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TESIS DOCTORAL:

DISTRIBUCIÓN DE LA BIOMASA ARBÓREA EN BOSQUES MIXTOS TEMPLADOS

Presentada por Eric Cudjoe para optar al grado
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PHD PROGRAMME IN CONSERVATION AND SUSTAINABLE USE OF FOREST SYSTEMS

DOCTORAL THESIS:

TREE BIOMASS ALLOCATION IN TEMPERATE MIXED FORESTS

Submitted by Eric Cudjoe in fulfilment of the requirements for the PhD degree by the Universidad de Valladolid

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To my parents, who planted the roots of my life

and will always be in my heart.

Forests are the lungs of our land, purifying the air
and giving fresh strength to our people.

Franklin D. Roosevelt

To plant a tree is to believe in tomorrow.

Audrey Hepburn

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TABLE OF CONTENTS

PREFATORY NOTE

Three (3) peer-reviewed original research articles, all published in prestigious international journals, served as the foundation for this doctoral thesis. The compendium of these 3 published original research papers is cited throughout the thesis using Roman numbers (I–III). The document is presented in English, adhering to standard conventions where decimals are indicated by a point and thousands by a comma. The thesis presents a summary in both English and Spanish (Resumen), as well as the methodologies, analyses, key findings, and general discussion. The doctoral thesis concludes with a section summarizing the conclusions, which have also been translated into Spanish (Conclusiones). The referenced original work generated from the thesis includes the following:

Eric Cudjoe, Felipe Bravo, Ricardo Ruiz-Peinado, 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.). Science of the Total Environment, Volume 953, 176061. https://doi.org/10.1016/j.scitotenv.2024.176061.

Eric Cudjoe, Ricardo Ruiz-Peinado, Hans Pretzsch, Shamim Ahmed, Felipe Bravo, 2025. Neighborhood competition improves biomass estimation for Scots pine (*Pinus sylvestris* L.) but not Pyrenean oak (*Quercus pyrenaica* Willd.) in young mixed forest stands. Forest Ecosystems, Volume 13, 100317. https://doi.org/10.1016/j.fecs.2025.100317.

Eric Cudjoe, Felipe Bravo, Hans Pretzsch, Pete Bettinger, Ricardo Ruiz-Peinado, 2025. Competition in mixed Scots pine and Pyrenean oak stands modifies allometry and partially affects biomass allocation during early stand development. Ecological Indicators, Volume 176, https://doi.org/10.1016/j.ecolind.2025.113713.

ABSTRACT

Forests are critical for global climate regulation, biodiversity conservation, and the provision of ecosystem services. However, estimating aboveground biomass (AGB) in mixed-species forests remains challenging because of the complex interactions among species, structural variability, and competitive dynamics. This study addresses this gap by investigating biomass allocation, allometric relationships, and competition effects in mixed and monospecific stands of Scots pine (*Pinus sylvestris* L.), sessile oak (*Quercus petraea*), and Pyrenean oak (*Quercus pyrenaica*) across different forest developmental stages (young and mature stands) in northern Spain.

The research combined empirical data from three complementary studies: mature triplet-based plots of Scots pine and sessile oak (Study I), young mixed stands of Scots pine and Pyrenean oak subjected to thinning treatments (Study II), and an analysis of competition effects on biomass allocation and tree structure using structural equation modeling (Study III). Tree attributes such as DBH, tree height, crown dimensions, and biomass components (stem, branches, foliage) were collected using destructive sampling and analyzed using log-transformed regression, nonlinear mixed-effects models, Dirichlet regression, and ANCOVA.

The results show that biomass allocation patterns and model performance are species and stand specific. While Scots pine displayed stable allometric relationships across stand types, sessile oak required distinct models for mixed and monospecific stands. Nonlinear mixed-effects models incorporating both DBH and height outperformed traditional log-linear approaches. Dirichlet regression effectively predicted biomass component proportions, preserving additivity. Neighborhood competition significantly improved AGB model performance for Scots pine but had negligible effects on Pyrenean oak, revealing differing sensitivities to interspecific and intraspecific competition. Furthermore, competition altered allometric scaling relationships and tree crown development, with Scots pine investing more in foliage and branches, whereas Pyrenean oak prioritized stem growth.

Structural equation modeling revealed indirect effects of competition on stem and branch biomass through modifications in tree height, supporting a mediation framework in tree allometry. These findings advance the understanding of biomass partitioning under mixed-species conditions and highlight the importance of incorporating species-specific traits and competitive interactions into biomass estimation models. Ultimately, this research provides refined modeling tools and insights to support adaptive forest management and carbon accounting under changing climatic and ecological conditions.

Keywords: Allometry, biomass equation, tree competition, mixed forests, modeling, monospecific forests, oak, Scots pine

RESUMEN

Los bosques desempeñan un papel esencial en la regulación climática global, la conservación de la biodiversidad y la provisión de servicios ecosistémicos. No obstante, la estimación de la biomasa aérea total (AGB, por sus siglas en inglés) en bosques mixtos sigue siendo un reto, debido a la complejidad de las interacciones interespecíficas, la variabilidad estructural y las dinámicas de competencia. Esta tesis aborda dicha brecha mediante el análisis de la asignación de biomasa, las relaciones alométricas y los efectos de la competencia en rodales mixtos y monoespecíficos de pino silvestre (*Pinus sylvestris* L.), roble albar (*Quercus petraea*) y roble melojo (*Quercus pyrenaica*), en diferentes estadios de desarrollo forestal (robles jóvenes y maduros) en el norte de España. La investigación integra datos empíricos de tres estudios complementarios: rodales maduros comparativos de pino silvestre y roble albar (Estudio I), rodales jóvenes mixtos de pino silvestre y roble melojo con tratamientos de claras (Estudio II), y un análisis de los efectos de la competencia sobre la estructura y la asignación de biomasa mediante modelos de ecuaciones estructurales (Estudio III). Se emplearon métodos de muestreo destructivo, regresión lineal log-transformada, modelos mixtos no lineales, regresión de Dirichlet y análisis de covarianza (ANCOVA) para analizar variables como el diámetro normal, la altura, atributos de copa y componentes de biomasa.

Los resultados muestran que los patrones de asignación de biomasa y el rendimiento de los modelos son específicos según la especie y el tipo de rodal. Mientras que el pino silvestre mantuvo relaciones alométricas consistentes, el roble albar requirió modelos diferenciados para rodales mixtos y puros. Los modelos mixtos no lineales que incorporan diámetro normal y altura superaron en rendimiento a los modelos log-lineales. La regresión de Dirichlet predijo eficazmente la proporción de biomasa por componente, garantizando la aditividad. Los índices de competencia entre vecinos mejoraron significativamente la predicción de AGB para el pino silvestre, pero no para el roble melojo, revelando diferencias en su sensibilidad competitiva. Además, la competencia modificó las relaciones alométricas y el desarrollo de la copa, asi en els casi del pino encontramos que invierte más en ramas y follaje, mientras que en el caso del roble favoreció el crecimiento del fuste.

