

Competition in mixed Scots pine and Pyrenean oak stands modifies allometry and partially affects biomass allocation during early stand development

Eric Cudjoe^{a,*}, Felipe Bravo^a, Hans Pretzsch^{a,c}, Pete Bettinger^d, Ricardo Ruiz-Peinado^b

^a SMART Ecosystems Research Group, Department of Plant Production and Forest Resources, University Institute of Research in Sustainable Forest Management (iuFOR), Associated R+D+I Unit of CSIC, Higher Technical School of Agricultural Engineering of Palencia, University of Valladolid, Avda. de Madrid 44, 34004 Palencia, Spain

^b Department of Forest Dynamics and Management, Institute of Forest Science (ICIFOR-INIA), CSIC, Ctra. A Coruña, km 7.5, 28040 Madrid, Spain

^c Chair for Forest Growth and Yield Science, Department of Life Science Systems, TUM School of Life Sciences, Technical University of Munich, Hans-Carl-von-Carlowitz-Platz 2, Freising 85354, Germany

^d Warnell School of Forestry and Natural Resources, University of Georgia, Athens, GA 30602, USA

ARTICLE INFO

Keywords:

Allometric scaling
Biomass partitioning
Resource allocation strategies
Structural equation modeling (SEM)
Tree competition
Tree structural attributes

ABSTRACT

Understanding how trees allocate growth and resources in response to competition is crucial for managing mixed-species forests under changing climatic conditions. Despite extensive research examining competition dynamics in mature forests, little is known about how competition influences biomass allocation strategies in early-stage mixed stands of Scots pine (*Pinus sylvestris* L.) and Pyrenean oak (*Quercus pyrenaica* Willd.). In this study, we examined the effects of competition on the allometric relationships between diameter at breast height (DBH) and tree height, crown base height (CBH), and crown length (CL) in both species. We also investigated how competition modifies biomass allocation among stem, branch, and foliage components and whether the two species adhere more closely to optimal allocation theory, where competition influences biomass distribution, or allometric partitioning theory, where it does not. Finally, we explored whether competition indirectly affects biomass allocation by altering its impact on structural attributes (DBH, tree height, CBH, and CL). Here, we destructively sampled 90 trees and then applied ANCOVA to quantify the direct effects of competition on tree structural attributes and biomass allocation. Additionally, we used structural equation modeling (SEM) to evaluate the indirect effects of competition. Our results demonstrated that competition significantly influenced allometric relationships (DBH–tree height, DBH–CBH, and DBH–CL). Moreover, biomass allocation between stem–branch and branch–foliage was not modified by competition and followed allometric partitioning theory, whereas stem–foliage allocation was modulated by competition and aligned with optimal allocation theory. We also found that Scots pine prioritized branch and foliage biomass under competition, whereas Pyrenean oak allocated more resources to the stem, reflecting contrasting adaptive strategies. SEM revealed that competition indirectly influences biomass allocation by modulating tree height, leading to a significant increase in stem and branch biomass but no effect on foliage biomass. These findings support early-stage silvicultural interventions, such as promoting drought-tolerant species, to guide stand development toward structurally resilient and climate-adaptive Mediterranean forests. While these findings offer informative results, they need to be interpreted with caution because of the single site and limited sample size, which may restrict broader generalizability.

1. Introduction

Forests play an important role in Earth's ecosystems by providing significant services such as carbon sequestration, biodiversity conservation, and water regulation. Tree–tree interactions, including

competition and facilitation, are crucial ecological processes that significantly influence individual tree growth, survival, and the overall structure of forest ecosystems (Carvalho et al., 2022). Notably, competition for limited resources, such as light, water, and nutrients, has emerged as a key interaction shaping tree allometry – the study of

* Corresponding author.

E-mail address: ericcudjoe09@yahoo.com (E. Cudjoe).

<https://doi.org/10.1016/j.ecolind.2025.113713>

Received 2 January 2025; Received in revised form 13 May 2025; Accepted 2 June 2025

Available online 10 June 2025

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relationships between tree structural attributes such as diameter at breast height (DBH), tree height, and crown variables – and biomass components such as stems, branches and foliage (Forrester et al., 2017b, 2017a; Pretzsch et al., 2015a, 2015b). Previous studies by Poorter et al. (2015) and Pretzsch et al. (2014) demonstrated that both intrinsic species factors (e.g., growth strategies, shade tolerance) and extrinsic environmental factors (e.g., competition, site conditions) shape allometric and biomass allocation patterns in trees. However, understanding how trees allocate resources in response to competition – either prioritizing tree height growth (i.e., to outcompete neighbors for light) or radial growth (i.e., to enhance structural stability) – can vary significantly across species and forest types (Forrester and Pretzsch, 2015; Niklas, 1994; Pretzsch, 2014).

Compared with monocultures, mixed-species forests are increasingly recognized for their higher productivity, greater biodiversity, and improved resilience to environmental stressors (Condés and del Río, 2015; Hilmers et al., 2024; Pretzsch et al., 2015a, 2015b). In southwestern Europe specifically, mixtures of Scots pine (*Pinus sylvestris* L.) and Pyrenean oak (*Quercus pyrenaica* Willd.) are of significant ecological and economic importance. Scots pine is among the most broadly dispersed conifer species in Europe and is appreciated due to its suitability for different environmental conditions and for being able to produce timber (Matías and Jump, 2015). In contrast, Pyrenean oak is a deciduous species native to the Iberian Peninsula, western France, and northern Morocco (Niéto Quintano et al., 2016) and is known for its resilience to drought and role in supporting biodiversity through its broadleaf canopy and associated understory flora (Gómez-Aparicio et al., 2011). Interestingly, Pyrenean oak grows more slowly but is extremely resilient to competition (Trouvé et al., 2017), unlike Scots pine, which is highly susceptible, especially during its early stages of growth and development (Zeng et al., 2024).

The ecological characteristics of the species studied further highlight their competitive strategies. Scots pine has a shade tolerance of 1.67 and a drought tolerance of 4.34 (Niinemets and Valladares, 2006), a specific leaf area of $4.28 \text{ m}^2 \text{ kg}^{-1}$ (Forrester et al., 2017b), a wood density of 0.422 g cm^{-3} (Brzeziecki and Kienast, 1994), and a root-to-shoot ratio of 0.279 (Ruiz-Peinado et al., 2011). In contrast, Pyrenean oak has a relatively high specific leaf area of $15.5 \text{ m}^2 \text{ kg}^{-1}$ (de Tomás Marín et al., 2023), a relatively high wood density of 0.665 g cm^{-3} (Cuny et al., 2025), and a root-to-shoot ratio of 0.353 (Ruiz-Peinado et al., 2012). These traits substantially influence how each species competes for resources and their respective biomass allocation strategies, particularly in Mediterranean regions characterized by high temperatures and limited water availability (Rodríguez de Prado et al., 2022).

As mixed forests mature, Scots pine generally dominates the overstory, whereas Pyrenean oak typically occupies the understory because of its greater shade tolerance and low tree height growth (Aldea et al., 2023; Pretzsch et al., 2020). A young mixed-species stand differs from a mature stand, however, because vertical stratification has not yet developed, competition is more direct, affecting the early growth trajectories of both species (Barbeito et al., 2014). Furthermore, shade tolerance and competitive strategies can change over time. For example, some oak species initially tolerate shade well and lose their tolerance as they grow taller (Thyroff et al., 2019). Early-stage competition plays an important role in determining the structure, stability, and composition of a stand over time, which underscores the importance of studying competition during stand development (Marqués et al., 2021).

Mixed-species forests in the early stages of growth are crucial for regulating species interactions and maintaining a balanced mixing proportion. During this critical establishment phase, if the competition dynamics are not adequately understood and managed, they can cause one species to dominate and others to disappear. A monospecific stand could result from this, undermining the mixture's ecological benefits (Pretzsch and Zenner, 2017). It is essential to regulate competition effectively at this early stage to avoid these outcomes and ensure that mixed forest stands meet their management objectives (Bravo-Oviedo

et al., 2014; Pretzsch, 2014). Despite the importance of both species in mixtures, research on allometric and biomass allocation patterns during the early stages of stand development has not been extensively conducted, making this a vital area for further investigation.

Tree species are likely to respond to competition and changing environmental conditions, which can be understood through two primary ecological theories: optimal allocation theory and allometric partitioning theory. According to optimal allocation theory, trees modify their biomass allocation patterns in response to environmental factors, such as competition, to optimize resource use for growth and survival under competitive stress (Dybzinski et al., 2015). Conversely, when competition does not substantially influence biomass allocation patterns, the allometric partitioning theory becomes more applicable, describing biomass allocation as a function of inherent allometric scaling laws, which are primarily size dependent and unaffected by competition (Liu et al., 2021; Mensah et al., 2016). Using young mixed-species stands to test these theories will help us better understand how species allocate resources and respond to competitive pressures.

Competition is more intense during the early stages of tree growth and development because trees grow quickly as they compete for a place in the canopy. At this critical stage, competitive pressures strongly affect tree growth rates and biomass allocation patterns, resulting in structural and functional changes (Dieler and Pretzsch, 2013). Despite their importance in shaping forest structure and ecosystem functioning, early-stage interactions among different species, particularly in mixed-species stands, have not received sufficient attention (Hynynen et al., 2011). For example, when trees compete for light in dense stands, they often prioritize vertical growth to improve their access to sunlight (Forrester et al., 2017a; Poorter et al., 2015). This strategy generally leads to the allocation of more biomass to stems, which support tree height growth and facilitate water and nutrient transport, potentially at the expense of branches and foliage, which are essential for photosynthesis (Hilmers et al., 2024; Litton et al., 2007). Conversely, in less competitive environments, radial growth may be prioritized, resulting in more balanced allometric relationships (Litton et al., 2007). These trees may allocate more biomass to branches and foliage, thereby boosting their photosynthetic capacity and general growth potential (Poorter et al., 2015; Ruiz-Peinado et al., 2021). Even though young mixed-species stands are increasingly recognized for their ecological and economic importance (Huuskonen et al., 2023; Pretzsch, 2018), the influence of competition – both direct and indirect – on tree allometric relationships as well as biomass allocation strategies remains poorly understood.

