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Neighborhood competition improves biomass estimation for Scots pine (*Pinus sylvestris* L.) but not Pyrenean oak (*Quercus pyrenaica* Willd.) in young mixed forest stands

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ABSTRACT

Neighborhood competition is a critical driver of individual tree growth, and aboveground biomass (AGB) accumulation, which together play key roles in forest dynamics and carbon storage. Therefore, accurate biomass estimation is essential for understanding ecosystem functioning and informing forest management strategies to mitigate climate change. However, integrating neighborhood competition into biomass estimation models, particularly for young mixed forest stands, remains unexplored. In this study, we examined how incorporating neighborhood competition improves biomass prediction accuracy and how the influence of neighborhood competition differs between Scots pine (*Pinus sylvestris* L.) and Pyrenean oak (*Quercus pyrenaica* Willd.), as well as the relative contributions of intra- and interspecific competition to AGB. Our findings revealed that including neighborhood competition alongside tree size variables (DBH and total tree height) significantly improved the predictive accuracy of AGB models for Scots pine. This addition reduced the root mean square error (RMSE) by 14% and improved the model efficiency factor (MEF) by 15%. Furthermore, intraspecific competition in Scots pine slightly reduced AGB, whereas interspecific competition had a significant negative effect on AGB. In contrast, DBH alone was the best predictor of AGB for Pyrenean oak, as neighborhood competition did not improve model performance. Also, intra- and interspecific competition in Pyrenean oak had positive but nonsignificant effects on AGB. These findings highlight the important role of competition in biomass models and suggest species-specific approaches in competition dynamics to inform sustainable forest management and climate change adaptation strategies.

1. Introduction

Forests are essential carbon sinks in the global carbon cycle and are integral to reducing the effects of climate change (Millar et al., 2007; Roe et al., 2019). The carbon sequestration process (i.e., the capacity of forests to sequester carbon) is predominantly determined by tree biomass, which is influenced by various factors such as species composition, tree age, and competition dynamics within the forest ecosystem (Zhou et al., 2008). Therefore, the accurate measurement and estimation of forest biomass, specifically aboveground biomass (AGB), are important for effective forest management, carbon accounting, and ecological research as a strategy to mitigate climate change (Pan et al., 2011).

Scots pine (*Pinus sylvestris* L.) and Pyrenean oak (*Quercus pyrenaica* Willd.) are two species that hold ecological and economic importance in Mediterranean and temperate European forests. Scots pine is a valuable species in Eurasia because of its ecological range and wood/timber value, however, it faces considerable challenges due to climate change caused by a combination of increased temperatures and drought stress (Jaime et al., 2019). Pyrenean oak is a deciduous oak species found in the Iberian Peninsula, southwestern France, and northern Morocco. This species plays a crucial role in biodiversity, soil and water conservation, and the supply of timber and nonwood resources; however, it is highly susceptible to climate change, which impacts productivity and habitat stability

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List of abbreviations

Adj. R^2	Adjusted coefficient of determination
AGB	Aboveground biomass
AIC	Akaike information criterion
CF	Correction factor
CI	Competition index
CI_{inter}	Interspecific competition index
CI_{intra}	Intraspecific competition index
DBH	Diameter at breast height
$\text{FW}_{\text{stem section}}$	Fresh weight of the stem section
HT	Total tree height
MEF	Model efficiency
NBA	Neighborhood basal area
R	Competition radius
RMSE	Root mean square error
SB	Biomass of the stem base
$\text{SDW}_{\text{stem section}}$	Subsample dry weight of the stem section
$\text{SFW}_{\text{stem section}}$	Subsample fresh weight of the stem section
SM	Biomass of the stem middle
ST	Biomass of the stem top
VIF	Variance inflation factor

(Gea-Izquierdo and Cañellas, 2014).

Monospecific forests are particularly vulnerable to climate change, with reduced resilience to drought, increased susceptibility to pests and diseases, and limited capacity for long-term adaptation (Liu et al., 2018). In contrast, mixed forests can mitigate these risks through complementary ecological strategies that increase resource use, promote biodiversity, and improve forest stability and productivity (Forrester et al., 2017; Rodriguez de Prado et al., 2023). Thus, integrating Scots pine and Pyrenean oak in mixed forests may provide advantages over monocultures (Pretzsch et al., 2013; Warner et al., 2023).

del Río and Sterba (2009) investigated the growth dynamics of Scots pine and Pyrenean oak in both monocultures and mixtures, especially in Spanish Mediterranean forests, reporting that mixed stands typically recorded higher volume increments per unit area than monoculture stands. Furthermore, Muñoz-Gálvez et al. (2021) reported that complementarity effects within mixtures enhanced the stability of forest productivity. Given their differing ecological strategies, Scots pine and Pyrenean oak may face varying competitive pressures, potentially resulting in distinct biomass allocation patterns that affect overall forest productivity and carbon sequestration (Cudjoe et al., 2024).

Neighborhood competition, defined as the degree of crowding among neighboring trees, is an important factor affecting individual tree growth and biomass accumulation (Metz et al., 2013). This form of competition is particularly pronounced during the early growth stages of trees (del Río et al., 2014), as trees compete with nearby trees for resources such as light, water, and nutrients (Oyden and Inkley, 2005). Importantly, competition occurs both within species (intraspecific competition) and between species (interspecific competition). While intraspecific competition arises among individuals of the same species, often leading to resource depletion due to similar ecological requirements, interspecific competition occurs among different species and can vary depending on their ecological traits, growth strategies, and resource use (Zhang et al., 2024). Intraspecific competition in dense Scots pine stands may lead to greater self-thinning and reduced growth due to intense competition for similar resources, whereas interspecific interactions between Scots pine and Pyrenean oak could either mitigate or exacerbate competition depending on their spatial arrangement and resource use (Aldea et al., 2023). Understanding the effect of neighborhood, intraspecific, and interspecific competition on tree biomass is crucial for developing accurate models of forest carbon storage and improving forest management practices.

Competition indices (CIs) are mostly used to quantify the intensity of competition for resources among individual trees, either within the same species or between different species. These indices are classified into two main groups: distance-dependent indices and distance-independent indices (Burkhart and Tomé, 2012; Lorimer, 1983; Sun et al., 2019). Distance-dependent indices require detailed spatial information (including spatial data of neighboring trees) as well as tree dimensions, which are often used in national forest inventories and field maps. In contrast, distance-independent indices are simpler and rely only on individual tree variables, making them more scalable and efficient for a wide range of applications (Kahriman et al., 2018; Rivas et al., 2005). Distance-independent indices prove advantageous in large-scale forest inventories and ecological studies where detailed spatial data may not be available (Burkhart and Tomé, 2012).