Los modelos de ecuaciones estructurales revelaron los efectos indirectos de la competencia sobre la biomasa del fuste y las ramas a través del aumento en altura del árbol, lo que respalda la hipótesis de mediación en la asignación de recursos. En conjunto, los hallazgos de esta tesis contribuyen al entendimiento de la dinámica de bosques mixtos, proporcionan herramientas de modelización más precisas y respaldan estrategias de gestión forestal sostenible y contabilización de carbono frente al cambio climático.

Palabras clave: Alometría, ecuación de biomasa, competencia entre árboles, bosques mixtos, modelización, bosques monoespecíficos, roble, pino silvestre.

1. INTRODUCTION

1.1. Forests in a changing world: Importance and challenges

Compelling evidence suggests that forests are complex and varied ecosystems that sustain the ecological and socioeconomic balance of the Earth. Forests, which constitute approximately 31% of the planet's land area, are the “lungs” of the Earth, sequestering carbon dioxide and stabilizing climate systems across the globe (Pan et al., 2011). In addition to their planetary function, forests supply numerous other ecosystem services, from conserving biodiversity to regulating the water cycle and soil stabilization (Brockerhoff et al., 2017). Their peculiar capacity to deliver these services makes them essential for ensuring planetary health.

Forests play a vital role in alleviating climate change on a global scale by acting as carbon sinks, capturing approximately 2.6 billion megagrams (Mg) of carbon each year (Fischer et al., 2023). This function is particularly crucial as the repercussions of climate change escalate, with increasing temperatures and erratic weather patterns jeopardizing ecosystems worldwide. Moreover, forests host an estimated 80% of terrestrial species, making them critical reservoirs of biodiversity (Toivonen et al., 2023). Thus, this causes canopy structures and root networks to create habitats and microclimates that sustain diverse flora and fauna, many of which are endemic and irreplaceable.

On a global, regional, and local scale, the function of forests extends beyond carbon regulation, offering key ecosystem services that enable ecological integrity as well as human welfare. Forests produce timber and non-timber forest products, as they regulate the water cycle, keep the soil in place, and provide cultural, spiritual, and recreational functions (Kolo et al., 2020). In temperate and Mediterranean regions, including certain regions of Europe, such services are typically provided by mixed forests of both broadleaf (e.g., oaks) and coniferous trees (e.g., pines). For example, in the northern part of Spain, Scots pine (*Pinus sylvestris* L) and oak (*Quercus* spp.) forests covered with mixed stands are ecologically and economically valuable and support biodiversity, carbon storage, and water regulation while also supporting local livelihoods through forestry and tourism.

However, despite forests playing a vital role, they are increasingly facing mounting threats from human-induced and climate-related disturbances (Hurmekoski et al., 2022).

Globally, an estimated 10 million hectares of forest are lost each year due to deforestation, which is driven primarily by agricultural expansion, infrastructure development, and illegal logging (Kumar et al., 2022). Fragmentation and land-use change diminish forest connectivity, reduce genetic diversity, and compromise ecosystem functioning. Simultaneously, climate change intensifies these threats by increasing the incidence and severity of wildfires, droughts, wind throw events, and pest and pathogen outbreaks (Stevens-Rumann et al., 2018).

These compounded stressors alter forest dynamics, reduce resilience, and challenge the capacity of forest ecosystems to deliver key services. Forests dominated by a limited number of species, which often exhibit reduced adaptability to changing environmental conditions, are particularly vulnerable. In contrast, species-diverse stands tend to show greater structural complexity and functional redundancy, buffering against environmental fluctuations and supporting long-term ecosystem stability (Goode et al., 2020; Miah et al., 2012).

Understanding how forest composition, structure, and species interactions respond to global change is essential for developing adaptive forest management strategies. Research has increasingly focused on enhancing forest resilience through biodiversity-based management, including the promotion of mixed-species stands, the restoration of degraded areas, and the integration of forest functions into broader landscape and climate policies. In this context, improving our scientific understanding of tree growth dynamics, biomass allocation, and competition in mixed versus monospecific forests has become a key priority for both ecology and forest science.

1.2. Importance and potential of mixed forests

Mixed-species forests, which include combinations of species such as Scots pine and oak, offer a resilient and ecologically sound alternative to traditional monoculture forestry systems. These forests are characterized by greater structural heterogeneity and functional diversity, which can enhance ecosystem processes such as productivity, nutrient cycling, and carbon sequestration (Forrester and Bauhus, 2016). In particular, combining resources by coexisting species, such as light, water, and soil nutrients, results in more efficient ecosystem functioning. This ecological complementarity not only increases the resilience of forest ecosystems to environmental stresses but also improves their overall stability and long-term sustainability.

Forests dominated by Scots pine and oak species are ecologically and economically prominent across most of Europe, where they are central to biodiversity, timber production, and ecosystem function (Pretzsch et al., 2020). These forests also regulate water flows and support traditional livelihoods and cultural practices. However, they are increasingly vulnerable to shifting climatic patterns and human exploitation. Addressing these challenges calls for adaptive, biodiversity-enhancing management approaches that maintain and restore forest functions (Loehle et al., 2024).

Empirical evidence supports the view that mixed-species forests often outperform monocultures across ecological and functional attributes. For example, studies have shown that mixed forests tend to have greater aboveground biomass production, greater resistance to insect outbreaks and disease, and faster recovery following disturbances such as storms or droughts (Pretzsch and Forrester, 2017a; Schuler et al., 2017). The presence of multiple species with varying tolerances and growth strategies contributes to a buffering effect, where the decline or failure of one species does not lead to total system collapse. This makes mixed forests especially valuable under the uncertain and increasingly variable conditions of a changing climate.

Moreover, mixed forests often provide a wider array of ecosystem services than monocultures. These include enhanced biodiversity support, better soil protection, improved water regulation, and increased recreational and cultural values (Zhao, 2014). The inclusion of broadleaf species such as oak improves soil fertility through leaf litter decomposition, whereas coniferous species such as Scots pine contribute to canopy closure and early stand development. Together, these species form synergistic interactions that strengthen ecosystem functioning at multiple scales.

Despite these advantages, mixed forests remain underutilized in both forest research and practical temperate silviculture. The legacy of industrial forestry has led to a dominance of even-aged, single-species stands designed for simplified management and maximized short-term yields. This approach, however, has often overlooked long-term ecological trade-offs, including reduced biodiversity, greater susceptibility to pests and diseases, and diminished resilience to climate extremes. From a scientific perspective, one major gap lies in the limited availability of species-specific models and tools tailored to mixed-species contexts (Coll et al., 2018). Most existing forest growth and biomass estimation models are calibrated for monospecific stands and fail to account for the complex inter- and intraspecific interactions that define mixed forests (Forrester et al., 2018; Pretzsch et al., 2015). These interactions influence growth trajectories and biomass partitioning among tree components (e.g., stems, branches, foliage), which is critical for accurate carbon accounting and forest planning.