Thus, the primary objective of this study was to examine how competition influences allometric relationships and biomass allocation within young mixed-species forest stands comprising Scots pine and Pyrenean oak. To the best of our knowledge, this study is one of the few that comprehensively analyzes the dynamics of these mixed stands during the early stages of forest development under Mediterranean conditions. The following research questions were investigated: (1) How does competition affect the allometric relationships between DBH and key tree structural attributes (tree height, crown base height, and crown length) in Scots pine and Pyrenean oak, and do these relationships differ significantly between the two species? (2) How does competition influence biomass allocation patterns of biomass among stem, branch, and foliage components in Scots pine and Pyrenean oak, and do these species conform more closely to optimal allocation theory or allometric partitioning theory given their distinct biological traits, such as regeneration strategies and growth forms? Competition may not have an equal impact on all tree components, with significant variations in its impacts on allocation to stems, branches, and foliage. (3) In what ways does competition indirectly modify tree biomass allocation (stems, branches, and foliage) through its influence on tree structural attributes (DBH, tree height, crown base height, and crown length)? This led us to hypothesize that competition may alter biomass allocation not only directly but also indirectly by modifying tree structural attributes. These tree structural attributes may then influence the distribution of biomass among the

various tree components. Our research questions represent an integrative approach to understanding the direct and indirect effects of competition on trees. The results are useful for improving forest management strategies and ensuring the ecological benefits of mixed-species forests under Mediterranean conditions.

2. Materials and methods

2.1. Study area

The research was conducted in young mixed forests of Scots pine and Pyrenean oak within the municipality of Quintanar de la Sierra, located in the province of Burgos, in northern Spain, as shown in Fig. 1. The study site was chosen because of its ecological significance as a Mediterranean mixed forest containing the species mentioned earlier, which are critically important for biodiversity conservation, forest resilience, and carbon sequestration under changing climatic conditions. In addition, it has a well-documented management history for both species studied, making it an ideal location to examine the effects of competition.

The stand composition resulted from natural regeneration, although the regeneration of Scots pine has been assisted by seed distribution so that Scots pine trees dominate Pyrenean oak trees, a common practice in the region (additional details are available in Cudjoe et al. (2025)). However, efforts were made in the study area to maintain a balanced mix of both studied species. Regeneration was successful, with an initial (pre-thinning) tree density of approximately 50,000 stems ha^{-1} . A pre-commercial thinning trial was established to test different density reductions. In 2016, the Institute of Research in Sustainable Forest Management (iuFOR) established nine experimental plots, each measuring $20 \times 40 \text{ m}$ (800 m^2) with three different treatments: the control plots retained 100 % of their original density, the light thinning plots were reduced by 40 %, and the heavy thinning plots were reduced by 70 %.

The experimental trial monitored the changes in stand development and species richness, diversity, and abundance of vegetation over time. The trees in the forest are located at $41^\circ 58' 41.16'' \text{ N}$ latitude and $3^\circ 01' 09.84'' \text{ W}$ longitude, with elevations between 1120–1150 m above

sea level and an age range of 15–18 years. In addition, a gentle terrain and a continental Mediterranean climate characterize the study site. The mean annual temperature is approximately 10.8°C , with average annual maximum and minimum temperatures of 16.7°C and 4.8°C , respectively. The study site's highest and lowest recorded temperatures are 33°C and -6.5°C , respectively (Fick and Hijmans, 2017).

2.2. Data collection

To test our research questions in this study, we used a random sampling method to select 90 target trees for destructive sampling between late 2022 and early 2023. The sample comprised 45 Scots pine trees and 45 Pyrenean oak trees, ensuring equal representation of both species, with 15 trees per species from each precommercial thinning treatment. As the costs of destructive sampling and biomass analysis are high, our sample size was necessarily limited while still maintaining a representative assessment of competition effects. Our target trees were selected in three different situations: (1) surrounding trees of the same species as themselves, (2) surrounding trees of the other species, and (3) surrounding trees of both species in varying proportions.

In this study, the tree structural attributes of target trees including diameter at breast height (DBH), tree height, and crown base height (CBH), were meticulously examined. At 1.3 m above ground level, the DBH was measured with a diameter tape, whereas the tree height and CBH were determined with a height stick. Consequently, the crown length (CL) was calculated as the difference between the tree height and the CBH. During the selection process, we selected target trees to ensure that each tree represented the full spectrum of size classes (both DBH and tree height distribution) present at the study site. This approach ensured a proportional representation of tree sizes, minimizing potential sampling bias in our results. We selected the target trees within interior buffer zones immediately adjacent to the main experimental plots, which had similar environmental characteristics and underwent the same silvicultural treatments. This was done to avoid removing trees from the main experimental plots. The trees in these buffer zones were comparable in size and growth conditions to those within the main experimental plots. Table 1 presents a summary description of the main tree measurements used in the study.

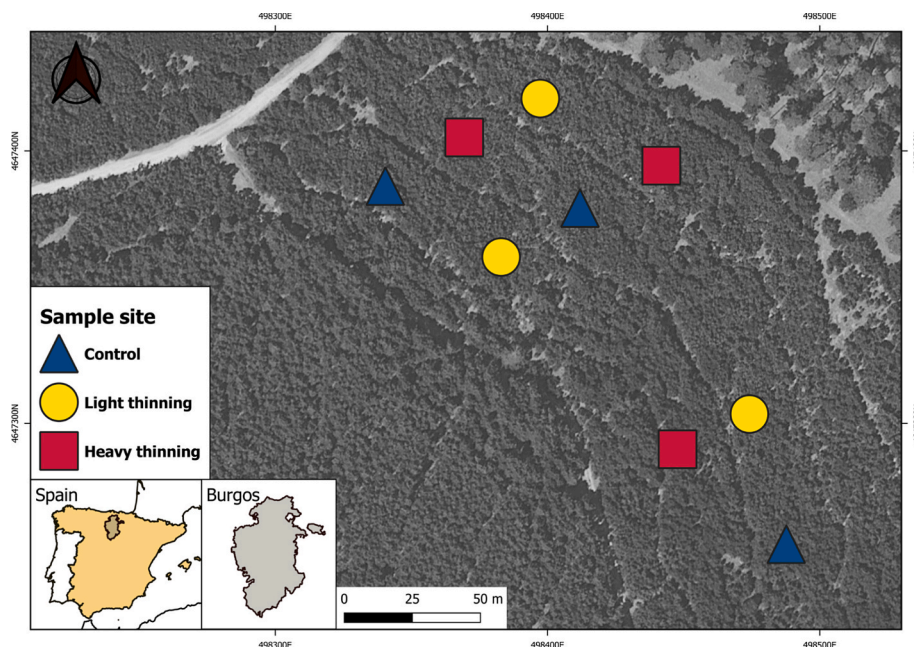


Fig. 1. Map of the sample site in Quintanar de la Sierra, Burgos (northern Spain), showing the young mixed forest of Scots pine and Pyrenean oak. The blue triangles represent control plots, the yellow circles represent lightly thinned plots, and the red squares represent heavily thinned plots in the experimental precommercial thinning site.

Table 1

Summary of the mean tree measurements for Scots pine and Pyrenean oak trees.

Species	Treatment	DBH (cm)	Tree height (m)	CBH (m)	CL (m)	Stem (kg)	Branch (kg)	Foliage (kg)	BAL (m ² ha ⁻¹)
S. pine	No thinning	6.22 (3.75–10.50)	6.37 (4.40–8.75)	3.36 (1.10–5.50)	3.01 (1.90–4.65)	6.90 (1.04–16.82)	2.35 (0.40–5.24)	1.74 (0.29–3.90)	12.71 (3.54–22.82)
S. pine	Light thinning	5.74 (3.50–8.65)	4.84 (3.00–6.45)	2.10 (0.90–3.25)	2.73 (1.75–3.50)	3.81 (1.82–6.88)	1.29 (0.29–5.24)	0.88 (0.24–2.08)	10.91 (2.35–29.26)
S. pine	Heavy thinning	7.03 (4.20–13.95)	5.88 (4.02–7.70)	2.52 (1.45–3.80)	3.36 (2.06–4.20)	5.63 (1.24–20.10)	1.72 (0.30–7.39)	1.09 (0.43–2.90)	16.36 (4.75–40.46)
P. oak	No thinning	6.71 (4.05–10.70)	7.62 (5.50–9.85)	2.96 (1.50–4.30)	4.66 (3.50–6.20)	9.32 (2.87–15.27)	1.62 (0.68–3.37)	0.47 (0.30–0.60)	14.93 (5.36–33.95)
P. oak	Light thinning	6.91 (4.30–8.90)	7.13 (4.55–8.85)	3.03 (1.75–4.20)	4.10 (2.80–6.70)	11.25 (5.14–20.16)	2.32 (0.92–5.59)	0.68 (0.30–1.84)	18.75 (6.52–37.57)
P. oak	Heavy thinning	7.68 (4.05–11.25)	6.80 (4.70–9.20)	2.45 (0.75–3.60)	4.35 (2.20–6.50)	11.55 (2.92–22.44)	3.45 (0.81–6.89)	0.64 (0.12–2.99)	17.52 (5.55–35.27)

Note: For each measurement variable, the table shows its mean and range (min–max), including the basal area of larger trees (BAL), diameter at breast height (DBH), tree height, crown base height (CBH), crown length (CL), stem biomass, branch biomass, and foliage biomass. Additionally, S. pine: Scots pine, and P. oak: Pyrenean oak.

2.3. Biomass component calculation

The biomass of individual tree components – stems (stem with bark), branches, and foliage – was quantified through a destructive sampling approach, following the biomass estimation method described by Williamson and Wiemann (2010) and Cudjoe et al. (2025). After the 90 target trees were selected and felled, each tree was carefully separated into its major components: stem, branches, and foliage. The stem was cut into three sections, and each section was weighed in the field for fresh (green) weight using a digital hanging scale (± 50 g accuracy, 50 kg maximum capacity). A representative subsample from each section was subsequently collected and dried in an oven at 105 °C in the laboratory until a constant weight was attained, ensuring accurate determination of dry weight.

The stem biomass was then determined by applying the dry-to-fresh weight ratio from subsamples to the fresh weight of the entire stem. The branches and foliage were also weighed in the field to obtain the fresh weight. Subsampling was not necessary for the branches and foliage. This occurred because the trees in this study were relatively young, with DBHs ranging from 3.50 cm to 13.95 cm for Scots pine and 4.05 cm to 11.25 cm for Pyrenean oak. Instead, the entire fresh weight was taken to the laboratory, where it was dried in an oven at 105 °C until a constant weight was reached. All biomass components were expressed in dry weight (kg) to ensure consistency in the data.

2.4. Neighbor tree selection and competition index calculation

To quantify the competitive environment, neighboring trees within an influence zone were identified for each target tree. The influence zone was defined as a radius equal to 25 % of the tree height of the target tree, following the approach of Cudjoe et al. (2025) and Pretzsch and Schütze (2021). In this approach, the size of the target tree is assumed to

be a determinant of the intensity of competition. Furthermore, to assess the competitive environment surrounding each tree, we calculated the basal area of larger trees (BAL) as the competition index (CI), as shown in Eq. (2). The BAL was calculated for each target tree as the cumulative basal area of all neighboring trees that had a greater DBH than the target tree within the influence zone radius. The index quantifies the cumulative competition from surrounding trees. Many models of tree growth use this distance-independent CI (Wyckoff et al., 1982). The distribution of BAL varied markedly across sampled trees, indicating differing competition levels for Scots pine and Pyrenean oak, as illustrated by the density plots in Fig. 2.

$$BAL_i = \sum_{j=1}^n \left(\frac{\pi \cdot d_j^2}{4} \right), \text{ where } d_j > d_i \quad (2)$$

where BAL_i represents the competition index of the target tree; n represents the number of neighboring trees with a DBH larger than the target tree; d_j represents the DBH of a neighboring tree; and d_i represents the DBH of the target tree.