Competition significantly alters tree biomass accumulation, stand structure, and ecosystem functioning (Jucker et al., 2014). Similarly, ignoring competition effects in biomass models may lead to inaccurate estimates (Forrester et al., 2017; Forrester and Albrecht, 2014). Despite good research evidence showing the role of competition in biomass estimation (Ali et al., 2020; González de Andrés et al., 2018; Nong et al., 2019; Rubio-Cuadrado et al., 2020; Zhou et al., 2018), most available models have focused predominantly on monocultures of young/mature trees or on mixed mature forests. As a result, these models fail to incorporate three important factors, namely, neighborhood competition, intraspecific competition, and interspecific competition, particularly in young mixed-species stands. This omission leaves a significant gap in the prediction of biomass dynamics (Nong et al., 2019; Zhou et al., 2018).

Certainly, young mixed-species forests, characterized by various species exhibiting diverse ecological characteristics and competing strategies, offer a more complex view of competition that is still not well understood (Pretzsch and Forrester, 2017; Werner et al., 2024). Hence, these ecosystems could display more intricate competitive relationships, resulting in varied biomass dynamics. The study of young mixed-species stands is important for understanding early successional dynamics, species complementarity, and resilience, which are essential for forest management and predicting future forest structure (Pretzsch and Forrester, 2017).

In this study, we investigated the impact of neighborhood competition (i.e., measured by the total basal area of competitors) on AGB estimation in these forests. In addition, we examined the impact of integrating intra- and interspecific competition on AGB prediction. Specifically, we hypothesized that: (H1) models that included neighborhood competition would enhance performance in the estimation of AGB in comparison with models that exclude competition; (H2) the effects of neighborhood competition on biomass predictions would differ between Scots pine and Pyrenean oak due to species-specific responses to growth patterns and competitive abilities; and (H3) intraspecific competition would affect AGB differently from that of interspecific competition. These findings are expected to contribute to developing more accurate biomass models, enhance carbon accounting, and promote sustainable forest management practices in mixed-species forests.

2. Materials and methods

2.1. Study site

This research was performed in a 15- to 18-year-old mixed forest of Scots pine and Pyrenean oak in the municipality of Quintanar de la Sierra (Burgos), which is located in the Sierra de la Demanda region of Spain (see Fig. 1). The study site is geographically located at 41.9781° N, −3.0194° W, ranging in elevation from 1,120 to 1,150 m above sea level (a.s.l.). The climate is Mediterranean, with mean annual maximum and minimum temperatures of 16.67 °C and 4.75 °C, respectively. The highest recorded temperature was 33 °C, whereas the coldest recorded temperature was −6.5 °C (Fick and Hijmans, 2017). The forest consists of

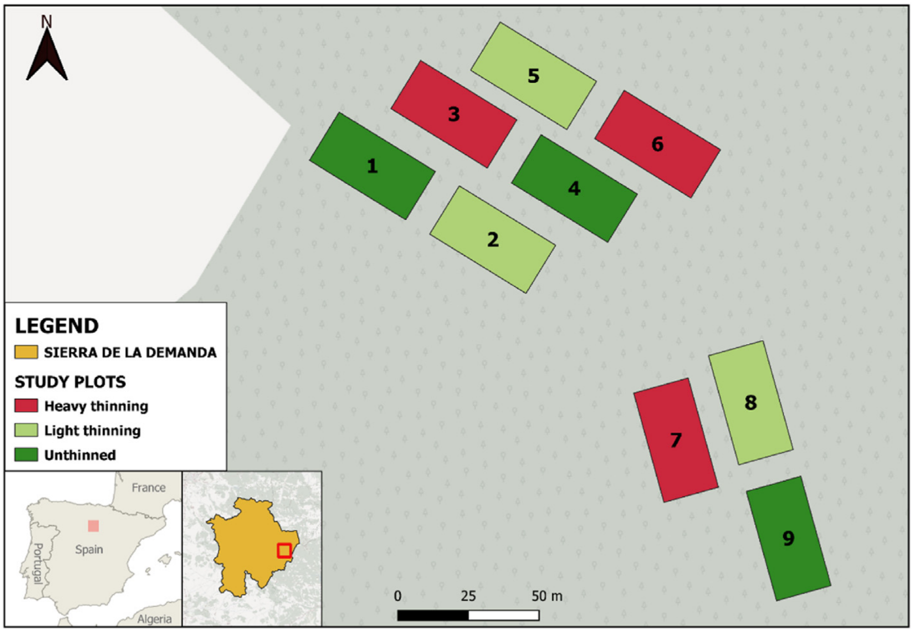

Fig. 1. Map of the study area and design of the sampling plots located in the Sierra de la Demanda region of Spain. Unthinned plots (Plots 1, 4, and 9) are represented in dark green, lightly thinned plots (Plots 2, 5, and 8) are represented in light green, and heavily thinned plots (Plots 3, 6, and 7) are represented in red.

naturally regenerating Scots pine and Pyrenean oak. The usual management practices in the area involved sowing seeds and planting young pines due to its faster growth and economic importance to promote pine regeneration. In addition, measures such as selective thinning and protection of existing oaks were part of the attempt to maintain a balance between the two species. At the beginning of the experiment (2016), the initial density was 50,000 stems per hectare and the dominant height was approximately 6 m. The experimental design consisted of 9 rectangular plots (20 m × 40 m each) with different precommercial thinning treatments. The first treatment was the control (unthinned), where no thinning was applied. The second treatment involved light thinning, which targeted a specific post-thinning density of approximately 30,000 stems per hectare. The third treatment involved heavy thinning, which aimed to achieve a density of 15,000 stems per hectare after thinning while maintaining a mixture of species to produce a more open forest structure – a less competitive environment at this stage – that allows for potentially economically profitable conditions.

2.2. *Sampling and measurement procedures*

The fieldwork was conducted from winter 2022 to spring 2023, with the primary goal of estimating the biomass of young trees. As part of the preliminary survey, the tree variables of both species in the experimental plots were measured (i.e., the diameter at breast height (DBH) was measured using a precision digital caliper, and the total tree height (HT) was measured using a graduated height pole). These tree measurements were conducted to provide a comprehensive overview of the range of DBH and HT to inform the selection of target trees before harvesting. Based on tree size (DBH and HT) and thinning densities (unthinned, light and heavy), we divided the trees into small, medium, and large classes to ensure representativeness and capture variation in both tree size and competition. Random sampling was then used to select target trees from each class. We harvested 90 target trees, including 45 Scots pine trees and 45 Pyrenean oak trees, to accurately represent the variability in DBH, HT, and thinning densities. We determined a competition radius (*R*, measured in meters) as 25% of the target HT for effective neighborhood

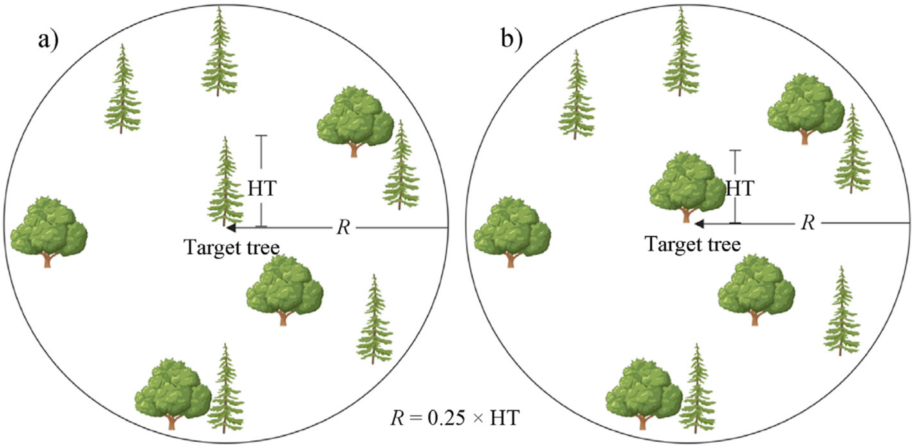

Fig. 2. Assessment of the zone of influence (not to scale) for target trees and their competitors within a specified competition radius under the **(a)** Scots pine target tree scenario and **(b)** Pyrenean oak target tree scenario.