Addressing this gap is vital for designing adaptive and multifunctional forest management strategies that align with ecological goals and climate mitigation targets. In regions such as northern Spain, where Scots pine and oak forests dominate and are culturally significant, transitioning toward mixed-stand forestry could yield long-term ecological and socioeconomic benefits. However, this transition must be supported by robust empirical data and refined modeling approaches that capture the dynamics of mixed-species interactions and their implications for forest development, productivity, and resilience.

1.3. Scots pine–oak stands: A model for temperate ecosystems

Scots pine (*Pinus sylvestris* L.), sessile oak (*Quercus petraea* (Matt.) Liebl.), and Pyrenean oak (*Quercus pyrenaica* Willd.) are key components of temperate forest ecosystems across Europe. These species exhibit distinct yet complementary ecological traits, making them ecologically significant in pure and mixed stands. Owing to their wide distribution, resilience under varying climatic conditions, and functional diversity, they are especially relevant for studying forest dynamics under changing environmental scenarios (Assefa et al., 2024).

Scots pine is one of the most widespread coniferous species in Eurasia and is known for its adaptability, fast growth, and high commercial value as a timber species (Jaime et al., 2019). It also plays a vital role in carbon sequestration, storing a substantial portion of aboveground carbon (Nave et al., 2019). The Iberian Peninsula typically inhabits montane zones between 800 and 2000 m above sea level, with annual precipitation between 600 and 1200 mm and more than 100 mm in the summer months (Giménez et al., 2004).

Sessile oak is a dominant broadleaf species in temperate European forests, occurring at elevations up to 1800 m. Sessile oak plays a crucial ecological role by enhancing habitat heterogeneity and supporting biodiversity. For example, it provides shelter and foraging areas for species such as the wild brown bear (*Ursus arctos arctos*). Its broad ecological range suggests potential resilience under future climate scenarios (Sáenz-Romero et al., 2017).

Pyrenean oak, meanwhile, is native to the Iberian Peninsula, with extensive distributions in the western and northern montane regions (Castilla y León, Galicia, Asturias, La Rioja, and parts of Portugal). This species also spread into southwestern France and the Rif and Middle Atlas ranges of northern Morocco. It thrives in subhumid, continental Mediterranean climates, typically between 400 and 1600 m in elevation, and receives approximately 650 to 1200 mm of annual rainfall (Lorite et al., 2008). Pyrenean oak forests are ecologically valuable because of their role in sustaining biodiversity, particularly compared with conifer-dominated stands, and their contribution to soil enrichment and water regulation (Bravo et al., 2019; Gómez-Aparicio et al., 2011; Löf et al., 2016).

Compared with Scots pine, both sessile and Pyrenean oak are generally more shade–tolerant than Scots pine, particularly during early developmental stages (Pretzsch et al., 2015). In addition, their deeper rooting systems, slower growth rates, and ability to resprout from the roots allow them to persist under canopy cover and exploit different resource niches (Pemán et al., 2017). In contrast, Scots pine is light-demand and grows rapidly when resources are abundant but tends to be more susceptible to competition (Niinemets and Valladares, 2006; Pretzsch et al., 2015).

When grown together, these species display complementary functional traits. The structural and physiological contrasts between Scots pine and oak species promote resource partitioning, reduce direct competition, and increase stand-level productivity and resilience (Forrester and Bauhus, 2016). Their co-occurrence in mixed forests provides an ideal model system for exploring interspecific interactions, allometric scaling, and biomass allocation across a gradient of environmental conditions (Waitz and Sheffer, 2021).

1.4. The ecological and productive benefits of mixed forests

Forests occupy nearly one-third of the Earth's land area, serving as crucial ecosystems that support biodiversity and provide essential environmental services (Brockerhoff et al., 2017). However, only a small fraction of these forests remain untouched by human activity, while managed forests often consist of either monocultures or limited species stands. In Europe, mixed forests constitute approximately 23% of the pan-European region (Pretzsch and Forrester, 2017b). With increasing concerns surrounding climate change, forestry research has increasingly explored the shift from single-species plantations to more ecologically diverse mixed forests (e.g., Bravo-Oviedo et al., 2014; Coll et al., 2018; del Río et al., 2019; Forrester et al., 2018; Pretzsch and Schütze, 2014; Pretzsch and Zenner, 2017).

Numerous studies indicate that mixed forests outperform monocultures in various ways, including increased biodiversity, greater resilience, and increased ecosystem productivity (Feng et al., 2022; Forrester and Bauhus, 2016; Pretzsch and Forrester, 2017a; Pretzsch and Schütze, 2016; Schnabel et al., 2019; Warner et al., 2023). Their structural complexity enables better adaptation to environmental changes, increased resistance to disturbances, and faster post disturbance recovery (Alvarez Arnesi et al., 2024). Recent findings by Rodríguez de Prado et al. (2022) further support the hypothesis that mixed stands exhibit higher growth rates than monocultures. However, further studies are needed to determine the universality of this pattern across different climatic and ecological contexts (Heym et al., 2017). The differences in the tree growth rates and final heights of different tree species contribute to the structural and functional complexity of mixed forests (Pretzsch and Forrester, 2017).

With the degradation of primary forests due to logging and land-use changes, tree plantations have become an essential means of sustaining forest ecosystem services (Chazdon, 2008). While monoculture plantations are common due to their simplified management and high timber yields, they often result in biodiversity losses (Paquette and Messier, 2011; Zhang et al., 2021). On the other hand, mixed-species plantations provide an alternative approach that supports ecosystem functionality, enhances biodiversity, and improves forest productivity (Paquette and Messier, 2011).

Research has demonstrated that biodiversity is crucial to tree growth and forest productivity (Yu et al., 2024). Mixed forests generally exhibit superior growth performance because of more efficient resource utilization, facilitated by niche differentiation and reduced competition among species (Pretzsch, 2018). However, not all mixed-species interactions result in positive outcomes, as interspecific competition can sometimes outweigh the benefits of diversity (Gross, 2008). Factors such as stand age, density, and environmental conditions, including temperature and precipitation, also influence species mixing outcomes (Pretzsch et al., 2015).

Tree functional traits play a key role in determining the success of species mixtures. For example, stands composed of tree species with similar growth cycles or leaf phenologies may experience heightened competition for resources (Kunstler et al., 2016; Melis et al., 2023). Similarly, conifer-only or broadleaf-only stands might exhibit higher levels of competition than mixed conifer-broadleaf forests, which tend to use resources more efficiently (Ishii and Asano, 2010). Differences in shade tolerance among species also contribute to better canopy space filling and overall resource utilization (Pretzsch, 2014).

Stand characteristics, such as tree age and stocking density, are important factors influencing the performance of mixed forests. Recent studies suggest that as mixed forests mature, they often become more productive than single-species plantations (Feng et al., 2022). The increase in productivity may be attributed to improved resource use efficiency (such as light, water, and nutrients) and complementary interactions between species, as mixed stands develop structurally and functionally over time (Pretzsch et al., 2015).