2.5. Statistical analysis

All the analyses were conducted using R software version 4.3.1 (R Core Team, 2023), with data visualization performed using the “ggplot2” package (Wickham, 2016). Structural equation modeling (SEM) was performed using the “lavaan” package (Rosseel, 2012), and the variance inflation factor (VIF) values were calculated using the “car” package (Fox et al., 2012). In the following sections, we describe the analysis procedures for each research question.

Statistical analysis for research question 1 (RQ1): ANCOVA was applied to assess how competition influences the allometric relationships between DBH and tree structural attributes in Scots pine and

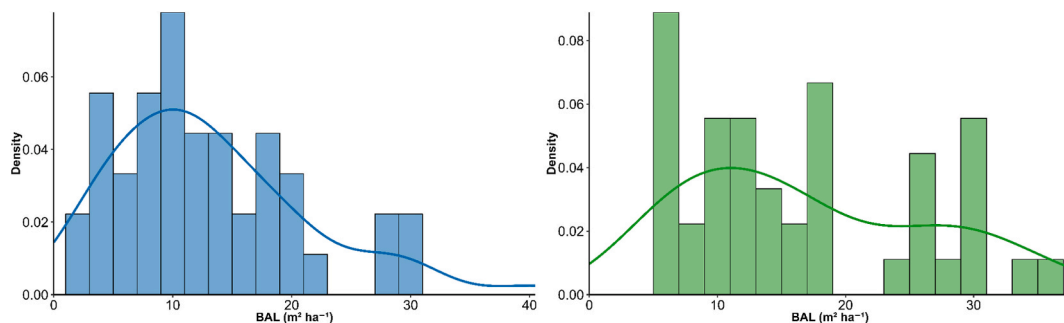


Fig. 2. Distribution of BAL (in m² ha⁻¹) for Scots pine (left) and Pyrenean oak (right), with a density curve providing a smooth representation of the overall distribution, showing the competitive status of the sampled trees.

Pyrenean oak, which allowed the interaction terms of competition and species on allometric scaling relationships to be tested. ANCOVA facilitates the incorporation of several covariates (continuous and categorical variables), thereby addressing challenges such as nonlinearity and heteroscedasticity, which are frequently encountered in ecological datasets (Akritas and Van Keilegom, 2001; Wilcox, 2005). All the variables were log-transformed to linearize scaling relationships and meet the assumptions of linear regression. This transformation is particularly suitable for analyzing tree allometry, as it captures the power-law nature of scaling between structural variables (Niklas, 2006). The log-transformed relationships were modeled using the following formula (Eq. (3)) for each tree structural attribute (Y):

$$\log(Y) = \beta_0 + \beta_1 * \log(X) + \beta_2 * \log(Z) + \beta_3 * [\log(X) * \log(Z)] + \beta_4 * \text{Species} + \varepsilon \quad (3)$$

where Y is the dependent variable (e.g., tree height, CBH, or CL), X is the independent variable (DBH), Z is the competition, β_{0-4} are the regression coefficients, and ε is the error term for the residuals. The significant interaction term (β_3) revealed if the allometric relationships were modified by competition. If a nonsignificant interaction effect was detected, we refitted the model without the interaction term. The “Species” variable was included in the model (Eq. (3)) as a categorical predictor. Furthermore, diagnostic checks were conducted to ensure the validity of the models: the residuals plotted against the fitted values showed no evidence of heteroscedasticity, and the Q–Q plots confirmed that the residuals were normally distributed (refer to [Supplementary Figs. S1 and S2](#) for details).

Statistical analysis for research question 2 (RQ2): To assess how competition influences the biomass relationships among the biomass components of Scots pine and Pyrenean oak. We applied ANCOVA, which is the same approach described in RQ1, where X and Y represent biomass components instead of tree structural attributes.

Statistical analysis for research question 3 (RQ3): Although competition did not directly affect all aspects of biomass allocation, we anticipate that it might have an indirect effect on these relationships through tree structural attributes such as DBH, tree height, CBH, and CL. These attributes likely mediate the relationship between biomass allocation and competition. To ensure the robustness, accuracy, and statistical reliability of the results, we did not differentiate the species, as the sample sizes for individual species were insufficient to conduct species-specific structural equation modeling (SEM). [Fig. 3](#) shows the conceptual model used to construct the SEM to investigate this possibility. To do so, all continuous variables, i.e., biomass (stems, branches, foliage)

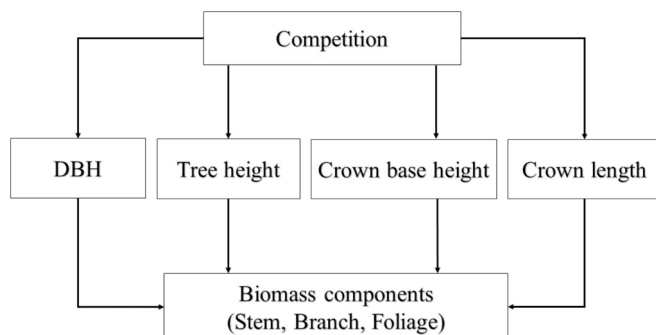


Fig. 3. The conceptual diagram illustrates how competition influences biomass allocation or components indirectly through tree structural attributes: DBH, tree height, crown base height, and crown length. These structural attributes mediate the effect of competition on biomass, serving as pathways through which competition indirectly determines the amount of biomass in different tree components. The arrows depict the flow of influence from competition to biomass components, with DBH, tree height, crown base height, and crown length acting as intermediaries.

and tree structural attributes (DBH, tree height, CBH, CL), were standardized to have a mean of zero and a standard deviation of one to allow for reasonable coefficient comparisons, following the approach used by [Mensah et al. \(2023\)](#). Multicollinearity checks using a correlation matrix and variance inflation factor (VIF) analysis led to the exclusion of CL due to redundancy and inflated standard errors. This decision was based on the strong correlation between tree height and CL ($r = 0.78$). In addition, five plausible sets of candidate SEMs were tested (see [Supplementary Material Table S1](#)), and the best-fitting model that accounts for the observed dataset was selected based on the Akaike information criterion (AIC) and Bayesian information criterion (BIC) ranking ([Burnham and Anderson, 2002; Garrido et al., 2022](#)). The purpose of this approach was intended to minimize model complexity and avoid overfitting. We used several standard indicators to evaluate the fit and validity of the optimal model. These indicators are: the chi-square (χ^2 , with $p > 0.05$), the comparative fit index (CFI > 0.90), the Tucker–Lewis index (TLI > 0.90), the root mean square error of approximation (RMSEA < 0.05), and the standardized root mean square residual (SRMR < 0.05) ([Schermelleh-Engel et al., 2003](#)). The best-fit model was then used for SEM analysis to assess the indirect pathways through which competition influences biomass allocation. Residual correlations between biomass components were modeled to account for unexplained shared variance and improve model fit, which is standard SEM practice.

3. Results

3.1. Effect of competition on allometric relationships (RQ1)

3.1.1. Allometric relationship between DBH and tree height

The ANCOVA results indicate that the model ($R^2 = 0.74$) had a significant effect on DBH (parameter estimate = 1.018, $p < 0.001$) and that competition (parameter estimate = 0.562, $p < 0.001$) had a significant effect on tree height ([Table 2](#)). As expected, competition significantly modified the allometric relationship between DBH and tree height in Scots pine and Pyrenean oak, revealing a significant interaction effect of DBH and competition on tree height (parameter estimate = -0.228 , $p < 0.001$). This interaction indicates that the strength of the relationship between DBH and tree height weakens as competition increases. In addition, we detected a significant difference in species (parameter estimate = -0.142 , $p < 0.001$), with Scots pine trees exhibiting lower tree heights than Pyrenean oak trees for the same DBH. This indicates distinct allometric patterns between both species in response to competition ([Fig. 4a](#)).

3.1.2. Allometric relationship between DBH and CBH

The model ($R^2 = 0.31$) revealed that DBH (parameter estimate = 1.380, $p < 0.01$) and competition (parameter estimate = 0.934, $p < 0.01$) were statistically significant, with a significant interaction effect of DBH and competition on CBH (parameter estimate = -0.380 , $p < 0.05$) as reported in [Table 2](#). This interaction suggests that competition modulates the relationship between DBH and CBH, which suggests that increasing competition reduces the influence of DBH on CBH. However, the observed effects were consistent across Scots pine and Pyrenean oak, with no significant species-specific differences (parameter estimate = 0.044, $p > 0.05$), as shown in [Fig. 4b](#). These results indicate that both species adjust their crown architecture to allocate resources similarly in competitive environments.

3.1.3. Allometric relationship between DBH and CL

After removing the interaction term (because it was nonsignificant, $p > 0.05$), the model ($R^2 = 0.65$) revealed that competition affects CL independently of DBH (parameter estimate = 0.070, $p < 0.05$). Additionally, DBH was correlated with CL (parameter estimate = 0.498, $p < 0.001$), which suggests that larger trees develop longer crown lengths. Importantly, this analysis revealed that competition influences the relationship between DBH and CL but not the interaction with DBH

Table 2
ANCOVA results for tree height, crown base height (CBH), and crown length (CL), including log-transformed predictors (DBH, competition, and their interaction effects) and species effects.

Model	Predictor	Estimate	Std. Error	t-value	p-value	Significance
Tree height	Intercept	−0.326	0.324	−1.006	0.3170	ns
	log (DBH)	1.018	0.174	5.861	8.51×10^{-8}	***
	log (Competition)	0.562	0.127	4.431	2.78×10^{-5}	***
	Species (Reference P. oak)	−0.142	0.028	−5.053	2.46×10^{-6}	***
	log (DBH): log (Competition)	−0.228	0.067	−3.428	0.0009	***
Crown base height (CBH)	Intercept	−2.205	0.867	−2.543	0.0128	*
	log (DBH)	1.380	0.466	2.963	0.0040	**
	log (Competition)	0.934	0.340	2.745	0.0074	**
	Species (Reference P. oak)	0.044	0.075	0.578	0.5647	ns
	log (DBH): log (Competition)	−0.380	0.179	−2.130	0.0361	*
Crown length (CL)	Intercept	0.302	0.141	2.135	0.0356	*
	log (DBH)	0.498	0.073	6.857	1.01×10^{-9}	***
	log (Competition)	0.070	0.031	2.249	0.0271	*
	Species (Reference P. oak)	−0.282	0.039	−7.225	1.90×10^{-10}	***
	log (DBH): log (Competition)	—	—	—	—	—

Notes: Dashes (—) indicate interaction terms not included in the model. Significance levels are denoted as follows: *** ($p < 0.001$), ** ($p < 0.01$), * ($p < 0.05$), and “ns” for nonsignificant results ($p \geq 0.05$).