analysis (as illustrated in Fig. 2), following the concept applied in other studies (Ahmed et al., 2024; Pretzsch, 2022; Pretzsch and Schütze, 2021). Accordingly, R was used to identify and measure the DBH of all neighboring trees within this distance. Studies on neighborhood competition have shown that tree species often exhibit considerable competitive interactions, reflecting the typical range of influence on resource competition. To guarantee precise data collection and reduce the influence of outside factors on biomass estimates, we adapted specific harvesting criteria for the target trees. We avoided trees with signs of structural damage or disease, dead trees, and trees with dead tops. In addition, the target trees near plot boundaries were omitted to facilitate accurate quantification of neighboring trees within R.

Each target tree was cut down, and its branches and foliage were removed from the stem and weighed separately in the field with an accuracy of 10 g using a portable scale. The entire stem was systematically divided into three sections (base, middle, and top), and each section was weighed separately. Representative stem subsamples were carefully taken from each section and weighed in the field. All the sample (branches and foliage) and subsample (stem) materials were subsequently transported to the laboratory and uniformly dried at a temperature of 102 °C (Williamson and Wiemann, 2010) until they reached a steady weight. The stem dry biomass was calculated from the dry and fresh masses of the subsamples, along with the fresh mass of each section of the stem biomass obtained from the field, as shown in Eq. 1. The total stem biomass was determined by summing the biomasses of the stems at the base, middle, and top. However, for the branches and foliage components, the total biomass was equal to the biomass dry weight obtained from the oven. The total dry aboveground biomass was calculated by summing the biomasses of the stem, branches, and foliage (refer to Eq. 2). Summary statistics (means ± standard deviations) for these biometric measurements, along with the number of trees harvested, are presented in Table 1.

$$\text{Biomass}_{\text{stem section}} = \text{FW}_{\text{stem section}} \times \frac{\text{SDW}_{\text{stem section}}}{\text{SFW}_{\text{stem section}}} \tag{1}$$

$$\text{AGB} = (\text{Biomass}_{\text{SB}} + \text{Biomass}_{\text{SM}} + \text{Biomass}_{\text{ST}}) + \text{Biomass}_{\text{branches}} + \text{Biomass}_{\text{foliage}} \tag{2}$$

where $\text{FW}_{\text{stem section}}$ represents the fresh weight of the stem section, $\text{SDW}_{\text{stem section}}$ represents the subsample dry weight of the stem section, and $\text{SFW}_{\text{stem section}}$ represents the subsample fresh weight of the stem section. $\text{Biomass}_{\text{SB}}$, $\text{Biomass}_{\text{SM}}$, and $\text{Biomass}_{\text{ST}}$ are the biomasses of the stem base (SB), stem middle (SM), and stem top (ST), respectively, whereas $\text{Biomass}_{\text{branches}}$ and $\text{Biomass}_{\text{foliage}}$ are the biomasses of the branches and foliage, respectively.

2.3. *Competition index calculation*

The total CI, hereinafter referred to as the neighborhood basal area (NBA), was used as a distance-independent metric for assessing and quantifying competitive interactions within young mixed pine–oak forest stands. The NBA has a straightforward formula, making it easy to calculate and interpret (Burkhart and Tomé, 2012; Dahlhausen et al., 2017). This competition metric is calculated by summing the basal areas of all neighboring trees within R, as delineated in Eq. 3:

$$\text{NBA}_i = \sum_{j=1}^{n_i} \left(\frac{\pi d_j^{\,2}}{4} \right) \tag{3}$$

where NBA_i is the neighborhood basal area (m^2) of trees in plot i, d_j is the diameter (cm) of the jth tree and n_i is the total number of trees within R of the target tree in plot i.

As part of the competition analysis, we separated NBA into intraspecific competition index (CI_{intra}) and interspecific competition index (CI_{inter}), based on the species composition of neighborhood trees relative to the target tree within the competition radius (R). Specifically, CI_{intra} represents the total basal area of neighboring trees of the same species as the target tree, whereas CI_{inter} represents the total basal area of neighboring trees of different species. A detailed summary of the competition indices, including NBA, CI_{intra}, and CI_{inter} for Scots pine and Pyrenean oak under the different thinning treatments, is provided in Table 1.

2.4. *Analyses and biomass modeling*

The entire suite of analyses was performed using R version 4.3.1 (R Core Team, 2023), with the “tidyverse” package specifically used for data manipulation and visualization (Wickham et al., 2019). Initially, plot and thinning treatments were included in the models as random effects. However, since both were not significant, we excluded them from further analysis. Hypotheses (H1) and (H2): Logarithmic regression was used to test whether competition, measured by the basal area of competitor trees, significantly affected the AGB models (Eqs. 4–11). This method was used to address the exponential growth patterns encountered in competitor trees and their associated AGB. By converting these exponential relationships into linear relationships, we effectively address the problem of heteroscedasticity in biomass data. This approach aligns with established biomass estimation methods documented in previous studies (Dutcă et al., 2018; Sun et al., 2024). The simplicity and interpretability of logarithmic models make them especially useful for ecological studies, where relationships are often multiplicative, allowing for a clearer understanding of biological interactions. Analyzing biomass data with this approach enhances the scientific rigor and relevance of our findings.

Furthermore, we selected four commonly used biomass estimation models (Eqs. 4, 6, 8 and 10) as reported by Cudjoe et al. (2024) and Sun et al. (2024). We then integrated neighborhood competition into these models, resulting in the development of additional models (Eqs. 5, 7, 9 and 11). We assessed eight models in total to evaluate the impact of incorporating competition into biomass models. We conducted a likelihood ratio test (LRT) to determine whether there was a significant difference between the models without competition factors and the models with competition factors, specifically for those models that included the same tree size variables (Supplementary Materials Tables S1 and S2). Next, we conducted the Shapiro–Wilk test for residual normality, the Studentized Breusch–Pagan test for homogeneity of variance, and the Durbin–Watson test for detecting residual autocorrelation (Supplementary Materials Table S3). We subsequently evaluated how the variables in

Table 1

Summary statistics (mean ± standard deviation) of the biometric measurements of Scots pine and Pyrenean oak target trees. DBH is the diameter at breast height; HT is the total tree height; n is the number of harvested trees; AGB ($\text{kg}\cdot\text{tree}^{-1}$) is the aboveground biomass per tree; CI_{intra} is the competition index within the same species; CI_{inter} is the competition index between different species; and NBA is the neighborhood basal area, which represents the total CI.