The stress–gradient hypothesis (SGH) proposes that positive interactions between tree species become more prominent in nutrient-poor environments, whereas competition prevails in resource-rich environments (Oduor et al., 2024; Toïgo et al., 2015). Climate variables, particularly temperature and precipitation, further modulate these effects (Jucker et al., 2016). An often overlooked aspect of mixed forests is their influence on tree crown development. The crown structure plays a crucial role in determining a tree's adaptation strategies, growth performance, and overall stand productivity (Pretzsch, 2021).

Diverse crown architectures in mixed forests enable better light capture and optimize canopy space utilization, leading to improved forest function and stability (Pretzsch, 2014). However, most research has focused on tree height and diameter growth, leaving crown development relatively underexplored (Burkhart and Tomé, 2012; Yang and Swenson, 2023). Another factor to consider is stand density variation, which can significantly impact species mixing effects. Many studies compare mixed and single-species stands under equal stand densities (Pretzsch, 2018; Pretzsch et al., 2020; Pretzsch and Schütze, 2016). However, because species mixing inherently alters stand density, failing to account for these differences could lead to misleading conclusions (Pretzsch et al., 2015).

1.5. Problem statement

Forests play a critical role in mitigating climate change by sequestering carbon, but accurately estimating forest biomass remains a challenge, particularly in mixed species stands (Pan et al., 2011; Pretzsch et al., 2015). Most biomass models have been developed for monospecific stands and often overlook complex interactions in mixed stands (Bravo et al., 2019; Forrester and Pretzsch, 2015). These stands are characterized by species-specific growth patterns and competition dynamics that significantly influence biomass allocation and carbon sequestration potential (Poorter et al., 2012). The effects of forest composition on tree allometry and biomass allocation remain poorly understood in mature mixed stands of Scots pine and sessile oak. Existing models, often designed for monospecific forests, may not accurately capture these dynamics, leading to biases in carbon accounting and suboptimal (i.e., ecologically and economically inefficient) management strategies (Menéndez-Miguélez et al., 2021; Pretzsch, 2019; Weiskittel et al., 2015).

Although competition influences both biomass allocation and structural traits such as DBH, crown base height, and crown length in young mixed stands of Scots pine and Pyrenean oak, the extent of intra- and interspecific effects remains insufficiently quantified (Bravo et al., 2019; Gómez-Aparicio et al., 2011). Addressing these knowledge gaps is essential for advancing forest ecology, improving biomass estimation accuracy, and supporting sustainable forest management practices (Weiskittel et al., 2015). To date, few models explicitly incorporate competition metrics and species-specific interactions across different forest compositions and developmental stages, which highlights the critical need for more accurate and adaptable models that can account for diverse real-world conditions.

1.6. Thesis focus and contributions

This study investigated biomass dynamics, allometric relationships, and competition effects in mixed and monospecific forests of Scots pine and oak species across different developmental stages. This study integrates data from mature forest stands comprising pure Scots pine, pure sessile oak, and mixed pine–oak stands, as well as from young mixed stands of Scots pine and Pyrenean oak. The key contributions of this thesis include the following:

- The development and validation of biomass models for Scots pine and sessile oak species involves the comparison of mixed and monospecific stands to assess the effects of forest composition on biomass allocation and allometric relationships (Pretzsch, 2019; Zhang et al., 2020).
- The exploration of neighborhood competition effects on biomass estimation for Scots pine and Pyrenean oak (mixed stands only) highlights species-specific responses to competitive pressures (Forrester et al., 2018).
- Analysis of competition-driven changes in biomass allocation patterns and structural attributes (e.g., DBH, crown dimensions) in young mixed Scots pine and Pyrenean oak forests (Bravo et al., 2019; Pretzsch and Schütze, 2016).
- The development of improved biomass estimation models that integrate competition metrics enhances their accuracy and applicability for mixed-species forests under Mediterranean and temperate conditions (Forrester and Pretzsch, 2015; Weiskittel et al., 2015).

By addressing these gaps and challenges, this thesis consisting Studies I, II and III collectively advances the theoretical understanding of mixed-species forest dynamics and provides practical tools for sustainable forest management, carbon accounting, and resilience strategies in a changing climate.

1.6.1. Competition and its role in forest dynamics

Competition among trees occurs when access to vital resources such as light, water, or nutrients is limited compared with the physiological needs of individual trees (Craine and Dybzinski, 2013). One of the principal factors affecting forest dynamics such as biomass accumulation, individual and stand-level growth, and species survival is competition either within (intraspecific) or between (interspecific) species.

With increasing density and size of neighbors, competition for resources intensifies (Canham et al., 2004; Clark et al., 2014). This competition not only suppress growth at the individual level but can also produce positive feedback effects by which competitive interactions produce increasing size heterogeneity in the stand (Bi and Turvey, 1996). In the long run, this growing heterogeneity in tree size distribution, in turn, further changes the nature of competition among trees and stand-level productivity.

Mostly complementing features allow for more effective resource usage, mixed-species stands frequently show less competition than monocultures (Feng et al., 2022; Pretzsch and Schütze, 2016). Interactions between species complicate the dynamics of competition in mixed-species forests, opening doors for niche differentiation and resource partitioning. Niche complementarity results from species' frequent differences in ecological niches, functional characteristics, and spatial resource usage in mixed forests. For example, species with deep root systems may cohabit peacefully with their shallow-rooted neighbors, whereas species that can withstand shade may flourish beneath the canopy produced by species that require light (Bartkowicz and Paluch, 2019; Valladares et al., 2016). These interactions not only reduce direct competition but can also lead to overyielding, where mixed stands produce more biomass than the average of their corresponding monocultures (Pretzsch and Schütze, 2016, 2009). This effect is particularly relevant in the context of global change, as forests face increasing pressure from climate variability and land-use change. These dynamics are crucial for understanding and predicting forest productivity (Pretzsch and Schütze, 2016).

Two main types of competition are distinguished as follows:

- Intraspecific competition**:** This phenomenon occurs among individuals of the same species and often results in self-thinning and size differentiation.

- Interspecific competition: Interspecific competition occurs between different species, potentially leading to complementarity effects and increased productivity in mixed stands (Forrester and Pretzsch, 2015).

In early stand development, trees still establish their structure and competitive hierarchies, making this a critical phase for studying how intra- and interspecific interactions shape future biomass dynamics (Bravo et al., 2019; Gómez-Aparicio et al., 2011). Moreover, young stands may exhibit more intense competition due to higher stem densities and uniform age structures, which can alter growth trajectories and complicate biomass modeling. Understanding the nuanced role of competition in forest dynamics is therefore essential not only for ecological theory but also for practical applications. The incorporation of competition into biomass estimation models and forest planning improves predictions of forest productivity and resilience, especially in complex systems like mixed-species stands (Forrester et al., 2018).