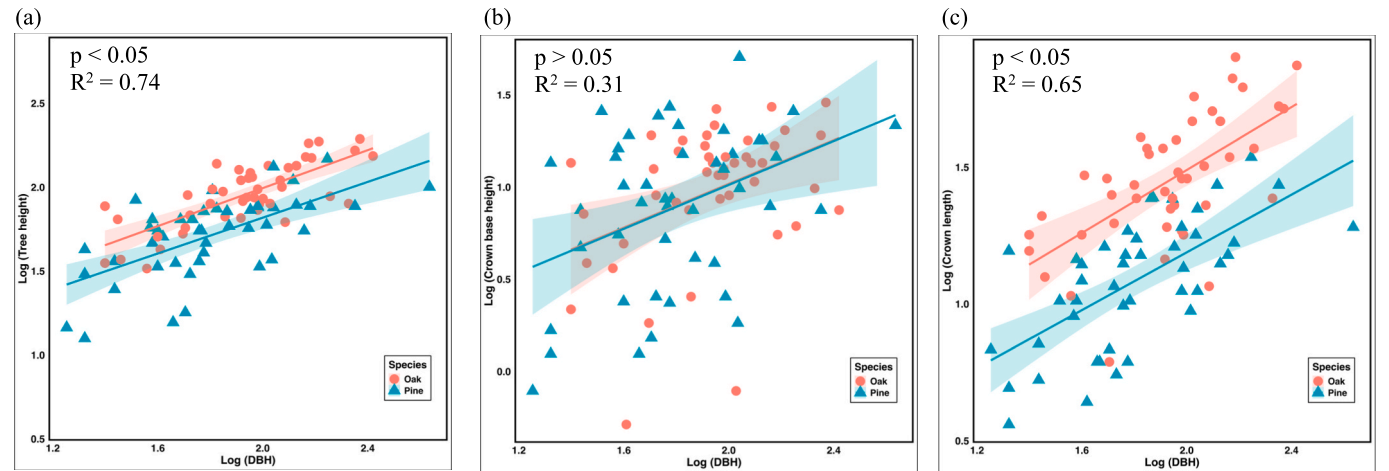


Fig. 4. Relationships between tree structural attributes for Pyrenean oak (red circles) and Scots pine (cyan triangles). Each panel depicts species differences in the response variable as indicated: (a): log (tree height) vs. log (DBH), showing a significant difference ($p < 0.05$). (b): log (crown base height) vs. log (DBH), with nonsignificant differences ($p > 0.05$). (c): log (crown length) vs. log (DBH), where the difference is not significant ($p > 0.05$). The significant differences in competition are further detailed in Table 2. The lines represent the fitted values, and the shaded regions represent the 95 % confidence intervals of the regression lines.

(Table 2). Scots pine and Pyrenean oak presented significantly different DBH–CL relationships (parameter estimate = -0.282 , $p < 0.001$), with Scots pine presenting shorter crown lengths than Pyrenean oak (Fig. 4c).

3.2. Competition and biomass allocation patterns (RQ2)

3.2.1. Biomass allocation between stems and branches

The ANCOVA results ($R^2 = 0.70$, $p > 0.05$) revealed that competition did not significantly influence the allocation relationship between stem

Table 3
The results of ANCOVA analyses were used to examine the effects of competition and species on the relationships among tree biomass components.

Model	Predictor	Estimate	Std. Error	t-value	p-value	Significance
Branch	Intercept	−1.384	0.241	−5.754	1.31×10^{-7}	***
	log (Stem)	1.051	0.083	12.671	$<2.00 \times 10^{-16}$	***
	log (Competition)	−0.100	0.076	−1.326	0.1883	ns
	Species (Reference P. oak)	0.289	0.111	2.607	0.0108	*
Stem	Intercept	2.112	0.175	12.080	$<2.00 \times 10^{-16}$	***
	log (Foliage)	0.619	0.054	11.370	$<2.00 \times 10^{-16}$	***
	log (Competition)	0.223	0.060	3.740	3.00×10^{-4}	***
	Species (Reference P. oak)	−1.111	0.085	−13.090	$<2.00 \times 10^{-16}$	***
Foliage	Intercept	−1.091	0.225	−4.852	5.41×10^{-6}	***
	log (Branch)	0.707	0.070	10.084	3.08×10^{-16}	***
	log (Competition)	−0.053	0.081	−0.656	0.5130	ns
	Species (Reference P. oak)	0.972	0.108	8.979	5.42×10^{-14}	***

Note: Significance levels are indicated as *** for $p < 0.001$, ** for $p < 0.01$, * for $p < 0.05$, and “ns” for nonsignificant results ($p \geq 0.05$).

and branch biomass, indicating that competitive intensity had a stable influence on branch–stem partitioning across both species. Interestingly, we found statistically significant differences in species ($p < 0.05$), suggesting inherent divergence in biomass allocation, with Scots pine consistently allocating more biomass to branches than Pyrenean oak does, regardless of competition (Table 3). This consistency in allocation aligns more closely with the established theory of allometric partitioning, implying that both species maintain similar allocation patterns across competitive pressures, as illustrated in Fig. 5a.

3.2.2. Biomass allocation between foliage and stems

The relationship between stem and foliage biomass was strongly affected by competition ($R^2 = 0.75$, $p < 0.001$), suggesting that competition influences resource allocation strategies. However, significant species-specific differences ($p < 0.001$) emerged, with Pyrenean oak allocating a greater proportion of biomass to stems, whereas Scots pine exhibited a lower relative allocation (Table 3). These findings support allometric partitioning theory by demonstrating unstable between foliage and stem allocation patterns under competition while highlighting unique species strategies in terms of biomass distribution (see Fig. 5b).

3.2.3. Biomass allocation between branches and foliage

The relationship between branch and foliage allocation indicates that competition does not significantly influence the biomass distribution between these components ($R^2 = 0.62$, $p > 0.05$), as shown in Table 3. This stability under competition suggests that a robust allocation pattern is unaffected by competition. However, significant species differences ($p < 0.001$) revealed that Scots pine allocates more biomass to foliage than Pyrenean oak does under competitive conditions, suggesting adaptive, species-driven strategies in terms of resource distribution (refer to Fig. 5c). Regardless of competition, the stability in branch–foliage allocation further supports the notion of allometric partitioning across both species, demonstrating inherent allocation strategies grounded in species traits.

3.3. Indirect effects of competition on biomass allocation (RQ3)

The SEM strongly fits the data, as indicated by the key fit indices (Fig. 6). In terms of direct effects, our results revealed that competition had a strong positive significant effect on tree height ($p < 0.001$). In addition, competition significantly indirectly affects stem and branch biomass through its influence on tree height. Specifically, competition

indirectly increased stem biomass (strong indirect effect: $p < 0.001$) and branch biomass (strong indirect effect: $p < 0.001$) through tree height. Although competition indirectly influenced foliage biomass mediated through tree height, this effect was not statistically significant ($p > 0.05$). This suggests that foliage biomass allocation may be less responsive to competitive pressures mediated by tree height. SEM explained the stem, branch, and foliage biomass variances in the following proportions: 0.611, 0.191, and 0.018, respectively. Significant residual correlations were found between biomass components, with strong relationships between stems and branches ($R^2 = 0.69$, $p < 0.001$), branches and foliage ($R^2 = 0.60$, $p < 0.001$), and stems and foliage ($R^2 = 0.38$, $p = 0.001$), indicating that neither tree height nor competition could fully explain the shared variance.

4. Discussion

4.1. Influence of competition on allometric relationships (RQ1)

Our findings demonstrated that competition significantly modifies the allometric relationships between DBH and tree attributes (eg., tree height, crown base height, and crown length) in Scots pine and Pyrenean oak (Table 2; Fig. 4a–c). Specifically, the relationship between DBH and tree height weakens as competition increases, suggesting that competition drives a shift in resource allocation. This aligns with earlier studies that emphasized the plasticity of tree architecture in response to competition, where tree height growth often supersedes diameter growth in denser stands (MacFarlane and Kane, 2017).

The significant interaction between DBH and competition further emphasized that taller trees are less likely to maintain tree height growth under competitive conditions, possibly due to limited light and nutrient availability (Chou et al., 2018). Moreover, our observation that Scots pine trees are shorter than Pyrenean oak trees at the same DBH in highly competitive environments suggests species-specific strategies, likely reflecting differences in growth prioritization (Pretzsch et al., 2020). This might also be because of the differences in physiological strategies and root system architecture between the two species studied.

Similarly, competition had an impact on the DBH–CBH relationship. Our findings revealed a substantial interaction effect between DBH and competitiveness, with higher levels of competition resulting in a decrease in CBH. This result supports the hypothesis that trees are forced to devote resources to tree height growth at the expense of crown development because of competition for light (Yamakawa et al., 2023). The lower branches in thick stands may be shaded and eventually die

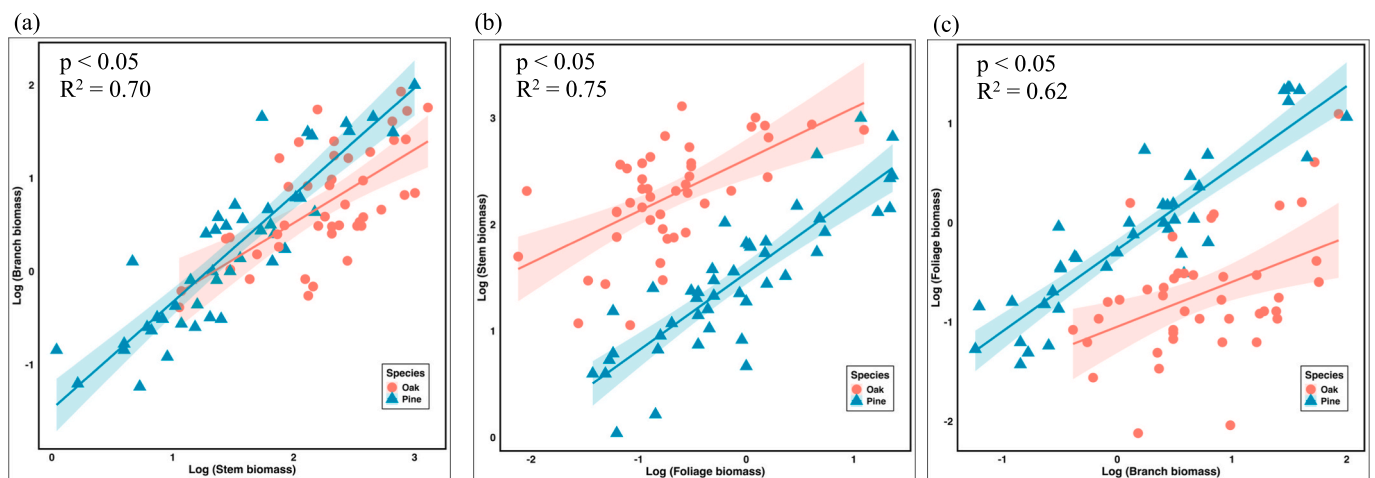


Fig. 5. Relationships between log-transformed biomass components for Pyrenean oak (red circles) and Scots pine (cyan triangles), with regression lines and 95 % confidence intervals. The following panels illustrate the significance level of competition: (a): log (branch biomass) vs. log (stem biomass) showing a nonsignificant difference ($p > 0.05$); (b): log (stem biomass) vs. log (foliage biomass) showing a significant difference ($p < 0.05$); and (c): log (foliage biomass) vs. log (branch biomass) with a nonsignificant difference ($p > 0.05$). The significant difference in competition is illustrated in Table 2.