Species	Treatment	n	DBH (cm)	HT (m)	AGB ($\text{kg}\cdot\text{tree}^{-1}$)	CI_{intra} (m^2)	CI_{inter} (m^2)	NBA (m^2)
Scots pine	No thinning	15	6.22 ± 1.87	6.37 ± 1.17	10.99 ± 8.02	0.0093 ± 0.0087	0.0067 ± 0.0057	0.0160 ± 0.0069
Scots pine	Light thinning	15	5.74 ± 1.60	4.84 ± 1.13	5.98 ± 3.13	0.0086 ± 0.0079	0.0051 ± 0.0071	0.0137 ± 0.0102
Scots pine	Heavy thinning	15	7.03 ± 2.34	5.88 ± 1.09	8.44 ± 6.79	0.0153 ± 0.0156	0.0053 ± 0.0050	0.0206 ± 0.0131
Pyrenean oak	No thinning	15	6.71 ± 1.80	7.62 ± 1.39	11.41 ± 3.92	0.0103 ± 0.0116	0.0085 ± 0.0108	0.0188 ± 0.0122
Pyrenean oak	Light thinning	15	6.91 ± 1.32	7.13 ± 1.29	14.25 ± 5.63	0.0166 ± 0.0144	0.0069 ± 0.0069	0.0236 ± 0.0114
Pyrenean oak	Heavy thinning	15	7.68 ± 2.10	6.80 ± 1.30	17.48 ± 11.36	0.0111 ± 0.0101	0.0109 ± 0.0104	0.0220 ± 0.0125

the models were related to each other to detect and prevent multicollinearity. This was done using the variance inflation factor (VIF), with a VIF greater than 5 considered indicative of significant multicollinearity (Supplementary Materials Table S3). In addition, we visually examined the relationship between predicted versus observed values and predicted versus residual values of the selected models (as shown in Fig. 3a–d). Statistical assumption checks were performed to ensure the model accuracy and validity of our regression fits.

$$\text{Model 1}: \log(\text{AGB}) = a + b \times \log(\text{DBH}) + \varepsilon \tag{4}$$

$$\text{Model 2}: \log(\text{AGB}) = a + b \times \log(\text{DBH}) + c \times \log(\text{NBA}) + \varepsilon \tag{5}$$

$$\text{Model 3}: \log(\text{AGB}) = a + b \times \log(\text{DBH}) + c \times \log(\text{HT}) + \varepsilon \tag{6}$$

$$\text{Model 4}: \log(\text{AGB}) = a + b \times \log(\text{DBH}) + c \times \log(\text{HT}) + d \times \log(\text{NBA}) + \varepsilon \tag{7}$$

$$\text{Model 5}: \log(\text{AGB}) = a + b \times \log\left(\text{DBH}^2 \times \text{HT}\right) + \varepsilon \tag{8}$$

$$\text{Model 6}: \log(\text{AGB}) = a + b \times \log\left(\text{DBH}^2 \times \text{HT}\right) + c \times \log(\text{NBA}) + \varepsilon \tag{9}$$

$$\text{Model 7}: \log(\text{AGB}) = a + b \times \log(\text{HT}) + \varepsilon \tag{10}$$

$$\text{Model 8}: \log(\text{AGB}) = a + b \times \log(\text{HT}) + c \times \log(\text{NBA}) + \varepsilon \tag{11}$$

where log() denotes the natural logarithm; a, b and c represent the coefficients of the model; and ε is the error term.

Hypothesis (H3): The best-selected model for each species was used to evaluate the separate effects of intra- and interspecific competition on AGB. We computed the log-transformed of intra- and interspecific competition indices to meet the normality assumptions required for linear modeling. Since these indices contained zero values, a constant of 1 was added before transformation (i.e., $\log(\text{CI}_{\text{intra}}+1)$ and $\log(\text{CI}_{\text{inter}}+1)$) to avoid undefined values. After the regression coefficients for the log-transformed CIs were obtained, the results were back-transformed to the original scale using the exponential function (exp(w) for intra-competition and exp(z) for interspecific competition). The competition terms were adjusted similarly to Eqs. 4–11 but with log(NBA) included, as shown here:

$$\log(\text{NBA}) = w \times \log(\text{CI}_{\text{intra}} + 1) + z \times \log(\text{CI}_{\text{inter}} + 1)$$

where w and z are the coefficients for the intra- and interspecific competition indices, respectively.

