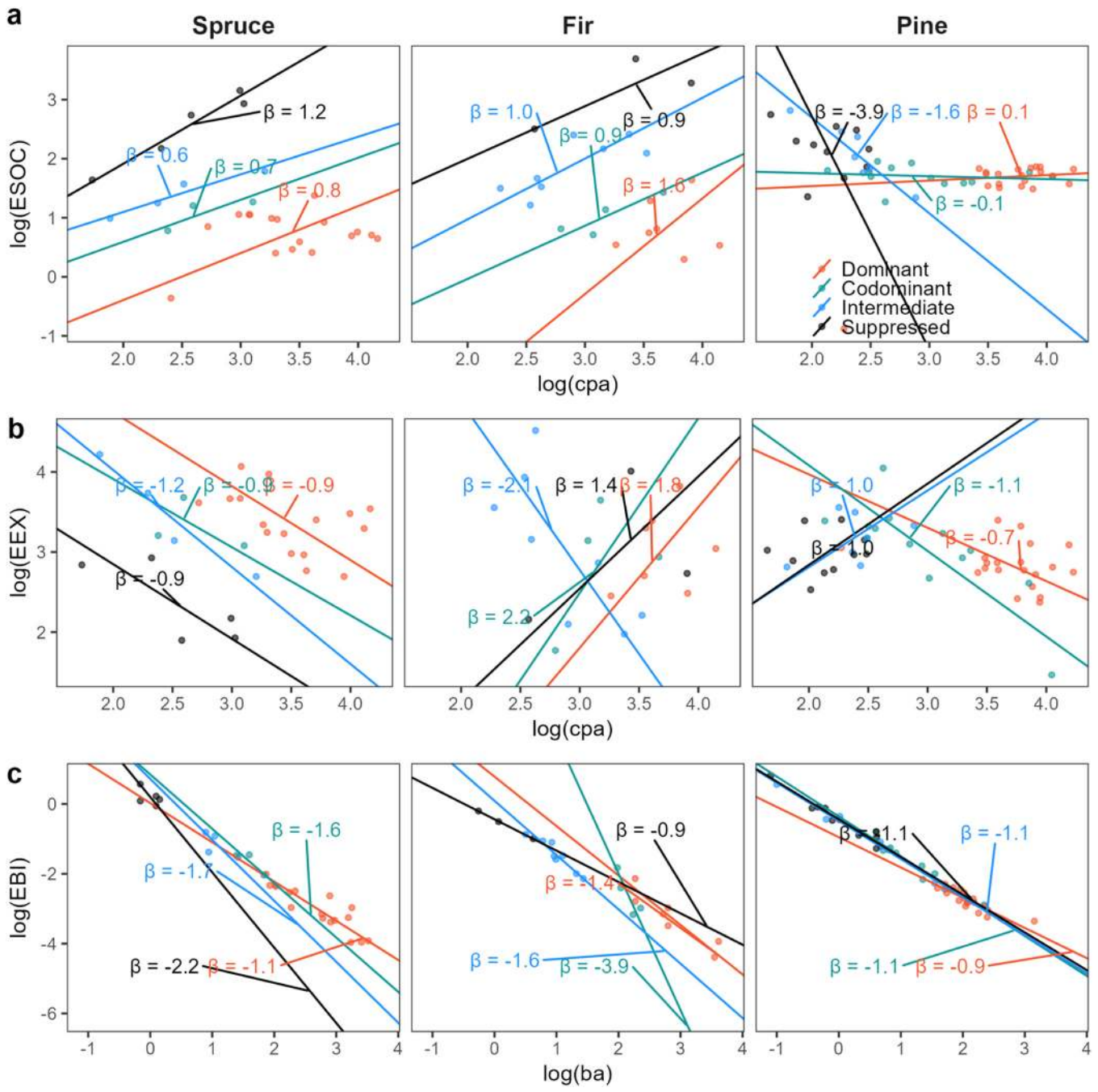


Fig. 7. Relationships between space occupancy (ESOC), exploitation (EEX), and biomass investment (EBI) across species and social strata. (a) relationships between efficient space occupation with crown size (CPA); (b), relationships between efficiency in EEX; and (c) Efficiency in biomass investment for tree size (ba). Legends are applicable for all subplots, and β values indicate slopes for the fitted lines.

adjustment to maximize light capture, consistent with their competitive dominance in open-canopy environments (Niinemets, 2010). In these environments, fluctuations in light and water availability can lead to more pronounced year-to-year variation in resource acquisition, which may explain the positive correlation between crown shape and tree-ring variability. Conversely, shade-tolerant fir developed top-heavy crowns under suppression to optimize light interception, prioritizing structural acclimation over rapid growth, a strategy documented in understory trees (Pretzsch, 1985; Valladares and Niinemets, 2008). However, such individuals are often close to their physiological limits, making them more sensitive to small changes in light or competition, which could amplify variability in radial growth. Intermediate trees showed no significant correlations, likely due to their opportunistic growth behavior; their conical crowns and vertical elongation (see Fig. 4b) reflect transitional efforts to escape suppression, akin to the "sit-and-wait" growth plasticity (Kitajima and Poorter, 2010). Notably, strong correlations in dominant trees suggest that expansive crowns experience heightened growth fluctuations, most likely driven by abiotic stressors (e.g., drought, wind exposure) rather than competition alone. This supports the hypothesis that dominant trees capitalize on resource abundance for growth efficiency (Ryan et al., 1997), while suppressed individuals invest relatively more in survival mechanisms, as observed in water-limited forests (McDowell et al., 2008).