As sustainable forest management shifts toward promoting diversity and multifunctionality, unraveling how competition shapes forest outcomes becomes even more critical. However, the integration competition in biomass estimation models, particularly for young mixed forest stands, remains unexplored. Most existing biomass models are developed for either mixed mature trees or monocultures of young or mature trees. These models are typically based on tree size and stand density and rarely differentiate between intra- and interspecific competition in young mixed forest stands.

1.6.2. Advancing biomass estimation through allometric relationships

Allometry, the study of size relationships among different parts of an organism, is central to biomass estimation. Allometric equations relate easily measurable variables, such as DBH and tree height, to biomass components. These equations are widely used in forestry for biomass accounting, ecosystem modeling, and resource management (Chave et al., 2014). Traditional allometric models often assume homogeneity within stands and ignore competition effects, limiting their applicability to mixed-species forests. Recent studies have emphasized incorporating competition indices and species-specific interactions to improve model accuracy (Forrester et al., 2018). By integrating these factors, this thesis aims to advance allometric modeling and provide robust tools for estimating biomass in diverse forest ecosystems.

1.7. Research questions and hypotheses

This thesis examines how forest composition and competition influence biomass estimation, allometric relationships, and biomass allocation in mixed and monospecific stands of Scots pine (*Pinus sylvestris* L.), sessile oak (*Quercus petraea*), and Pyrenean oak (*Quercus pyrenaica*) at different developmental stages, specifically young and mature. Each of the three studies presented in this thesis (i.e., published papers) focused on distinct and original research questions, but related research issues collectively enhance biomass modeling and support sustainable forest management under changing environmental conditions.

Study I was conducted to examine how mature mixed species stands composed of Scots pine and sessile oak differ from their respective monospecific stands in terms of allometric relationships and the way biomass is distributed. In addition, the study investigated the estimation of AGB and biomass component proportions (using a proportion-based modeling approach, Dirichlet regression to ensure additivity). Allometric relationships are hypothesized to differ significantly between mixed species and monospecific stands because of interactions between the species. Consequently, models developed separately for mixed and monospecific stands are expected to yield more accurate estimates than are generalized models.

Study II focused on young mixed stands of Scots pine and Pyrenean oak and evaluated whether incorporating total neighborhood competition, and intra- and interspecific competition metrics improved the prediction accuracy of the biomass models. This study hypothesized that Scots pine, being light-demanding and competitively sensitive, may benefit more from the inclusion of competition variables than Pyrenean oak, which exhibits greater shade tolerance and slower growth and may be less responsive to neighborhood effects in early developmental stages (Niinemets and Valladares, 2006; Pretzsch et al., 2015). Furthermore, interspecific competition is expected to exert a more substantial effect than intraspecific competition on the biomass prediction of Scots pine.

Study III also focused on young mixed stands of Scots pine and Pyrenean oak, examining how competition influences both tree structural attributes (e.g., tree height, crown base height, and crown length) and biomass partitioning. We aimed to understand whether competitive pressures alter allometric relationships and lead to species-specific adjustments in the distribution of biomass among stems, branches, and foliage. We hypothesize that competition has both direct and indirect effects on biomass partitioning and that these effects differ between Scots pine and Pyrenean oak due to their contrasting ecological strategies.

2. RESEARCH OBJECTIVE

2.1. General objectives

This study investigated biomass dynamics, allometric relationships, and competition effects in mixed and monospecific stands of Scots pine and oak species at different forest developmental stages to improve biomass estimation models that can support sustainable forest management.

2.2. Specific objectives

The specific objectives of this study are as follows:

2.2.1. Forest composition and allometry (Study I)

- To evaluate how forest composition (mixed vs. monospecific stands) influences tree allometry and biomass allocation for Scots pine and sessile oak in mature forests.
- To estimate and model the biomass allocation patterns among tree components in Scots pine and sessile oak using Dirichlet regression, and to assess how these patterns vary with tree size (DBH and tree height) and forest composition.

This objective is addressed in Study I, as presented in the results section.

2.2.2. Competition effects on biomass estimation (Study II)

- To investigate the impact of neighborhood competition on the accuracy of biomass estimation for Scots pine and Pyrenean oak in young mixed forests.
- To assess differences in how intra- and interspecific competition affect biomass predictions for these species.

This aspect is discussed in Study II, as reported in the results section.

2.2.3. Biomass allocation and structural attributes (Study III)

- To analyze how competition alters biomass allocation patterns across stems, branches, and foliage in young mixed Scots pine and Pyrenean oak forests.
- To explore the indirect effects of competition on biomass distribution through modifications in structural attributes such as crown length, DBH, and tree height.

This matter is explored in Study III of the results section.

2.3. Research framework

The research framework (see Figure 1) outlines the structured sequence of processes guiding Studies I, II, and III, where key starting points represent stand development stages and stand composition (monospecific vs. mixed-species). Study I focused on mature forest stands, both monospecific and mixed, to investigate patterns in allometric relationships, AGB estimation, and biomass component proportions. The subsequent studies (Studies II and III) concentrated on young mixed stands, where the influence of competitive dynamics was investigated.

Studies II and III introduce distance-independent neighborhood analysis to assess the following: Study II specifically examines the influence of total competition, and intra- and interspecific competition on biomass estimation, whereas Study III also explores how competition affects allometric relationships and biomass allocation among tree components. Together, these studies (Studies I, II and III) enhance our understanding of species-specific growth patterns and biomass estimation and support sustainable forest management across different stages of forest development.

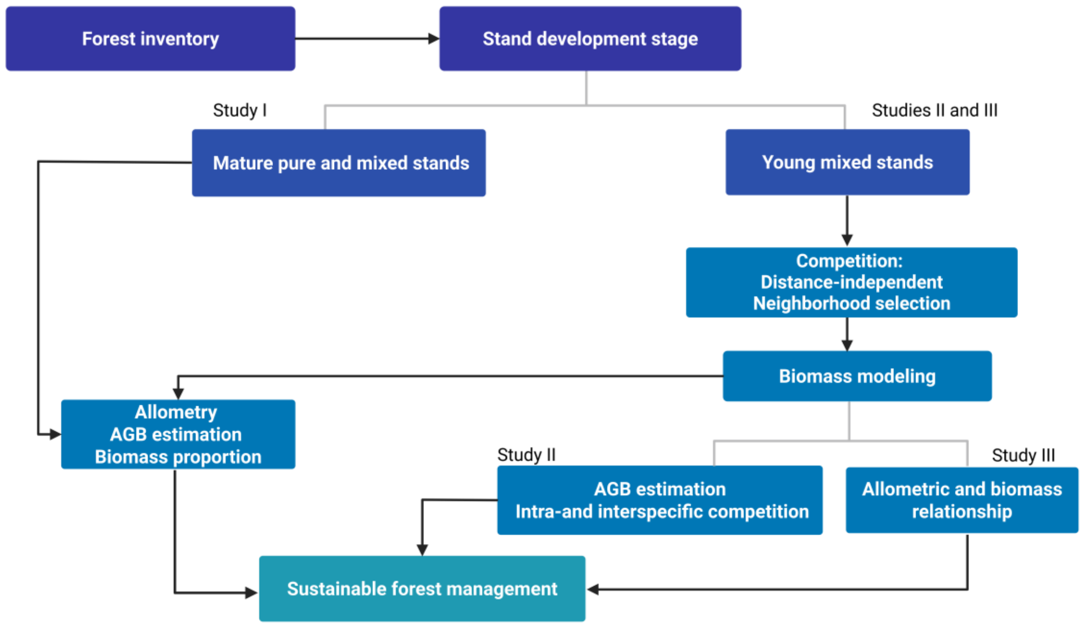

Figure 1. The conceptual framework for the thesis illustrates the integration of three interconnected studies (Studies I, II, and III) to address improving aboveground biomass (AGB) estimation, allometry, and competition across young and mature forest types. Study I focused on forest composition and allometry in mature stands; Study II explored the role of competition in biomass estimation in young stands; and Study III examined how competition and structural attributes influence biomass partitioning.