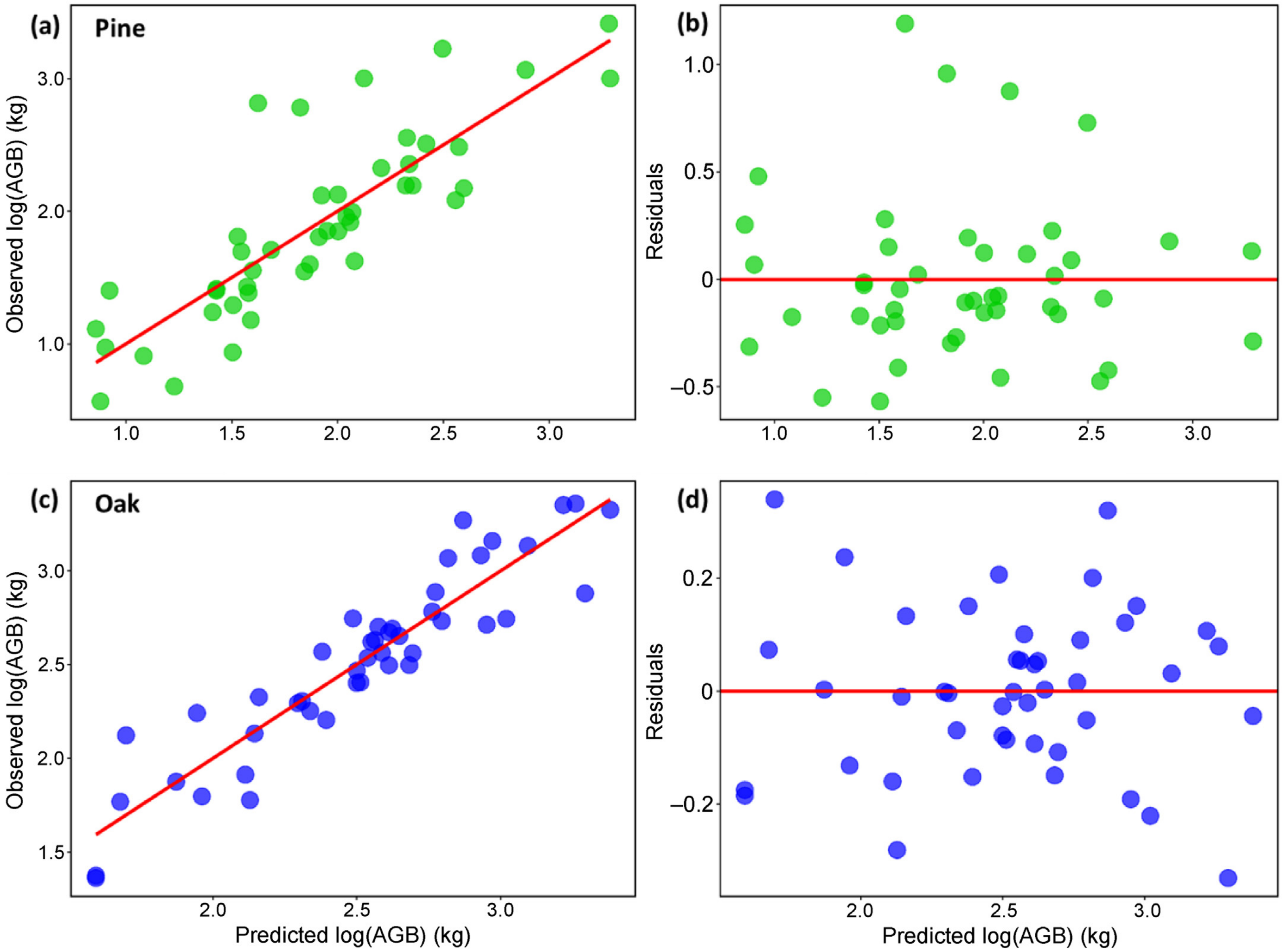

Fig. 3. Panels **(a)** and **(b)** show the relationships between predicted versus observed values and predicted versus residual log-transformed AGB for Scots pine (green), respectively, using the best-performing model, Model 6. In addition, panels **(c)** and **(d)** illustrate a similar relationship between predicted versus observed values and predicted versus residual log-transformed AGB for Pyrenean oak (blue), respectively, using the optimal model, Model 1.

A correction factor (CF) is required when converting logarithmic transformations back to biomass units (kg). The CF can be calculated using Eq. 12 to eliminate or minimize the bias inherent during the conversion process. According to Baskerville (1972), the predicted log values are corrected by multiplying them by the CF:

$$\mathrm{CF} = \exp\left(\frac{\mathrm{SEE}^2}{2}\right) \tag{12}$$

where SEE is the standard error of the estimate.

2.5. Statistical criteria

Initially, the significance of the parameters in the models was assessed. The models were then evaluated using four metrics in this order: AIC, RMSE, Adj. R^2, and MEF. Finally, a graphical analysis assessed residuals vs. predicted values and observed vs. predicted values. The first metric considers the Akaike information criterion (AIC) because of its ability to assess the goodness of fit of the models (Akaike, 1974), as shown in Eq. 13:

$$\mathrm{AIC} = -2 + \ln(L) + 2 + p \tag{13}$$

where L = the maximum likelihood of the model and p = the number of parameters in the model. The lowest AIC value indicated the best-performing model. The models were subsequently assessed using the root mean square error (RMSE) to evaluate the model's performance, as illustrated in Eq. 14:

$$\mathrm{RMSE} = \frac{\sum_{i=1}^{n}(y_i - \hat{y}_i)^2}{n-p} \tag{14}$$

where n = the number of target trees, y_i and $\hat{y}_i$ = the observed and predicted AGB values, respectively, and p = the number of parameters in the equation. The lower the RMSE, the more accurate the model. Furthermore, the Adj. R^2 values were analyzed to measure the model's predictive accuracy (Sun et al., 2024), as depicted in Eq. 15:

$$\text{Adj. } R^2 = 1 - \frac{\sum_{i=1}^{n}(y_i - \hat{y}_i)^2}{\sum_{i=1}^{n}(y_i - \bar{y}_i)^2} \times \frac{n-1}{n-p} \tag{15}$$

where n = the number of target trees, y_i and $\hat{y}_i$ = the observed and predicted AGB values, respectively, $\bar{y}_i$ = the mean of the observed value, and p = the number of parameters in the equation. The higher the Adj. R^2, the greater the proportion of variance in AGB that is explained by the model. Finally, the model efficiency (MEF) was used to evaluate the models, as shown in Eq. 16:

$$\mathrm{MEF} = 1 - \frac{\sum_{i=1}^{n}(y_i - \hat{y}_i)^2}{\sum_{i=1}^{n}(y_i - \bar{y}_i)^2} \tag{16}$$

where n = the number of target trees, y_i and $\hat{y}_i$ = the observed and predicted AGB values, respectively, and $\bar{y}_i$ = the mean of the observed value. Higher MEF values indicate better model performance.

3. Results

3.1. Evaluating biomass predictive models for Scots pine and Pyrenean oak in mixed stands (H1 and H2)

Eight different models were evaluated to determine the best variables and the role of neighborhood competition in estimating the biomass of Scots pine and Pyrenean oak, as shown in Tables 2 and 3, respectively. For Scots pine, Model 6, which used DBH, HT, and NBA yielded the best performance with AIC of 45.931, RMSE of 0.353, Adj. R^2 of 0.789, and MEF of 0.803. Consequently, the RMSE was reduced by 14%, the Adj. R^2 was increased by 12%, and the MEF was improved by 15%. The incorporation of CI was significant in three out of the four models ($p < 0.05$), except in Model 1, which underscores its importance in predicting biomass (Supplementary Materials Table S1). For Pyrenean oak, the CI did not improve model performance, as it was not significant in any of the models tested ($p > 0.05$). Although Model 2, which included CI surpassed Model 1 in terms of regression fit quality, the CI was not statistically significant ($p > 0.05$). Accordingly, DBH was the only variable considered in this model. Model 1, which included only DBH, performed best with an AIC of −12.980, an RMSE of 0.196, an Adj. R^2 of 0.850, and an MEF of 0.854 (Supplementary Materials Table S2).

Table 2
Parameter estimates, standard errors (SE), p-values, and model fit metrics, such as the Akaike information criterion (AIC), root mean square error (RMSE), adjusted coefficient of determination (Adj. R^2), model efficiency factor (MEF), and correction factor (CF) for the log models were calculated for Scots pine.

Model No.	Coefficient	Estimate	SE	p–value	AIC	RMSE	Adj. R^2	MEF	CF
1	a	−1.510	0.403	0.001 ***	54.842	0.416	0.622	0.630	1.095
	b	1.889	0.221	$7.680\mathrm{e}^{-11}$ ***					
2	a	−2.119	0.695	0.004 **	52.619	0.411	0.623	0.640	1.095
	b	1.971	0.233	$1.300\mathrm{e}^{-10}$ ***					
	c	−0.107	0.100	0.288 ns					
3	a	−1.893	0.474	$3.000\mathrm{e}^{-04}$ ***	54.549	0.406	0.632	0.649	1.092
	b	1.617	0.285	$1.140\mathrm{e}^{-06}$ ***					
	c	0.510	0.344	0.146 ns					
4	a	−4.698	1.003	$3.060\mathrm{e}^{-05}$ ***	47.073	0.365	0.695	0.715	1.076
	b	1.433	0.266	$3.220\mathrm{e}^{-06}$ ***					
	c	1.396	0.424	0.002 **					
	d	−0.377	0.122	0.004 **					
5	a	−1.997	0.445	$5.250\mathrm{e}^{-05}$ ***	53.020	0.408	0.637	0.645	1.091
	b	0.732	0.083	$3.180\mathrm{e}^{-11}$ ***					
6	a	**−3.824**	**0.757**	**$8.980\mathrm{e}^{-06}$ *****	**45.931**	**0.353**	**0.789**	**0.803**	**1.077**
	b	**0.850**	**0.087**	**$2.160\mathrm{e}^{-12}$ *****					
	c	**−0.280**	**0.097**	**0.006 ****					
7	a	−1.137	0.598	0.064 ns	78.198	0.540	0.364	0.379	1.165
	b	1.770	0.346	$6.810\mathrm{e}^{-06}$ ***					
8	a	−5.150	1.290	$3.000\mathrm{e}^{-04}$ ***	69.150	0.477	0.491	0.514	1.130
	b	2.800	0.432	$7.990\mathrm{e}^{-08}$ ***					
	c	−0.524	0.153	0.002 **					