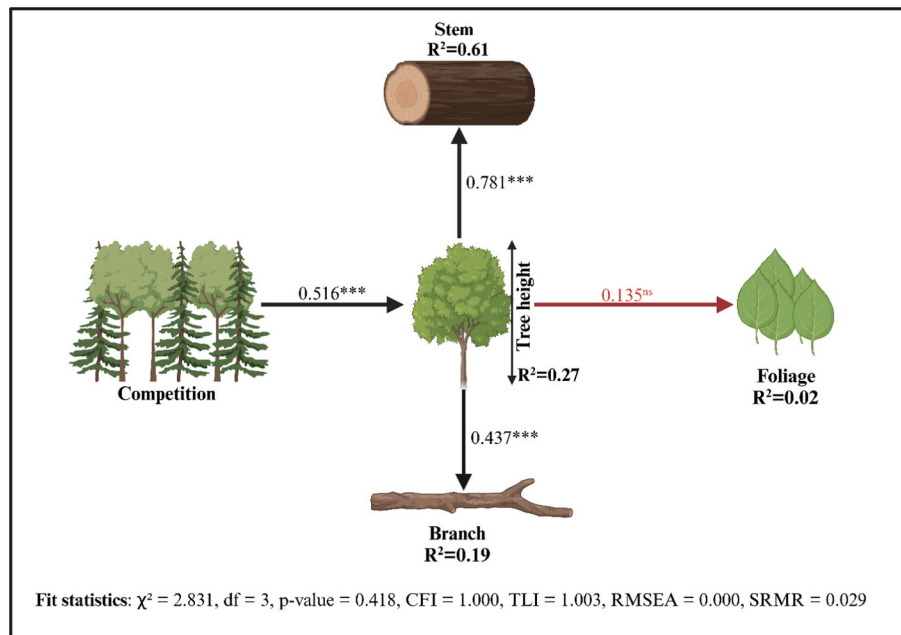


Fig. 6. The structural equation model (SEM) diagram illustrates the effects of competition on biomass allocation through tree height. The numbers adjacent to the arrows represent standardized pathway coefficients, with black arrows indicating significant pathways ($p < 0.05$) and red arrows representing nonsignificant pathways ($p > 0.05$). The coefficients of determination (R^2) indicate that the model $R^2 = 0.61$ for stems, whereas $R^2 = 0.27$ for tree height, $R^2 = 0.19$ for branches, and $R^2 = 0.02$ for foliage represent the explained variances. The goodness-of-fit statistics ($\chi^2 = 2.831$, $df = 3$, $p\text{-value} = 0.418$, $CFI = 1.000$, $TLI = 1.003$, $RMSEA = 0.000$, and $SRMR = 0.029$) indicate good model-data fit.

off, reducing the base height of the crown (Saarinen et al., 2022). Both Scots pine and Pyrenean oak showed this impact, and there were no significant variations in CBH across the species when they competed, indicating that their responses to competition in terms of crown architecture were comparable. Despite contrasting life-history traits (e.g., growth strategies), this lack of significant interspecies differences indicates a convergent strategy in crown architecture. This finding may be explained by the competitive dynamics in these stands differing from those typically observed in pure stands. This adaptive response, particularly evident in dense or crowded stands, may be attributed to light capture optimization, as suggested by studies on crown plasticity in mixed-species forests (Jucker et al., 2015).

We removed the interaction term from the model because, in contrast to tree height and CBH, the interaction between DBH and competition did not significantly alter the DBH–CL relationship. In contrast, the competition term significantly increased CL, indicating that trees in more competitive conditions grow longer crowns, perhaps as a means of maximizing light capture in crowded areas (del Río et al., 2019; Jucker et al., 2016). This finding is consistent with research suggesting that CL, as opposed to other tree structural attributes such as tree height or CBH, may be more malleable in response to environmental conditions such as light availability (Antin et al., 2013; Pretzsch et al., 2012; Yang and Swenson, 2023).

Pyrenean oak had a longer CL than Scots pine at the same DBH, indicating a species-specific variation in crown shape, even if competition had a favorable effect on CL. This confirms earlier observations that, under similar environmental conditions, broadleaf species such as oaks tend to have broader, more expansive crowns than conifers (Longuetaud et al., 2013). Given that light availability is essential for growth in mixed-species stands, the longer CL of Pyrenean oak may be a tactic to improve light interception (Ishii and Asano, 2010; Pretzsch et al., 2020).

4.2. Influence of competition on biomass allocation (RQ2)

The results reported here indicate that competition selectively modulates specific biomass allocation strategies, particularly

foliage–stem partitioning, whereas other biomass relationships, such as branch–stem and branch–foliage allocation, remain remarkably stable (Table 3; Fig. 5a–c). This stability observed in this study supports allometric partitioning theory (unaffected by competition), which posits that biomass allocation follows predictable scaling laws driven primarily by tree size (tree height and DBH) rather than by environmental changes such as competition (Liu et al., 2021). This pattern may withstand short-term competitive pressures. However, prolonged environmental stresses, such as ongoing drought or nutrient depletion, could disrupt these relationships, especially as stands continue to mature (Touche et al., 2024).

Typically, foliage–stem partitioning is highly sensitive to competition, highlighting that trees dynamically adjust their foliage biomass investment to optimize light capture and physiological efficiency in response to environmental constraints. These findings suggest that competition for light probably causes Scots pine to invest more in its foliage biomass. In contrast, Pyrenean oak, which can withstand greater shade, maintains its foliage–stem allocation more conservatively. These findings are consistent with optimal allocation theory (i.e., affected by competition), which posits that trees prioritize biomass investment into the most limiting organ to maximize growth and fitness under current conditions (Tsogtsaikhan et al., 2025).

Additionally, significant species-specific differences were evident across all allocation relationships. Compared with Pyrenean oak, Scots pine consistently allocated more biomass to branches and foliage for the same stem mass, while the latter allocated more biomass to stems. These interspecific differences suggest adaptive strategies unique to each species. The greater branch and foliage biomass allocation of Scots pine may reflect its strategy to increase light capture in dense stands, which aligns with previous findings on its shade-intolerant growth habits (Wertz et al., 2020). In contrast, Pyrenean oak allocated more biomass to its stem for the same foliage mass, a strategy that may enhance its ability to outcompete other species in mixed stands through stronger below-ground resource competition (Aldea et al., 2021). In contrast to the results of Pretzsch and Biber (2010) and Aspinwall et al. (2013), who reported pronounced effects of competition on biomass partitioning

across forest ecosystems, our findings indicate that competition may not uniformly disrupt allocation patterns. The potential explanation for this discrepancy could be the stage of development and distinct ecological context of the mixed Scots pine and Pyrenean oak stands in northern Spain, where competition dynamics may influence biomass distribution differently from that of mature forests (Prior and Bowman, 2014).

Additionally, research has shown that vertical stratification – the natural layering of trees into distinct canopy heights (i.e., overstory of pine, and understory of oak trees) – has not yet developed in young mixed stands, unlike mature forests. Consequently, trees in young mixed stands compete directly for light and resources (Barbeito et al., 2014). As shade tolerance shifts with age, Pyrenean oak may allocate biomass differently in the early stages, whereas Scots pine, although light-demanding, may initially struggle before gaining a tree height advantage (Franceschini and Schneider, 2014). This suggests that extrapolating competition effects from mature to young stands may be misleading (West and Ratkowski, 2022). Understanding these early-stage interactions is key to adaptive forest management and long-term stand resilience (Cattaneo et al., 2018).

4.3. Indirect effects of competition on biomass allocation (RQ3)

The outcomes of structural equation modeling (SEM) revealed that competition indirectly influenced biomass allocation through its effect on tree height. As competition increased, tree height increased, which, in turn, positively influenced stem and branch biomass allocation, whereas foliage biomass remained unaffected (Fig. 6). These results emphasize the role of tree height as a mediator in biomass allocation under competition, which aligns with growth prioritization models (Yang et al., 2024). However, the lack of significant effects on foliage biomass suggests that competitive environments prioritize vertical growth over foliar development to gain an advantage in terms of light acquisition (Gruntman et al., 2017). This could be a strategy that some trees use when under competition for light.

Recent studies have indicated that changes in tree allometry are associated with both species diversity and competition intensity (del Río et al., 2019; Forrester et al., 2017a). According to Gilbert et al. (2001), some species prioritize tree height growth more strongly in competitive contexts, whereas others might allocate biomass differently depending on their ecological traits, such as shade tolerance and successional status. Therefore, the indirect effects of competition on tree height, as measured by the model, represent a generalized trend across species rather than a species-specific response to competition. Therefore, caution should be exercised when generalizing across species with potentially divergent growth strategies.

Moreover, the residual correlations between biomass components highlighted the complexity of biomass allocation, with strong correlations between stem, branch, and foliage biomass. These findings suggest that unmeasured environmental factors, such as soil nutrients or microclimate variations, may further influence biomass allocation patterns, supporting the conclusions of Valor et al. (2024) that tree responses to competition are multifactorial and context dependent.

The combination of the two species studied in our analysis allowed us to increase the overall sample size, allowing us to perform more robust statistical modeling and reducing the risk of overfitting due to the presence of more species. The nature of this approach, however, may have influenced our findings in a variety of ways. Variations in growth strategy, allometric relationships, and competitive responses among species may affect the observed patterns because of differences in their growth strategies, allometric relationships, and competitive responses (Rollinson et al., 2016).