4.2. Relationships between crown shape and tree ring patterns modulated by local neighborhood competition and competition-driven canopy space-filling (HII)

Crown structure -growth ring patterns relationships are significantly influenced by local neighborhood competition (KKL) and canopy space-filling (LCSF) that were calculated based on the current status of the stands, with site-specific crown-growth link variations reflecting changes in growth dynamics between sites. In moisture-rich forests, LCSF dominated growth modulation, suppressed radial growth variability through interactions with crown projection area (cpa: LCSF, $p < 0.05$, Fig. 6) and maximum crown size (maxcr: LCSF, $p < 0.05$). This aligns with the "asymmetric competition" paradigm (Weiner, 1990), where dense canopies amplify light competition, prioritizing vertical over lateral growth (Pretzsch, 2014). However, variation in local tree-level LCSF significantly influenced how trees shaped their crowns and allocated growth, reflecting structural adaptations to local competition intensity.

Additionally, we found that KKL was the primary driver in dry sites, which we hypothesize is related to the competition for water. Alternatively, the lower density in a dry site may have reduced competition for light and canopy filling. However, we noticed that suppressed trees in dry site are still growing annually; it could be due to facilitative interactions (one can pump water and another can live better) due to complementarity under drought stress or dry conditions (Pretzsch, 2024). The role of competition (KKL) through interactions with crown traits (cpa: KKL, $p < 0.05$ cvcr: KKL, $p < 0.01$) further supports the stress gradient hypothesis (Maestre et al., 2009). The influence of climate conditions on tree growth was more pronounced under high competition, whereas trees experiencing lower competition showed reduced climate sensitivity and generally better growth performance. This pattern, observed across our study sites, supports findings from temperate mixed forests that thinning, by reducing competition, can buffer trees against climate stress, enhancing their resilience (D'Amato et al., 2013; Sohn et al., 2016). However, these site-specific contrasts—LCSF-driven suppression in comparatively wet forests versus KKL-mediated in dry stands—support our second hypothesis (HII), demonstrating how local competitive pressures and abiotic stressors shape crown plasticity and growth behavior.

The interaction between KKL and crown metrics also revealed that suppressed trees in dense neighborhoods exhibited steeper declines in growth variability, highlighting the critical role of neighborhood competition in determining growth outcomes. Conversely, dominant trees benefited from reduced competition, leveraging abundant resources for efficient growth. These observations underscore the importance of considering local competition and canopy structure when assessing forest growth patterns. The absence of LCSF effects in dry sites further underscores how open canopies in Mediterranean systems reduce light competition, shifting growth constraints to abiotic stressors, which in our case might be related to reduced water availability (Gomez-Aparicio et al., 2011). LCSF and KKL's consistent adverse effects across regions emphasize competition for canopy space as a driver of growth limitation. However, we hypothesize its dual role in sites—as both a constraint (universal) and facilitator (site-specific)—mirrors findings in water-limited ecosystems, where competition might shift from resource-driven to stress-mediated depending on neighborhood density (Grossiord et al., 2017).

The positive correlation between crown variability (cvcr) and growth variability (cvcr) ($\beta = 0.22$) aligns with studies linking crown plasticity to resilience in mixed forests (Bauhus et al., 2017). In Germany, suppressed growth under high LCSF reflects a "to grow or wait" strategy, where trees invest in structural persistence over radial growth (Kunstler et al., 2016). In contrast, Spain's crown-KKL synergy suggests a "grow-with-the-flow" tactic, where trees exploit facilitative interactions to offset arid conditions—a pattern observed in Mediterranean woody species (Sánchez-Gómez et al., 2006). Therefore, thinning to reduce LCSF (canopy density) could alleviate light competition, particularly for shade-intolerant species (Puettmann et al., 2015).