Note: a, b, and c are the estimates of the coefficients. The significance levels are * $p < 0.05$, ** $p < 0.01$, and *** $p < 0.001$. Nonsignificant (ns) values, with $p > 0.05$, are indicated as "ns". The bold values indicate the final model selected for AGB for Scots pine.

Table 3

Parameter estimates, standard errors (SE), p-values, and model fit metrics such as the Akaike information criterion (AIC), root mean square error (RMSE), adjusted coefficient of determination (Adj. R^2), model efficiency factor (MEF), and correction factor (CF) for the log models were calculated for Pyrenean oak.

Model No.	Coefficient	Estimate	SE	p–value	AIC	RMSE	Adj. R^2	MEF	CF
1	*a*	**−1.046**	**0.228**	**$3.890e^{-05}$ *****	**−12.980**	**0.196**	**0.850**	**0.854**	**1.020**
	b	**1.857**	**0.117**	**$2.000e^{-16}$ *****					
2	*a*	−0.643	0.357	0.079 ns	−13.192	0.191	0.854	0.861	1.020
	b	1.806	0.121	$2.000e^{-16}$ ***					
	c	0.076	0.052	0.153 ns					
3	*a*	−0.914	0.474	0.005 **	−11.401	0.195	0.848	0.855	1.021
	b	1.944	0.285	$1.420e^{-13}$ ***					
	c	−0.153	0.344	0.533 ns					
4	*a*	−0.323	0.461	0.488 ns	−12.478	0.188	0.855	0.865	1.020
	b	1.948	0.178	$9.180e^{-14}$ ***					
	c	−0.271	0.248	0.282 ns					
	d	0.092	0.054	0.096 ns					
5	*a*	−1.494	0.298	$9.54e^{-06}$ ***	−1.674	0.222	0.808	0.812	1.026
	b	0.693	0.051	$2.000e^{-16}$ ***					
6	*a*	−1.231	0.461	0.011 *	−0.273	0.221	0.826	0.814	1.026
	b	0.680	0.054	$9.270e^{-16}$ ***					
	c	0.046	0.061	0.457 ns					
7	*a*	−1.037	0.594	0.088 ns	45.811	0.377	0.447	0.460	1.077
	b	1.828	0.302	$3.120e^{-07}$ ***					
8	*a*	−0.496	0.903	0.586 ns	47.137	0.374	0.542	0.468	1.078
	b	1.725	0.330	$5.190e^{-06}$ ***					
	c	0.084	0.106	0.430 ns					

Note: *a*, *b*, and *c* are the estimates of the coefficients. The significance levels are * $p < 0.05$, ** $p < 0.01$, and *** $p < 0.001$. Nonsignificant (ns) values, with $p > 0.05$, are indicated as "ns". The bold values indicate the final model selected for AGB for Pyrenean oak.

3.2. *Effects of intra- and interspecific competition on AGB (H3)*

Table 4 presents the results of the logarithmic regression, where NBA was modeled as a function of CI_{intra} and CI_{inter} and applied to both Scots pine and Pyrenean oak. The analysis of the Scots pine revealed that intraspecific competition was associated with a slight decrease in AGB (estimated coefficient = −12.995), but this effect was not statistically significant ($p = 0.055$), as shown in Table 4. This accounted for 8.44% of the variance in AGB. In addition, we observed a significant decrease in AGB (estimated coefficient = −34.049) under interspecific competition, with a statistically significant effect ($p = 0.003$), contributing to 7.09% of the variance in AGB. In contrast, intraspecific competition had a positive effect on AGB of oak trees (estimated coefficient = 5.063), although this effect was not statistically significant ($p = 0.091$). Despite a slight increase in AGB (estimated coefficient = 2.593), interspecific competition was not significant ($p = 0.467$).

4. Discussion

4.1. *Evaluation of the role of independent variables in biomass estimation*

In this study, we found that the best-fitting biomass estimation model for Scots pine included DBH, HT, and CI, suggesting that combining these variables improved AGB estimation performance. These results are consistent with those reported by Dahlhausen et al. (2017), who reported that the inclusion of DBH, HT, and CI resulted in a more accurate AGB in Nelder trials for young *Quercus robur* trees. In contrast, for Pyrenean oak, DBH was the main independent variable for biomass estimation. HT and CI were not statistically significant and were not considered in the models. This finding aligns with previous research indicating that using DBH alone is often sufficient for estimating AGB in certain tree species (Sileshi, 2014; Xiao and Ceulemans, 2004). These findings highlight the importance of adopting species-specific approaches for biomass estimation in mixed-species forests (Cudjoe et al., 2024).

4.2. *Impact of neighborhood competition dynamics*

Our study explored the impact of neighborhood competition on biomass estimation, revealing nuanced interactions that significantly affect biomass estimation. The role of neighborhood competition in biomass estimation models within forest ecosystems has been extensively debated. Several studies (Ford et al., 2017; Rivas et al., 2005; Zhang et al., 2016) have highlighted how neighboring trees affect individual tree growth and biomass accumulation. Our findings contribute to this body of knowledge by demonstrating that incorporating the competition index into biomass models significantly improves the model accuracy of Scots pine in young mixed forests but does not improve the accuracy of Pyrenean oak in young mixed forests.

For Scots pine, the biomass predictions that included neighborhood competition outperformed those that did not, emphasizing the importance of accounting for neighborhood competition in biomass modeling. This finding is consistent with studies by Forrester et al. (2017), Zhou

Table 4

Summary of the regression models for intra- and interspecific competition. Parameter estimates, standard errors (SE), p-values, model fit metrics, and CF values for the log models were calculated. The coefficients (a, b, w, z) are the estimates of the model parameters. Statistical significance is indicated by *** ($p < 0.001$), ** ($p < 0.01$), and ns (not significant).