4.4. Implications and future research for forest management

While this study provides critical insights into early stage of stand development (aged 15–18 years) of competitive dynamics of Scots pine

and Pyrenean oak, it is important to recognize that competitive interactions evolve with stand development, especially under changing climate conditions. As stands mature, structural differentiation, species dominance, and resource partitioning may shift considerably, potentially altering the observed patterns in biomass allocation and allometric scaling (Pretzsch et al., 2020; Zeng et al., 2024).

In forests of similar composition to those in southwestern Europe, early precommercial thinning activity interventions ideally using light thinning methods should be prioritized in management plans not only to maintain species coexistence and balance competitive dynamics but also to promote drought-tolerant species such as Pyrenean oak. This can be achieved cost-effectively during early stand development through simple silvicultural measures that involve the use of a rotary mower or hatchet to reduce tree density and consequently decrease competition for resources. These interventions can help regulate species mixing ratios and structural diversity, guiding stand composition before costly and disruptive methods involving larger equipment (e.g., chainsaw thinning) become necessary in later stages. Understanding allometric relationships and competition effects in this early phase can inform species-targeted management and promote forest resilience in Mediterranean ecosystems, which are increasingly vulnerable to environmental stress (Altieri et al., 2024). Therefore, forest management measures should consider these differences in biomass allocation (Cudjoe et al., 2024; Fernández-de-Uña et al., 2015).

Further research on increasing destructive sampling efforts across diverse forest types and environmental gradients is needed to provide a more comprehensive understanding of how competition influences biomass allocation and species interactions in mixed-species forests. Further research should explore the role of abiotic factors, such as water availability and soil nutrients, in modulating these competitive dynamics. Moreover, future studies should conduct species-specific SEM analyses to more effectively capture the biomass allocation patterns and competitive responses of each species. Furthermore, alternative statistical frameworks, such as Bayesian SEM, could be explored in future work in handling small sample sizes.

5. Limitations

Despite this study providing valuable insights, several limitations should be noted. First, a limited destructive sampling dataset of aboveground biomass in mixed stands remains challenging, especially for capturing the full range of tree structural attributes and biomass allocation variability. Larger sample sizes across more diverse sites would provide stronger statistical power and more generalizable results. Second, the competition index (i.e., BAL) relies on a fixed influence zone radius, which may not capture all interactions in mixed stands. Third, our study did not account for scale variations in abiotic factors such as soil fertility, microclimatic conditions, and water availability, which could significantly influence biomass allocation. Finally, we combined all the tree species for our SEM to ensure adequate statistical power and reliable model estimates. However, species-specific responses to competition and biomass allocation might influence pathway identification.

6. Conclusion

Overall, this study provides novel insights into how competition shapes allometric relationships and biomass allocation patterns in young Scots pine and Pyrenean oak mixed-stands. Our results indicate that competition significantly modifies the allometric relationships of DBH–tree height, DBH–crown base height, and DBH–crown length, with both species exhibiting convergent adjustments to optimize resource use. Moreover, competition altered biomass allocation patterns, particularly foliage–stem partitioning, where greater competition reduced the proportion of biomass allocated to foliage. Scots pine was more responsive to competition, allocating more biomass to branches and foliage to

increase light capture, whereas Pyrenean oak prioritized stem biomass for belowground resource acquisition. Interestingly, branch-foliage and branch-stem biomass allocation remained stable despite the effects of competition.

Additionally, SEM demonstrated that competition indirectly alters biomass allocation through its influence on tree height, highlighting the importance of tree structural attributes as mediators of resource allocation. This nuanced understanding of direct and indirect effects enriches our knowledge of forest dynamics and species interactions in young mixed stands.

In conclusion, these findings demonstrate that competition and species-specific traits jointly influence biomass allocation and allometric patterns in young mixed forests growing in conditions representative of southwestern Europe. Recognizing these early dynamics is essential for designing adaptive, cost-effective silvicultural strategies to promote forest resilience under changing Mediterranean conditions.

CRedit authorship contribution statement

Eric Cudjoe: Writing – review & editing, Writing – original draft, Validation, Methodology, Investigation, Formal analysis, Conceptualization. **Felipe Bravo:** Writing – review & editing, Validation, Supervision, Project administration, Methodology, Funding acquisition, Conceptualization. **Hans Pretzsch:** Writing – review & editing. **Pete Bettinger:** Writing – review & editing. **Ricardo Ruiz-Peinado:** Writing – review & editing, Validation, Supervision, Methodology, Formal analysis, Conceptualization.

Funding

We express our deepest appreciation to the University of Valladolid and Banco Santander for their financial support, as well as to the following research projects: “CLU-2019-01 – Unidad de Excelencia Instituto iuFOR,” (Grant PID2021-126275OB-C21), and “Integrated Forest Management along complexity gradients, IMFLEX – (Grant PID2021-126275OB-C22),” funded by MCIN/AEI/10.13039/501100011033 and also European Regional Development Fund (ERDF). Support from the Regional Government of Castilla and León was also received by the project.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Acknowledgments

This research was carried out in the context of a PhD program in Conservation and Sustainable Use of Forest Systems at the University of Valladolid. Thank you to José Carlos Porto Rodríguez for his help in creating the research area map. We are incredibly thankful to everyone who helped make this research work successful in various ways.

Appendix A. Supplementary data

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.ecolind.2025.113713>.

References

- Akritas, M.G., Van Keilegom, I., 2001. ANCOVA methods for heteroscedastic nonparametric regression models. *J. Am. Stat. Assoc.* 96, 220–232. <https://doi.org/10.1198/016214501750332802>.
Aldea, J., Bravo, F., Vázquez-Piqué, J., Ruiz-Peinado, R., del Río, M., 2021. Differences in stem radial variation between *Pinus pinaster* Ait. and *Quercus pyrenaica* Willd. may

- release inter-specific competition. *For. Ecol. Manage.* 481, 118779. <https://doi.org/10.1016/j.foreco.2020.118779>.
Aldea, J., del Río, M., Cattaneo, N., Riofrío, J., Ordóñez, C., Uzquiano, S., Bravo, F., 2023. Short-term effect of thinning on inter- and intra-annual radial increment in Mediterranean Scots pine-oak mixed forests. *For. Ecol. Manage.* 549, 121462. <https://doi.org/10.1016/j.foreco.2023.121462>.
Altieri, S., Niccoli, F., Kabala, J.P., Liyaqat, I., Battipaglia, G., 2024. Influence of drought and minimum temperature on tree growth and water use efficiency of Mediterranean species. *Dendrochronologia* 83, 126162. <https://doi.org/10.1016/j.dendro.2023.126162>.
Antin, C., Péliissier, R., Vincent, G., Couteron, P., 2013. Crown allometries are less responsive than stem allometry to tree size and habitat variations in an Indian monsoon forest. *Trees - Struct. Funct.* 27, 1485–1495. <https://doi.org/10.1007/s00468-013-0896-7>.
Aspinwall, M.J., King, J.S., McKeand, S.E., 2013. Productivity differences among loblolly pine genotypes are independent of individual-tree biomass partitioning and growth efficiency. *Trees - Struct. Funct.* 27, 533–545. <https://doi.org/10.1007/s00468-012-0806-4>.
Barbeito, I., Collet, C., Ningre, F., 2014. Crown responses to neighbor density and species identity in a young mixed deciduous stand. *Trees - Struct. Funct.* 28, 1751–1765. <https://doi.org/10.1007/s00468-014-1082-2>.
Bravo-Oviedo, A., Pretzsch, H., Ammer, C., Andenmatten, E., Barbat, A., Barreiro, S., Brang, P., Bravo, F., Coll, L., Corona, P., Den Ouden, J., Ducey, M.J., Forrester, D.I., Gieregiczny, M., Jacobsen, J.B., Lesinski, J., Löf, M., Mason, B., Matovic, B., Metslaid, M., Morneau, F., Motiejunaite, J., O'Reilly, C., Pach, M., Ponette, Q., Del Río, M., Short, I., Skovsgaard, J.P., Soliño, M., Spathelf, P., Sterba, H., Stojanovic, D., Strelcova, K., Svoboda, M., Verheyen, K., Von Lüpke, N., Zlatanov, T., 2014. European mixed forests: Definition and research perspectives. *For. Syst.* 23, 518–533. <https://doi.org/10.5424/fs/2014233-06256>.
Brzeziecki, B., Kienast, F., 1994. Classifying the life-history strategies of trees on the basis of the Grime model. *For. Ecol. Manage.* 69, 167–187. [https://doi.org/10.1016/0378-1127\(94\)90227-5](https://doi.org/10.1016/0378-1127(94)90227-5).
Burnham, K.P., Anderson, D.R., 2002. Multimodel inference: A Practical Information-Theoretic Approach, Sociological Methods and Research.
Carvalho, B., de la Cruz, M., Escudero, A., Bastias, C.C., Valladares, F., Benavides, R., 2022. The effect of plant-plant interactions as a key biotic process mediating the spatial variation of phenotypes in a *Pinus sylvestris* forest. *Trees - Struct. Funct.* 36, 1401–1412. <https://doi.org/10.1007/s00468-022-02299-9>.
Cattaneo, N., Bravo-Oviedo, A., Bravo, F., 2018. Analysis of tree interactions in a mixed Mediterranean pine stand using competition indices. *Eur. J. For. Res.* 137, 109–120. <https://doi.org/10.1007/s10342-017-1094-8>.
Chou, C.B., Hedin, L.O., Pacala, S.W., 2018. Functional groups, species and light interact with nutrient limitation during tropical rainforest sapling bottleneck. *J. Ecol.* 106, 157–167. <https://doi.org/10.1111/1365-2745.12823>.
Condés, S., del Río, M., 2015. Climate modifies tree interactions in terms of basal area growth and mortality in monospecific and mixed *Fagus sylvatica* and *Pinus sylvestris* forests. *Eur. J. For. Res.* 134, 1095–1108. <https://doi.org/10.1007/s10342-015-0912-0>.
Cudjoe, E., Bravo, F., Ruiz-Peinado, R., 2024. Allometry and biomass dynamics in temperate mixed and monospecific stands: Contrasting response of Scots pine (*Pinus sylvestris* L.) and sessile oak (*Quercus petraea* (Matt.) Liebl.). *Sci. Total Environ.* 953, 176061. <https://doi.org/10.1016/j.scitotenv.2024.176061>.
Cudjoe, E., Ruiz-Peinado, R., Pretzsch, H., Ahmed, S., Bravo, F., 2025. Neighborhood competition improves biomass estimation for Scots pine (*Pinus sylvestris* L.) but not Pyrenean oak (*Quercus pyrenaica* Willd.) in young mixed forest stands. *For. Ecosyst.* 13, 100317. <https://doi.org/10.1016/j.fecs.2025.100317>.
Cuny, H., Leban, J.M., Hervé, J.C., Bontemps, J.D., Kerfriden, B., Jacquin, P., Lacarin, M., Dauffy, V., Duprez, C., Wurrpillot, S., 2025. XyloDensMap: a georeferenced dataset for the wood density of 110,000 trees from 156 European species in France. *Sci. Data* 12, 380. <https://doi.org/10.1038/s41597-025-04645-1>.
de Tomás Marín, S., Rodríguez-Calcerrada, J., Arenas-Castro, S., Prieto, I., González, G., Gil, L., de la Riva, E.G., 2023. *Fagus sylvatica* and *Quercus pyrenaica*: Two neighbors with few things in common. *For. Ecosyst.* 10, 100097. <https://doi.org/10.1016/j.fecs.2023.100097>.
del Río, M., Bravo-Oviedo, A., Ruiz-Peinado, R., Condés, S., 2019. Tree allometry variation in response to intra- and inter-specific competitions. *Trees - Struct. Funct.* 33, 121–138. <https://doi.org/10.1007/s00468-018-1763-3>.
Dieler, J., Pretzsch, H., 2013. Morphological plasticity of European beech (*Fagus sylvatica* L.) in pure and mixed-species stands. *For. Ecol. Manage.* 295, 97–108. <https://doi.org/10.1016/j.foreco.2012.12.049>.
Dybzinski, R., Farrior, C.E., Pacala, S.W., 2015. Increased forest carbon storage with increased atmospheric CO₂ despite nitrogen limitation: A game-theoretic allocation model for trees in competition for nitrogen and light. *Glob. Chang. Biol.* 21, 1182–1196. <https://doi.org/10.1111/gcb.12783>.
Fernández-de-Uña, L., Cañellas, I., Gea-Izquierdo, G., 2015. Stand competition determines how different tree species will cope with a warming climate. *PLoS One* 10, e0122255. <https://doi.org/10.1371/journal.pone.0122255>.
Fick, S.E., Hijmans, R.J., 2017. WorldClim 2: new 1-km spatial resolution climate surfaces for global land areas. *Int. J. Climatol.* 37, 4302–4315. <https://doi.org/10.1002/joc.5086>.
Forrester, D.I., Benneter, A., Bouriaud, O., Bauhus, J., 2017a. Diversity and competition influence tree allometric relationships – developing functions for mixed-species forests. *J. Ecol.* 105, 761–774. <https://doi.org/10.1111/1365-2745.12704>.
Forrester, D.I., Pretzsch, H., 2015. On the strength of evidence when comparing ecosystem functions of mixtures with monocultures. *Tamm Rev. For. Ecol. Manag.* 356, 41–53.