3. MATERIALS AND METHODS

This section comprehensively describes the study sites, experimental design, data collection, biomass estimation methods, competition assessment, and statistical analyses employed in this thesis.

3.1. Study sites

In this study, the research was conducted across three sites in the Castilla y León region of northern Spain. Study I was carried out at two separate sites (Busnela and Valberzoso), which are different from Studies II and III. However, Studies II and III were both conducted at the same site. The study sites were chosen for their ecological characteristics, climate conditions, and natural progression of mixed-species forest stands as well as their suitability for the specific experimental design and research objectives.

3.1.1. Mature triplet-based mixed and monospecific stands (Study I)

This research used a triplet design ((Pretzsch et al., 2015); see Pretzsch et al., 2020 for more information) to examine mature forest stands, allowing for direct comparisons of biomass dynamics and allometric relationships. Each triplet included a monospecific Scots pine plot, a monospecific sessile oak plot, and a mixed-species plot where both species were grown together under similar environmental conditions. Each plot ranged from 760 to 897 m² in size and shared a uniform soil type, elevation, slope, and silvicultural practices to minimize variability unrelated to species composition between the plots. The site selected included two locations: (1) Busnela in Burgos Province (03°47′19″ W, 43°02′52″ N) which was established in April 2018, where Scots pine was planted 58 years ago, while sessile oak regenerated naturally; and (2) Valberzoso, in Palencia Province (04°14′32″ W, 42°53′41″ N), which was established in March 2020, where both species regenerated naturally and are approximately 60 years old.

The experimental triplets were located within the Cantabrian Mountain Range, characterized by a transitional climate with both Atlantic and continental influences. The mean annual temperature is 9.9°C, ranging from summer highs of 25.3°C to winter lows of -1.9°C. Yearly precipitation averages 1044 mm, peaking in October and November (82 mm) and reaching its lowest value in July (29 mm) (Pizarro et al., 2021). The parent material of the soil originated from the Triassic period and is composed primarily of sandstone and conglomerate, with some oil-bearing strata of carboniferous age, which can be found in the western sector. In this landscape, steep slopes, a cold climate, and historical deforestation limit soil development, although less steeply vegetated areas support deep, well-developed acidic soils (López et al., 2009). The sites are characterized by distinct climatic and edaphic conditions, as summarized in Table 1 and illustrated in Figure 2.

Table 1. Site characteristics and stand composition of the triplet experimental plots in Busnela and Valberzoso, Spain.

Location	**Plot**	**Longitude (°W)**	**Latitude (°N)**	**Altitude (m)**	**Slope (%)**	**Area (ha)**	**Number of trees (tree ha^{-1})**	**Basal area (m^2 ha^{-1})**
Busnela	Pure pine	03° 47'19"	43°02'55"	810	22	0.062	1102	66.17
	Pure oak	03° 47'21"	43°02'51"	760	34	0.058	1461	47.65
	Mixed	03° 47'19"	43°02'52"	785	28	0.089	1203	52.65
Valberzoso	Pure pine	04°14'31"	42°53'52"	897	16	0.062	1134	71.30
	Pure oak	04°14'22"	42°53'43"	880	10	0.062	1240	58.70
	Mixed	04°14'32"	42°53'41"	810	11	0.089	1165	54.20

Geographical coordinates (longitude and latitude) are given in degrees (°), minutes ('), and seconds ("). The altitude is recorded in meters (m); the slope is expressed as a percentage (%); the plot area is measured in hectares (ha); the tree density is reported as the number of trees per hectare (trees ha^{-1}); and the basal area is represented in square meters per hectare (m^2 ha^{-1}).

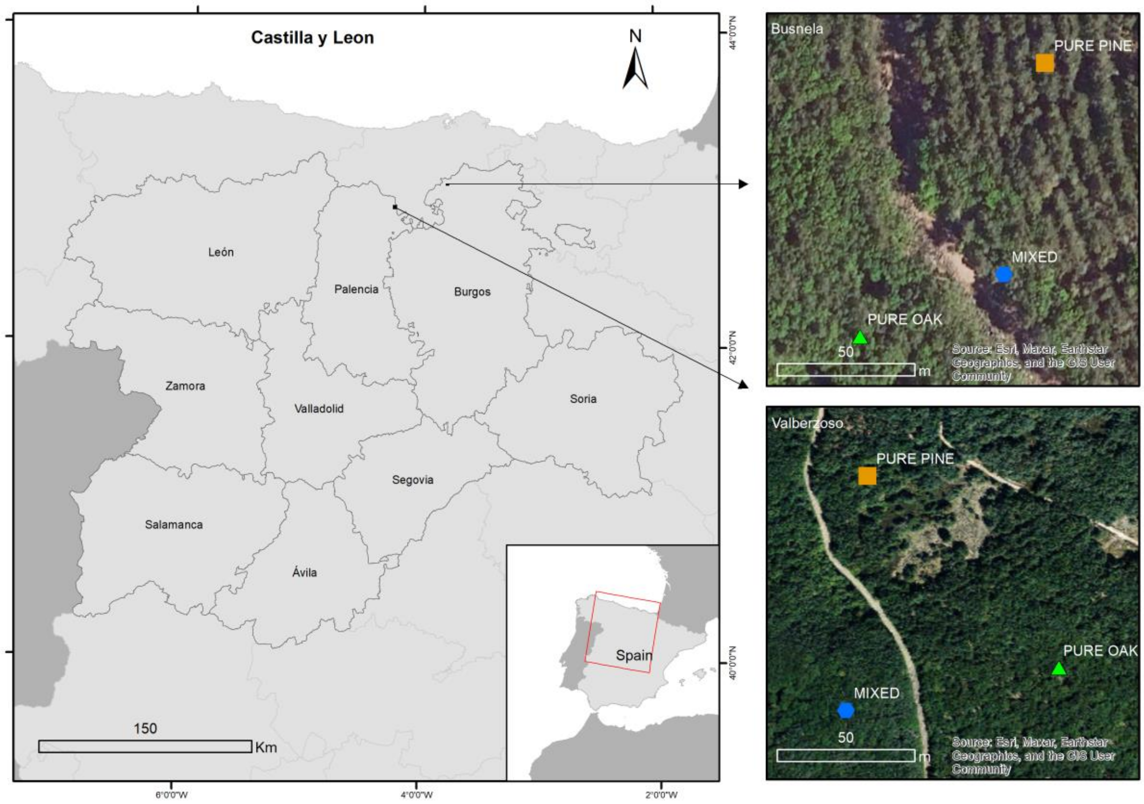

Figure 2. Locations and layouts of the triplet experiments in Busnela and Valberzoso in the Cantabrian Mountain Range, Castilla y León region (Spain).