Species	Model No.	Coefficient	Estimate	SE	p–value	AIC	RMSE	Adj. R^2	MEF	CF
Scots pine	6 with CI_{intra} and CI_{inter}	*a*	−2.104	0.438	$2.110e^{-05}$ ***	47.051	0.365	0.695	0.716	1.050
		b	0.815	0.089	$1.620e^{-11}$ ***					
		w	−12.995	6.565	0.055 ns					
		z	−34.049	10.939	0.003 **					
Pyrenean oak	1 with CI_{intra} and CI_{inter}	*a*	−0.987	0.236	$1.460e^{-04}$ ***	−12.153	0.189	0.854	0.864	1.020
		b	1.782	0.125	$2.000e^{-16}$ ***					
		w	5.063	2.927	0.091 ns					
		z	2.593	3.529	0.467 ns					

et al. (2018), and Nong et al. (2019), who reported that competition is a key factor in explaining allometric relationships and biomass allocation in pine-dominated forests. Similarly, Ahmed et al. (2024) and Canham et al. (2004) found that competition factors equally affect tree growth predictions. The light-demanding trait of Scots pine underscores the importance of competitive conditions in biomass accumulation. These conclusions are supported by our results, emphasizing the critical role of neighborhood competition in improving the biomass estimation of Scots pine.

Neighborhood competition plays a different role in Pyrenean oak trees than in Scots pine trees growing in mixtures in terms of biomass prediction. Some studies suggest that oak trees are less sensitive to neighborhood competition than pine trees (Ferrio et al., 2021; Lamonica et al., 2020). Oaks may coexist effectively with pines in mixed stands, potentially tolerating pine encroachment (Pretzsch et al., 2020). For oaks, factors such as soil fertility, moisture availability, and disturbance regimes may have greater influences on growth and biomass accumulation than direct competition with neighboring trees (Jensen and Löf, 2017). As a result, the effects of competition on biomass modeling are species-specific.

Studies showing that oaks respond neutrally to mixing, especially during dry seasons (e.g., Muñoz-Gálvez et al., 2021; Steckel et al., 2020), support our findings. Oaks may benefit from adaptation in warmer, drier regions due to their well-known resistance to heat stress and drought (Jucker et al., 2014; Schroeder et al., 2021). In contrast, pines may have a reduced competitive advantage under changing climatic conditions because of their susceptibility to stress factors, including drought, which increases the effects of competition on biomass growth. In addition, pine species frequently exhibit aggressive competitive traits, such as quick early growth and a propensity to invest in height growth to outcompete neighbors for light. These characteristics increase the vulnerability of Scots pine to light competition (Pitkänen et al., 2022). Pyrenean oak, by contrast, is known for its adaptability and capacity to thrive in a wide range of environmental conditions, including low light. The tolerance of these trees to competitive pressures, with comparatively less impact on their biomass accumulation, can be attributed to their tolerance to shade, slower growth rates, and more efficient resource use (Britton et al., 2023). This variability in response to neighborhood competition reflects diverse ecological strategies and competitive interaction characteristics. For example, Pyrenean oak in mixed forests differ in their ecological characteristics and species-specific responses to competition (Forrester and Albrecht, 2014; Pretzsch and Schütze, 2009). Our results further confirm that competition dynamics differ widely between species (Dahlhausen et al., 2017).

As mixed forests are complex due to species diversity as well as structural and functional variability, biomass models must accurately address these features and adapt accordingly. Forest compositions and competitive dynamics differ significantly between mixed forests, underscoring the need for tailored modeling approaches (Forrester and Albrecht, 2014). According to Reyer et al. (2010), who examined competitive interactions in mixed forests under the lens of climate change, model adaptability is essential for accounting for environmental swifts. Pioneering species such as Scot pine are generally adapted to open, high-light environments where competition is strong for light, meaning that their biomass is sensitive to changes in neighborhood competition. In contrast, Pyrenean oaks, which occupy a wide range of niches, including shaded and open areas, are less affected by changes in competition and can utilize resources under diverse conditions (Martin et al., 2021).

4.3. Intra- and interspecific competition dynamics

Attention to mixed forest management has increased interest in competitive effects, particularly intra- and interspecific competition. Species identity within mixed forests determines whether trees promote growth through facilitation or experience hindered development because of competition (Pretzsch, 2022). Trees benefit from local trees that provide resources such as light, water or nutrients through facilitation. The acquisition of these resources together with other trees creates competition which reduces the growth of trees. We found that Scots pine and Pyrenean oak responded differently to competitive interactions (as shown in Fig. 4a–d). Although intraspecific competition was not statistically significant for Scots pine, a negative influence on AGB indicated possible resource limitations within the species that may inhibit biomass growth (Pretzsch, 2014).

Studies have shown that intraspecific competition among Scots pine species can reduce individual performance (Pretzsch and Biber, 2010). Conversely, Pyrenean oak trees presented a different pattern of response. AGB was positively influenced by intraspecific competition. However, the positive effect was not statistically significant. These findings suggest that intraspecific competition may not be an important driving force regulating AGB. Other factors, such as resource availability or environmental factors, may be more important in determining AGB.

The effects of interspecific competition on Scots pine trees were substantial, reducing their biomass accumulation. This finding corroborates previous research demonstrating that interspecific competition can lead to intense competition for light, water, and nutrients due to differences in ecological niches and resource use. For example, species with deeper or more extensive root systems can be more competitive for water than some pine trees, including Scots pine, leading to reduced growth rates and biomass accumulation (Ogaya and Penuelas, 2007). Unlike Scots pine, interspecific competition did not significantly affect AGB of Pyrenean oak. A reduction in interspecific competition in mixtures was reported in a shaded stand of Pyrenean oak and European beech (de Tomás Marín et al., 2023).

In mixtures with Scots pine, the roots of Pyrenean oak are deep and extensive, so they can access water and nutrients from deeper soil layers that are less competitive. When surface resources are scarce, Pyrenean oak can still grow with such a root structure (Germon et al., 2020). Furthermore, Pyrenean oak is a moderately shade-tolerant species, allowing it to maintain photosynthetic activity even when competing trees shade it. Despite competing for light with light-demanding conifers, Pyrenean oak can grow in shaded environments (Xi et al., 2023). Pyrenean oak trees may benefit from niche complementarity or facilitative interactions with heterospecific neighbors, thus reducing adverse interspecific competition effects. The dynamics of facilitation and competition reduction may be subject to modulation by various environmental factors (González de Andrés et al., 2018; Muñoz-Gálvez et al., 2021).

4.4. Limitations and future directions

A single competition index (NBA) and a fixed radius based on a target tree height approach to identify tree competitors have inherent limitations. However, several studies have demonstrated the robustness of NBA and fixed radius in similar forest contexts, making it an appropriate choice for our study (Ahmed et al., 2024; Biging and Dobbertin, 1995; Pretzsch, 2022; Rozendaal et al., 2020; Zhang et al., 2016). Future studies should explore additional CIs, including distance-dependent metrics and varying competition radii, to refine these findings and offer a deeper understanding of competition dynamics in mixed-species forests. While our statistical analyses confirmed that the assumptions of normality, homoscedasticity, and multicollinearity were met, the sensitivity of logarithmic regression to extreme values remains a consideration. Visual assessment of residual plots indicated no strong violations, however, the use of alternative modeling approaches, such as mixed-effects models and machine learning approaches, could improve predictive accuracy (Burnham and Anderson, 2002). In addition, our sample size of 90 trees was determined based on feasibility and logistical constraints, and a larger dataset could further improve the statistical power of our models and provide a more comprehensive representation of competition dynamics. Future research could consider a larger number of samples to ascertain variations in biomass accumulation and competition effects.