- Forrester, D.I., Tachauer, I.H., Annighoefer, P., Barbeito, I., Pretzsch, H., Ruiz-Peinado, R., Stark, H., Vacchiano, G., Zlatanov, T., Chakraborty, T., Saha, S., Sileshi, G.W., 2017b. Generalized biomass and leaf area allometric equations for European tree species incorporating stand structure, tree age and climate. *For. Ecol. Manage.* 396, 160–175. <https://doi.org/10.1016/j.foreco.2017.04.011>.
- Fox, J., Weisberg, S., Adler, D., Bates, D., Baud-Bovy, G., Ellison, S., Firth, D., Friendly, M., Gorjanc, G., Graves, S., 2012. Package ‘car’. *Vienna R Found. Stat. Comput.* 16, 333.
- Franceschini, T., Schneider, R., 2014. Influence of shade tolerance and development stage on the allometry of ten temperate tree species. *Oecologia* 176, 739–749. <https://doi.org/10.1007/s00442-014-3050-3>.
- Garrido, M., Hansen, S.K., Yaari, R., Hawlena, H., 2022. A model selection approach to structural equation modelling: A critical evaluation and a road map for ecologists. *Methods Ecol. Evol.* 13, 42–53. <https://doi.org/10.1111/2041-210X.13742>.
- Gilbert, I.R., Jarvis, P.G., Smith, H., 2001. Proximity signal and shade avoidance differences between early and late successional trees. *Nature* 411, 792–795. <https://doi.org/10.1038/35081062>.
- Gómez-Aparicio, L., García-Valdés, R., Ruiz-Benito, P., Zavala, M.A., 2011. Disentangling the relative importance of climate, size and competition on tree growth in Iberian forests: implications for forest management under global change. *Glob. Chang. Biol.* 17, 2400–2414. <https://doi.org/10.1111/j.1365-2486.2011.02421.x>.
- Gruntman, M., Groß, D., Májeková, M., Tielbörger, K., 2017. Decision-making in plants under competition. *Nat. Commun.* 8, 2235. <https://doi.org/10.1038/s41467-017-02147-2>.
- Hilmers, T., Mehtälä, L., Bielak, K., Brazaitis, G., del Río, M., Ruiz-Peinado, R., Schmed, G., Uhl, E., Pretzsch, H., 2024. Towards resource-efficient forests: Mixing species changes crown biomass allocation and improves growth efficiency. *Plants People Planet* 117–132. <https://doi.org/10.1002/ppp3.10562>.
- Huuskonen, S., Lahtinen, T., Miina, J., Uotila, K., Bianchi, S., Niemistö, P., 2023. Growth Dynamics of Young Mixed Norway Spruce and Birch Stands in Finland. *Forests* 14, 56. <https://doi.org/10.3390/f14010056>.
- Hynynen, J., Repola, J., Mielikäinen, K., 2011. The effects of species mixture on the growth and yield of mid-rotation mixed stands of Scots pine and silver birch. *For. Ecol. Manage.* 262, 1174–1183. <https://doi.org/10.1016/j.foreco.2011.06.006>.
- Ishii, H., Asano, S., 2010. The role of crown architecture, leaf phenology and photosynthetic activity in promoting complementary use of light among coexisting species in temperate forests. *Ecol. Res.* 25, 715–722. <https://doi.org/10.1007/s11284-009-0668-4>.
- Jucker, T., Avacaritei, D., Bămoaiea, I., Duduman, G., Bouriaud, O., Coomes, D.A., 2016. Climate modulates the effects of tree diversity on forest productivity. *J. Ecol.* 104, 388–398. <https://doi.org/10.1111/1365-2745.12522>.
- Jucker, T., Bouriaud, O., Coomes, D.A., 2015. Crown plasticity enables trees to optimize canopy packing in mixed-species forests. *Funct. Ecol.* 29, 1078–1086. <https://doi.org/10.1111/1365-2435.12428>.
- Litton, C.M., Raich, J.W., Ryan, M.G., 2007. Carbon allocation in forest ecosystems. *Glob. Chang. Biol.* 13, 2089–2109. <https://doi.org/10.1111/j.1365-2486.2007.01420.x>.
- Liu, R., Yang, X., Gao, R., Hou, X., Huo, L., Huang, Z., Cornelissen, J.H.C., 2021. Allometry rather than abiotic drivers explains biomass allocation among leaves, stems and roots of *Artemisia* across a large environmental gradient in China. *J. Ecol.* 109, 1026–1040. <https://doi.org/10.1111/1365-2745.13532>.
- Longuetaud, F., Piboule, A., Wernsdörfer, H., Collet, C., 2013. Crown plasticity reduces inter-tree competition in a mixed broadleaved forest. *Eur. J. For. Res.* 132, 621–634. <https://doi.org/10.1007/s10342-013-0699-9>.
- MacFarlane, D.W., Kane, B., 2017. Neighbour effects on tree architecture: functional trade-offs balancing crown competitiveness with wind resistance. *Funct. Ecol.* 31, 1624–1636. <https://doi.org/10.1111/1365-2435.12865>.
- Marqués, L., Camarero, J.J., Zavala, M.A., Stoffel, M., Ballesteros-Cánovas, J.A., Sancho-García, C., Madrigal-González, J., 2021. Evaluating tree-to-tree competition during stand development in a relict Scots pine forest: how much does climate matter? *Trees - Struct. Funct.* 35, 1207–1219. <https://doi.org/10.1007/s00468-021-02109-8>.
- Matías, L., Jump, A.S., 2015. Asymmetric changes of growth and reproductive investment herald altitudinal and latitudinal range shifts of two woody species. *Glob. Chang. Biol.* 21, 882–896. <https://doi.org/10.1111/gcb.12683>.
- Mensah, S., Noulékoun, F., Dimobe, K., Seifert, T., Glèlè Kakaï, R., 2023. Climate and soil effects on tree species diversity and aboveground carbon patterns in semi-arid tree savannas. *Sci. Rep.* 13, 509. <https://doi.org/10.1038/s41598-023-38225-3>.
- Mensah, S., Seifert, T., Glèlè Kakaï, R., 2016. Patterns of biomass allocation between foliage and woody structure: The effects of tree size and specific functional traits. *Ann. For. Res.* 59, 49–60. <https://doi.org/10.15287/afr.2016.458>.
- Nieto Quintano, P., Caudullo, G., de Rigo, D., 2016. *Quercus pyrenaica* in Europe: distribution, habitat, usage and threats. In: San-Miguel-Ayán, J., de Rigo, D., Caudullo, G., Houston Durrant, T., Mauri, A. (Eds.), *European Atlas of Forest Tree Species*. Publ. Off. EU, Luxembourg, p. e01f807.
- Niinemets, Ü., Valladares, F., 2006. Tolerance to shade, drought, and waterlogging of temperate northern hemisphere trees and shrubs. *Ecol. Monogr.* 76, 521–547. [https://doi.org/10.1890/0012-9615\(2006\)076\[0521:TTSDAW\]2.0.CO;2](https://doi.org/10.1890/0012-9615(2006)076[0521:TTSDAW]2.0.CO;2).
- Niklas, K.J., 2006. A phyletic perspective on the allometry of plant biomass-partitioning patterns and functionally equivalent organ-categories. *New Phytol.* 171, 27–40. <https://doi.org/10.1111/j.1469-8137.2006.01760.x>.
- Niklas, K.J., 1994. *Plant Allometry: The Scaling of Form and Process*. University of Chicago Press, Chicago.
- Poorter, H., Jagodzinski, A.M., Ruiz-Peinado, R., Kuyah, S., Luo, Y., Oleksyn, J., Usoltsev, V.A., Buckley, T.N., Reich, P.B., Sack, L., 2015. How does biomass distribution change with size and differ among species? An analysis for 1200 plant species from five continents. *New Phytol.* 208, 736–749. <https://doi.org/10.1111/nph.13571>.
- Pretzsch, H., 2018. Growth and Structure in Mixed-Species Stands Compared with Monocultures: Review and Perspectives. https://doi.org/10.1007/978-3-319-91953-9_5.
- Pretzsch, H., 2014. Canopy space filling and tree crown morphology in mixed-species stands compared with monocultures. *For. Ecol. Manage.* 327, 251–264. <https://doi.org/10.1016/j.foreco.2014.04.027>.
- Pretzsch, H., Biber, P., 2010. Size-symmetric versus size-asymmetric competition and growth partitioning among trees in forest stands along an ecological gradient in Central Europe. *Can. J. For. Res.* 40, 370–384. <https://doi.org/10.1139/X09-195>.
- Pretzsch, H., Biber, P., Schütze, G., Uhl, E., Rötzer, T., 2014. Forest stand growth dynamics in Central Europe have accelerated since 1870. *Nat. Commun.* 5, 4967. <https://doi.org/10.1038/ncomms5967>.
- Pretzsch, H., del Río, M., Ammer, C., Avdagic, A., Barbeito, I., Bielak, K., Brazaitis, G., Coll, L., Dimberger, G., Drössler, L., Fabrika, M., Forrester, D.I., Godvold, K., Heym, M., Hurt, V., Kurylyak, V., Löf, M., Lombardi, F., Matović, B., Mohren, F., Motta, R., den Ouden, J., Pach, M., Ponette, Q., Schütze, G., Schweig, J., Skrzyszewski, J., Sramek, V., Sterba, H., Stojanović, D., Svoboda, M., Vanhellemont, M., Verheyen, K., Wellhausen, K., Zlatanov, T., Bravo-Oviedo, A., 2015a. Growth and yield of mixed versus pure stands of Scots pine (*Pinus sylvestris* L.) and European beech (*Fagus sylvatica* L.) analysed along a productivity gradient through Europe. *Eur. J. For. Res.* 134, 927–947. <https://doi.org/10.1007/s10342-015-0900-4>.
- Pretzsch, H., Forrester, D.I., Rötzer, T., 2015b. Representation of species mixing in forest growth models: A review and perspective. *Ecol. Modell.* 313, 276–292. <https://doi.org/10.1016/j.ecolmodel.2015.06.044>.
- Pretzsch, H., Matthew, C., Dieler, J., 2012. Allometry of Tree Crown Structure. Relevance for Space Occupation at the Individual Plant Level and for Self-Thinning at the Stand Level 287–310. https://doi.org/10.1007/978-3-642-30645-7_13.
- Pretzsch, H., Schütze, G., 2021. Tree species mixing can increase stand productivity, density and growth efficiency and attenuate the trade-off between density and growth throughout the whole rotation. *Ann. Bot.* 128, 767–786. <https://doi.org/10.1093/aob/mcab077>.
- Pretzsch, H., Steckel, M., Heym, M., Biber, P., Ammer, C., Ehbrecht, M., Bielak, K., Bravo, F., Ordóñez, C., Collet, C., Vast, F., Drössler, L., Brazaitis, G., Godvold, K., Jansons, A., de-Dios-García, J., Löf, M., Aldea, J., Korboulewsky, N., Reventlow, D.O., J., Nothdurft, A., Engel, M., Pach, M., Skrzyszewski, J., Pardos, M., Ponette, Q., Sitko, R., Fabrika, M., Svoboda, M., Cerný, J., Wolff, B., Ruiz-Peinado, R., del Río, M., 2020. Stand growth and structure of mixed-species and monospecific stands of Scots pine (*Pinus sylvestris* L.) and oak (*Q. robur* L., *Quercus petraea* (Matt.) Liebl.) analysed along a productivity gradient through Europe. *Eur. J. For. Res.* 139, 349–367. <https://doi.org/10.1007/s10342-019-01233-y>.
- Pretzsch, H., Zenner, E.K., 2017. Toward managing mixed-species stands: from parametrization to prescription. *For. Ecosyst.* 4, 19. <https://doi.org/10.1186/s40663-017-0105-z>.
- Prior, L.D., Bowman, D.M.J.S., 2014. Across a macro-ecological gradient forest competition is strongest at the most productive sites. *Front. Plant Sci.* 5, 1–12. <https://doi.org/10.3389/fpls.2014.00260>.
- R Core Team, 2023. *R: A Language and Environment for Statistical Computing*. R Foundation for Statistical Computing, Vienna, Austria.
- Rodríguez de Prado, D., Riofrio, J., Aldea, J., Bravo, F., Herrero de Aza, C., 2022. Competition and climate influence in the basal area increment models for Mediterranean mixed forests. *For. Ecol. Manage.* 506, 119955. <https://doi.org/10.1016/j.foreco.2021.119955>.
- Rollinson, C.R., Kaye, M.W., Canham, C.D., 2016. Interspecific variation in growth responses to climate and competition of five eastern tree species. *Ecology* 97, 1003–1011. <https://doi.org/10.1890/1515-549.1>.
- Rosseel, Y., 2012. *lavaan: An R Package for Structural Equation Modeling*. *J. Stat. Softw.* 48, 1–36. <https://doi.org/10.18637/jss.v048.i02>.
- Ruiz-Peinado, R., del Río, M., Montero, G., 2011. New models for estimating the carbon sink capacity of Spanish softwood species. *For. Syst.* 20, 176–188. <https://doi.org/10.5424/fs/2011201-11643>.
- Ruiz-Peinado, R., Montero, G., del Río, M., 2012. Biomass models to estimate carbon stocks for hardwood tree species. *For. Syst.* 21, 42–52. <https://doi.org/10.5424/fs/2112211-02193>.
- Ruiz-Peinado, R., Pretzsch, H., Löf, M., Heym, M., Bielak, K., Aldea, J., Barbeito, I., Brazaitis, G., Drössler, L., Godvold, K., Granhus, A., Holm, S.O., Jansons, A., Makrickienė, E., Metslaid, M., Metslaid, S., Nothdurft, A., Otto Juel Reventlow, D., Sitko, R., Stankevičienė, G., del Río, M., 2021. Mixing effects on Scots pine (*Pinus sylvestris* L.) and Norway spruce (*Picea abies* (L.) Karst.) productivity along a climatic gradient across Europe. *For. Ecol. Manage.* 482, 118834. <https://doi.org/10.1016/j.foreco.2020.118834>.
- Saarienen, N., Kankare, V., Huuskonen, S., Hynynen, J., Bianchi, S., Yrttimaa, T., Luoma, V., Junttila, S., Holopainen, M., Hyyppä, J., Vastaranta, M., 2022. Effects of Stem Density on Crown Architecture of Scots Pine Trees. *Front. Plant Sci.* 13, 1–14. <https://doi.org/10.3389/fpls.2022.817792>.
- Schermelleh-Engel, K., Moosbrugger, H., Müller, H., 2003. Evaluating the fit of structural equation models: Tests of significance and descriptive goodness-of-fit measures. *Methods Psychol. Res.* online 8, 23–74.
- Thyoff, E.C., Burney, O.T., Mickelbart, M.V., Jacobs, D.F., 2019. Unraveling Shade Tolerance and Plasticity of Semi-Evergreen Oaks: Insights From Maritime Forest Live Oak Restoration. *Front. Plant Sci.* 10, 1526. <https://doi.org/10.3389/fpls.2019.01526>.
- Touche, J., Calvaruso, C., De Donato, P., Turpault, M.P., 2024. Drought events influence nutrient canopy exchanges and green leaf partitioning during senescence in a deciduous forest. *For. Ecosyst.* 11, 100173. <https://doi.org/10.1016/j.fecs.2024.100173>.