3.1.2. Young mixed forest site (Studies II and III)

Figure 3 shows the location of the study site: a young mixed forest of Scots pine and Pyrenean oak (*Quercus pyrenaica* Willd.) in the municipality of Quintanar de la Sierra, within the Sierra de la Demanda area of Spain. The site was selected because of its ecological importance as a Mediterranean mixed forest ecosystem that plays a crucial role in biodiversity conservation, forest resilience, and carbon sequestration under changing climatic conditions.

The site has a well-documented history of forest management, making it an ideal location for studying the effects of competition and precommercial thinning treatments on tree growth and biomass allocation. The site is a naturally regenerated mixed forest composed of Mediterranean vegetation, including Pyrenean oak, Erica species shrubs, and Scots pine, forming a diverse ecosystem with both natural and semi managed components.

With an age range between 15 and 18 years, the forest spans an elevation range of 1120 to 1150 m above sea level (a.s.l.) and is located at 41°58′41.16″ N latitude and 3°01′09.84″ W longitude. The site has a continental Mediterranean climate, with an annual mean temperature of 11.1 °C, reaching a summer maximum of 16.67 °C. Precipitation averages approximately 850 mm annually, with a pronounced dry season in July and August (Gavilán et al., 2007). In addition, frost events are common in the winter months, particularly between December and February.

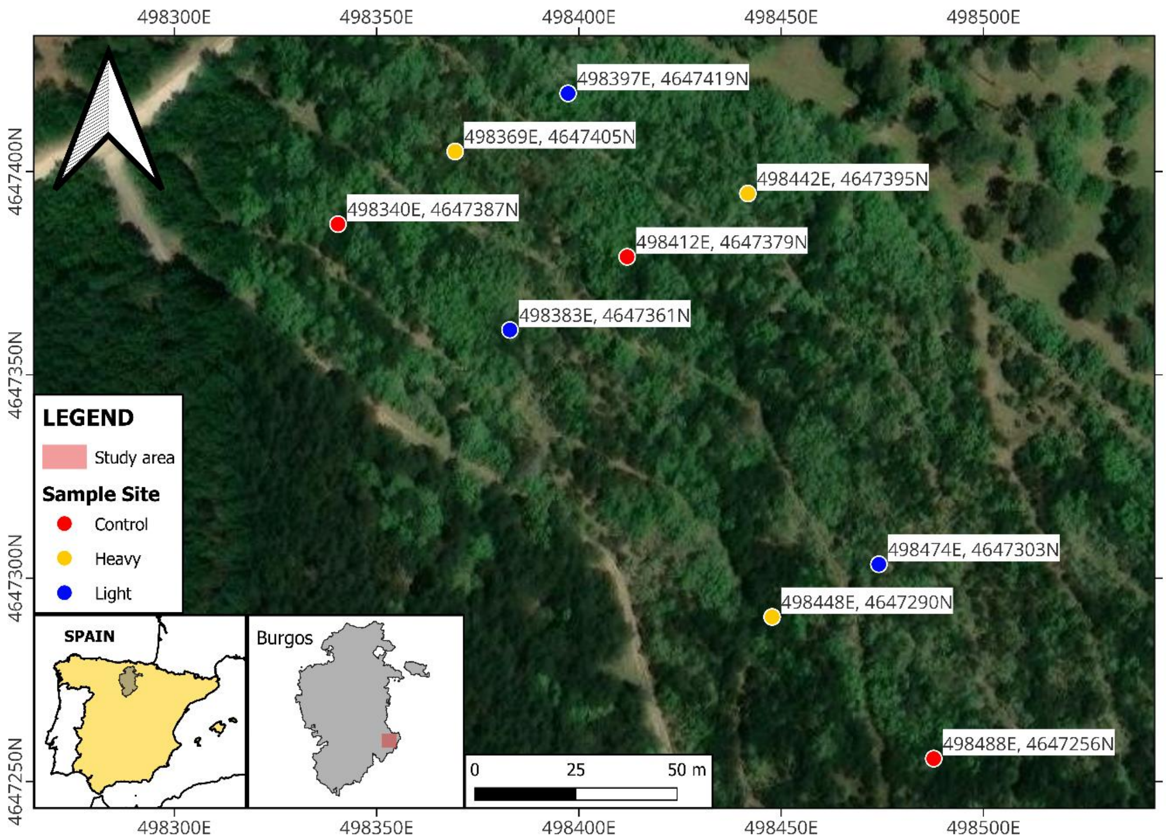

Figure 3. Location of the study site in Quintanar de la Sierra, Burgos (Spain), illustrating the mixed forest of Scots pine (*Pinus sylvestris* L.) and Pyrenean oak (*Quercus pyrenaica*). The different thinning treatments are indicated: control plots (red circles), light thinning plots (blue circles), and heavy thinning plots (yellow circles).

3.2. Experimental design

3.2.1. Mixed vs. monospecific plots (Study I)

The experimental design for Study I was based on the triplet approach (presented in subsection 3.1.1), which allowed comparisons between mixed and monospecific forest stands under identical environmental conditions. Each triplet consisted of three adjacent plots – one with Scots pine, one with sessile oak, and one with a mixture of both species – ensuring a balanced design for statistical comparisons. The triplets were selected from two study locations, Busnela and Valberzoso, to account for potential local site effects.

3.2.2. Thinning treatments (Studies II and III)

In 2016, the experimental setup for precommercial thinning used in studies II and III was established, following a randomized complete block design. At the start of the experiment, the young forest stand had an initial density of approximately 50,000 stems per hectare, with dominant trees reaching a height of approximately 6 meters. The experimental setup included nine rectangular plots, each measuring 40 × 20 m, where different levels of precommercial thinning were applied. One set of plots served as the control group, which was not subjected to thinning. The second group underwent light thinning, reducing the stand density to approximately 30,000 stems per hectare. The final group was heavily thinned, aiming for a post-treatment density of approximately 15,000 stems per hectare. This heavier thinning approach was designed to promote a more open stand structure while preserving species diversity, thereby reducing competitive pressure and potentially improving future economic returns (see Table 1 in Study II and Table 1 in Study III).

3.3. Data collection

The study was conducted at three distinct sites employing different methodologies for data collection and AGB estimation. Despite differences in experimental design and methodologies, both approaches aim to estimate AGB through precise tree measurements and random destructive sampling.