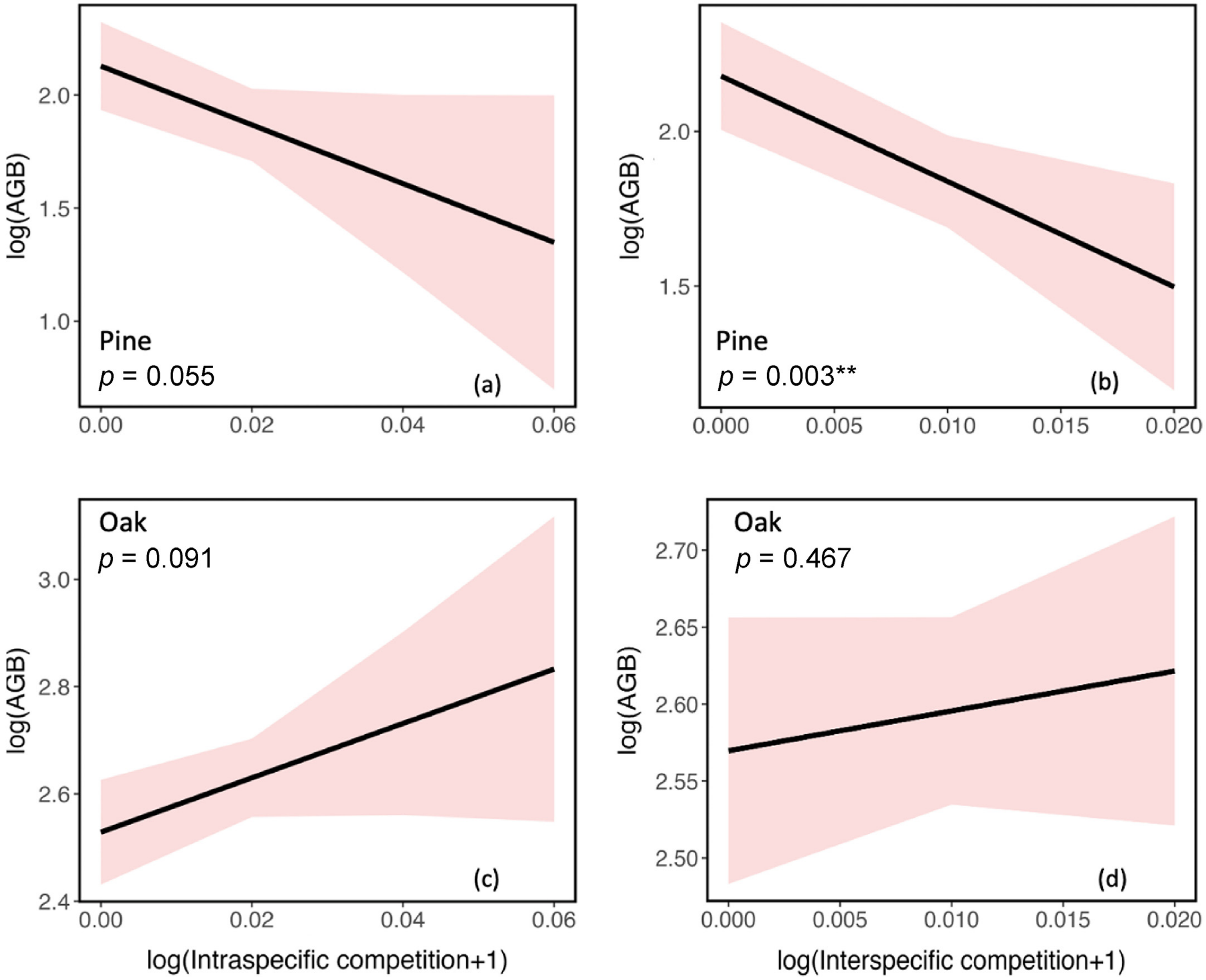

Fig. 4. Relationships between AGB and competition (intraspecific and interspecific) for Scots pine and Pyrenean oak. **(a)** and **(c)** Effects of intraspecific competition on AGB for Scots pine and Pyrenean oak, respectively, whereas **(b)** and **(d)** effects of interspecific competition on AGB for Scots pine and Pyrenean oak, respectively. The shaded areas indicate the 95% confidence intervals and a significant p-value is indicated (** $p < 0.01$).

The size of trees (DBH and total tree height) and thinning density were the main factors considered in assessing competition. Although these measurements are standard and useful, other variables that affect biomass estimation are tree age, tree health conditions, canopy composition, and site conditions (slope and soil properties). Future research should incorporate these ecological factors to enhance the accuracy of biomass predictions.

4.5. Practical and broader ecological implications

From a forest management point of view, the use of species-specific models makes it easier to monitor the stages of forest development and accurately assess the carbon stock and biomass (Pretzsch et al., 2015). The development of young mixed species is especially critical because small changes in the growth rates of different species can significantly influence future stand dynamics, competitive interactions, and survival rates. Thus, species-specific variable sets and models, need to be employed to ensure accurate biomass estimation. For example, acknowledging that Scots pine responds more strongly to competitive pressure than Pyrenean oak can help managers adopt targeted thinning that reduces competition around Scots pine, which can increase its growth and carbon sequestration potential, whereas less intensive management may suffice for Pyrenean oak. Furthermore, better predictions of carbon stocks require forest managers to use models that include all variables (DBH, HT, and CI), especially for Scots pine species, especially during early growth stages. For Pyrenean oak, models based on DBH will be used since they are easier to apply and accurate enough. The specific model approach for each species enables better management decisions in forest operations, which in turn promotes the sustainable development of mixed-species stands while improving carbon sequestration efforts.

5. Conclusion

The results of our study revealed different responses of Scots pine and Pyrenean oak to competitive interactions in terms of biomass accumulation in young Scots pine and Pyrenean mixed forests. For Scots pine, incorporating neighborhood competition into biomass models significantly improved the prediction accuracy and efficiency. In contrast, neighborhood competition did not significantly enhance the model performance for Pyrenean oak. These results indicate that neighborhood competition plays a more critical role in shaping AGB of Scots pine as compared to that of Pyrenean oak. Furthermore, Scots pine showed a significant reduction in AGB under interspecific competition but had a nonsignificant negative response to intraspecific competition. For Pyrenean oak, neither intraspecific nor interspecific competition affected AGB, although the response of intra- and interspecific competition was positive but not significant. This nonsignificant effect on Pyrenean oak is probably attributed to its deep roots and greater shade tolerance. Overall, these findings underscore the importance of species-specific responses to neighborhood competition and support sustainable forest management practices, particularly in the context of mixed-species forests and climate change.

CRediT authorship contribution statement

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

Data availability

Data will be made available on request.

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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.

Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.fecs.2025.100317.

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