- Trouvé, R., Bontemps, J.D., Collet, C., Seynave, I., Lebourgeois, F., 2017. Radial growth resilience of sessile oak after drought is affected by site water status, stand density, and social status. *Trees - Struct. Funct.* 31, 517–529. <https://doi.org/10.1007/s00468-016-1479-1>.
- Tsogtsaikhan, T., Yang, X., Gao, R., Liu, J., Tang, W., Liu, G., Ye, X., Huang, Z., 2025. Biomass allocation between reproductive and vegetative organs of *Artemisia* along a large environmental gradient. *BMC Plant Biol.* 25, 27. <https://doi.org/10.1186/s12870-024-06030-3>.
- Valor, T., Coll, L., Forrester, D.I., Pretzsch, H., del Río, M., Bielak, K., Brzeziecki, B., Binder, F., Hilmers, T., Sitková, Z., Tognetti, R., Ameztegui, A., 2024. Competitive effect, but not competitive response, varies along a climatic gradient depending on tree species identity. *For. Ecosyst.* 11, 100176. <https://doi.org/10.1016/j.fecs.2024.100176>.
- Wertz, B., Bembek, M., Karaszewski, Z., Ochał, W., Skorupski, M., Strzeliński, P., Wegiel, A., Mederski, P.S., 2020. Impact of stand density and tree social status on aboveground biomass allocation of scots pine *Pinus sylvestris* L. *Forests* 11, 765. <https://doi.org/10.3390/f11070765>.
- West, P.W., Ratkowsky, D.A., 2022. Problems with models assessing influences of tree size and inter-tree competitive processes on individual tree growth: a cautionary tale. *J. For. Res.* 33, 565–577. <https://doi.org/10.1007/s11676-021-01395-9>.
- Wickham, H., 2016. *ggplot2: Elegant Graphics for Data Analysis*. Springer-Verlag, New York, Media.
- Wilcox, R.R., 2005. An Approach to Ancova that Allows Multiple Covariates, Nonlinearity, and Heteroscedasticity. *Educ. Psychol. Meas.* 65, 442–450. <https://doi.org/10.1177/0013164404268670>.
- Williamson, G.B., Wiemann, M.C., 2010. Measuring wood specific gravity...Correctly. *Am. J. Bot.* 97, 519–524. <https://doi.org/10.3732/ajb.0900243>.
- Wykoff, R.W., Crookston, N.L., Stage, A.R., 1982. User's Guide to the Stand Prognosis Model. General Technical Report INT-133 118.
- Yamakawa, M., Onoda, Y., Kurokawa, H., Oguro, M., Nakashizuka, T., Hikosaka, K., 2023. Competitive asymmetry in a forest composed of a shade-tolerant species depends on gap formation. *For. Ecol. Manage.* 549, 121442. <https://doi.org/10.1016/j.foreco.2023.121442>.
- Yang, J., Swenson, N.G., 2023. Height and crown allometries and their relationship with functional traits: An example from a subtropical wet forest. *Ecol. Evol.* 13, e9804. <https://doi.org/10.1002/ece3.9804>.
- Yang, M., Zhou, X., Liu, Z., Li, P., Liu, C., Huang, H., Tang, J., Zhang, C., Zou, Z., Xie, B., Peng, C., 2024. Dynamic carbon allocation trade-off: A robust approach to model tree biomass allometry. *Methods Ecol. Evol.* 15, 886–899. <https://doi.org/10.1111/2041-210X.14315>.
- Zeng, X., Li, J., Peng, Q., Gong, C., Ran, H., Xie, T., Liao, T., Zhou, T., Huang, D., Song, Q., Liu, J., Yang, Q., 2024. Differences in Response of Tree Species at Different Succession Stages to Neighborhood Competition. *Forests* 15, 435. <https://doi.org/10.3390/f15030435>.