4.3. Efficiency in space occupation, exploitation, and biomass investment across species behavior and social classes (HIII)

Our space uses and exploitations efficiency metrics (ESOC, EEX, EBI) revealed stark contrasts in resource allocation strategies across species and social classes (Fig. 7), supporting the third hypothesis (HIII). With crown expansion, dominant spruce and fir exhibited high space occupation efficiency (ESOC). Still, lower biomass investment efficiency (EBI) reflects a growth-fast of height or crown that prioritizes light capture over carbon accumulation in stems—a hallmark of canopy dominance in stratified forests (Pretzsch and Schütze, 2005). This aligns with the vertical growth prioritization paradigm, where dominant trees invest disproportionately in height to secure light (Ryan et al., 1997a; Ryan, Yoder, 1997b). Conversely, suppressed trees displayed higher or comparable EBI and structural plasticity, favoring a wait-and-persist strategy that allocates resources to roots and defense compounds under chronic stress (Kunstler et al., 2016). These growth or wait dynamics indicate that trees may persist with diverse ecological strategies (e.g., secondary growth over height growth or maintaining a static crown for better light or canopy space efficiency). However, in reality, biomass investment proportionality is comparable based on tree size across social strata.

Furthermore, dominant trees in spruce and fir exhibited tight crown-growth coupling, optimizing light exploitation through expansive crowns. However, their low EBI underscores the vulnerability of this strategy to sudden canopy disturbances (e.g., windthrow), as excessive height growth compromises mechanical stability (Larjavaara and Muller-Landau, 2012). In contrast, suppressed trees retained smaller, plastic crowns that efficiently captured transient light gaps, mirroring the shade tolerance syndrome, where slow growth enhances survival under low light (Pretzsch, 1985; Messier et al., 2022). Intermediate fir's conical crowns and efficiency patterns represent a transitional strategy, balancing vertical growth with lateral light interception to maximize light capture and escape suppression—a behavior observed in gap-phase regenerators (Nagel and Diaci, 2006; Nagel et al., 2010), or in gap-cut systems.

Light-demanding pine diverged sharply from shade-tolerant spruce and fir, with static crown architectures and declining EEX in suppressed individuals. This reflects a wait-for-gap strategy, which is common to drought-adapted species, where static crowns await disturbance-triggered release (creates gap or open canopy) (Oliver et al., 1996). However, pine's inability to adjust crown structure under suppression highlights a critical vulnerability in dense stands, aligning with studies showing reduced drought resilience in rigid-crowned species (Bose et al., 2020; DeSoto et al., 2020).

Despite the limitations of our dataset, arising from the high cost and time required for data collection (TLidar) and the availability of expected close-to-nature forests data, our findings reveal clear crown structure-growth variability in tree ring relationships. These relationships provide valuable insights into underlying ecological patterns, particularly how tree crown plasticity indicates growth behavior (whether to grow or wait for better light). Future studies incorporating more extensive datasets, including the same species across varying environmental conditions with a temporal scale, will likely improve our understanding of growth dynamics, allowing for a more comprehensive exploration of the mechanisms driving these processes.

5. Conclusions

We found that crown shape positively correlated with tree ring patterns across different species and social strata despite significant variations in tree growth behavior and growing conditions. Furthermore, our findings showed that local canopy packing and neighborhood

competition are crucial in shaping the relationship between crown structure and growth patterns. Under wet and light-limited conditions, we found that canopy space filling is critical as trees acclimate and adjust crowns based on light availability. In dry sites, water availability and below-ground competition are likely to be the key factors influencing the crown shape and space use efficiency. We also found that trees display different behaviors in space use efficiency to persist and coexist. However, despite these differences, they show similar patterns in biomass accumulation and investment, suggesting a convergence in long-term growth potential. Understanding these dynamics can help predict future tree growth and guide forest management strategies. By integrating TLS-derived crown metrics with dendrochronological data, we provide a comprehensive understanding of tree growth dynamics, especially trees from suppressed to dominant, offering valuable insights for precision forestry. Linking crown traits to growth potential allows forest managers to design targeted thinning and restoration practices, promoting resilience in forests facing climate change. Although our sampling design aimed to capture a range of social classes, some groups were underrepresented due to natural stand structure and tree availability, Nonetheless, this study provides an important baseline for understanding species–social class interactions in mixed, unmanaged ecosystems. To build on these findings, we recommend that future studies incorporate a broader dataset, including more species (such as broadleaves), a wider range of sites, and temporal laser scanning data to better explain the changes in crown and growth patterns.

CRediT authorship contribution statement

Richard L. Peters: Writing – review & editing, Resources. **Hans Pretzsch:** Writing – review & editing, Supervision, Methodology, Funding acquisition, Conceptualization. **Cristóbal Ordóñez:** Resources, Data curation. **Miren del Río:** Writing – review & editing, Supervision. **Felipe Bravo:** Writing – review & editing, Resources, Project administration. **Enno Uhl:** Project administration, Conceptualization. **Frederico Tupinambá-Simões:** Writing – review & editing, Data curation. **Shamim Ahmed:** Writing – review & editing, Writing – original draft, Visualization, Validation, Software, Methodology, Investigation, Formal analysis, Data curation, Conceptualization. **Torben Hilmers:** Writing – review & editing, Conceptualization.

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Declaration of Competing Interest

The authors declare no competing interests.

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Appendix A. Supporting information

Supplementary data associated with this article can be found in the online version at doi:10.1016/j.foreco.2025.122814.

Data availability

Link is shared

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