3.3.1. Tree attribute measurements

In terms of the age classes of the trees, the key tree attributes were measured using different instruments. For young trees, tree height (HT, in meters) was measured using a graduated height pole, whereas DBH was determined using a digital caliper, which provides high precision for smaller stem diameters. For mature trees, tree height was measured using a Vertex IV hypsometer (Haglöf Sweden AB, Långsele, Sweden) to capture the vertical distance to the tree apex accurately, as direct measurement was not feasible because of the tree height. The

DBH of these larger trees was measured using a diameter tape, which is more suitable for large-diameter stems and provides reliable circumference-based diameter estimates (Ormerod, 1986).

Crown attributes were also carefully recorded. The crown base height (CBH) refers to the vertical distance from the ground level to the lowest point of the tree's live branches, offering insight into the tree's growth patterns and crown development. It was also measured using a hypsometer. The crown length (CL) is the vertical distance from the crown base to the apex of the tree's canopy, which helps assess the extent and form of the tree's crown and was calculated as the difference between HT and CBH.

3.3.2. Biomass component sampling

For biomass sampling, the thesis strategically focused on mature and young forest stands to capture the full spectrum of structural and developmental variability within mixed-species ecosystems. This approach allowed for a comprehensive assessment of biomass dynamics under varying ecological conditions. Different sampling methods, which are as follows, were employed to suit each forest composition:

3.3.2.1. Mature forests (Study I)

Field sampling was conducted at Busnela in April 2018 and at Valberzoso in March 2020. Within each plot, trees were selected to represent the full DBH and tree height range, excluding suppressed or diseased trees, as well as those with structural deformities (Budhathoki et al., 2008). A total of 52 trees were destructively sampled across six plots (two triplets). At Busnela, 8 trees were sampled from each monospecific plot, and 16 were sampled from the mixed-species plot. At Valberzoso, 5 trees were selected from each monospecific plot, and 10 were selected from the mixed-species plot (see Table 2 in Study I).

The AGB was estimated for individual trees through destructive sampling, which involved harvesting and weighing the tree components, following the procedures outlined by Ruiz-Peinado et al. (2012, 2011). The study considered the following biomass components: stems with bark, thick branches (minimum diameter greater than 2 cm), thin branches (diameter less than 2 cm), and foliage (for only Scots pine, oak leaves were excluded because of their seasonal absence). Fresh weight was measured in the field using digital hanging balances with 0.05 kg accuracy and 50 kg capacity. Fresh subsamples (2–4 kg) of the various components were collected and stored in sealed, heavy-duty polyethylene bags to prevent moisture loss before oven-drying. The subsamples were then transported to the laboratory for determination of the dry weight of the biomass. These subsamples were weighed and then oven-dried at 102°C (Williamson and Wiemann, 2010) until a constant mass was reached.

Since stems cannot be weighed directly in the field, their diameter was recorded at 1-meter intervals down to a minimum diameter of 7 cm known as the merchantable volume. Smalian's formula was therefore used to calculate volume. Wood density was calculated from the stem disks (with a thickness of 1–3 cm) that were taken at the stem base, at breast height (1.3 m), and at the stem tip. The water displacement method involves immersing the subsample in water and measuring the amount of water displaced to accurately measure the sample's fresh (or green) volume. This step was used to calculate the fresh volume of each stem disk. The subsamples were then dried in an oven. The wood density was calculated as the dry mass-to-volume ratio (kg m^{-3}), incorporating variations across stem height (Demol et al., 2021). The biomass of the stem ($\text{Biomass}_{\text{stem}}$) was calculated using Equation (1.0) as follows:

$$\text{Biomass}_{\text{stem}} = \text{volume}_{\text{stem}} * \text{wood density} \quad (1.0)$$

where $\text{volume}_{\text{stem}}$ represents the stem volume, and where wood density refers to the density of the wood.

The biomass of each component ($\text{Biomass}_{\text{component}}$) was determined using Equation (1.1):

$$\text{Biomass}_{\text{component}} = \text{FW}_{\text{component}} * \frac{\text{SDW}_{\text{component}}}{\text{SFW}_{\text{component}}} \quad (1.1)$$

where$\text{FW}_{\text{component}}$ represents the fresh weight of the component, $\text{SDW}_{\text{component}}$ represents the dry weight of a subsample, and $\text{SFW}_{\text{component}}$ represents the fresh weight of the subsample.

The total aboveground biomass (AGB) was then computed as shown in Equation (1.2).

$$\text{AGB} = \text{Biomass}_{\text{stem}} + \text{Biomass}_{\text{branches}} + \text{Biomass}_{\text{foliage}} \quad (1.2)$$

where $\text{Biomass}_{\text{stem}}$, $\text{Biomass}_{\text{branches}}$, and $\text{Biomass}_{\text{foliage}}$ represent the biomasses of the stem, branches, and foliage, respectively.

3.3.2.2. Young mixed forests (Studies II and III)

The fieldwork for this study was conducted using destructive sampling to estimate the AGB. On the Iberian Peninsula, Pyrenean oak often keeps its dead leaves through winter due to marcescence (withering of the leaves without abscission and leaf fall during autumn and winter). Therefore, most of the leaves were still present from December 2021 to March 2023 and were included in the destructive biomass harvest. A total of 90 trees were harvested (target trees), including 45 Scots pines and 45 Pyrenean oaks (details in Table 3). Trees were selected across all diametric ranges, tree heights, and stand densities to ensure representativeness. The trees were classified into three DBH classes: small (3.5–6.9 cm), medium (7.0–10.4 cm), and large (10.5–13.9 cm), allowing for a comprehensive representation of stand structure and competition scenarios.

The target trees were then harvested through destructive sampling to determine their biomass. To ensure accurate and unbiased biomass measurements, specific criteria were applied during tree selection: trees with structural damage, disease, dead tops, or those located near plot boundaries were excluded. After each tree was felled, the branches and foliage of the tree were separated from the stem and weighed individually in the field using a portable scale with 10-gram precision. The stem was divided into three sections for easy management and handling of the samples – the base, middle, and top – and each section was weighed separately. Representative subsamples were collected from each tree component for dry biomass analysis. For stem sections, the samples were 2–5 cm thick slices. The branches and foliage were sampled in their entirety and placed in sealed plastic bags before being transported to the laboratory. All the samples, including the branch, foliage, and stem subsamples, were dried uniformly at 102°C (Williamson and Wiemann, 2010) until a constant weight was achieved.

The dry biomass of each stem section was calculated from the fresh and dry weights of the subsamples, as well as the fresh weight of each section recorded in the field (Equation (1.3)). The total stem biomass was obtained by summing the biomasses of the base, middle, and top sections. For branches and foliage, the total biomass was directly derived from the oven-dried weights. Finally, the AGB was calculated as the sum of the biomasses of the stem, branches, and foliage, as expressed in Equation (1.4). Summary statistics (means ± standard deviations) for these biometric measurements, along with the number of trees harvested, are presented in Table 2 of Study I.

$$\text{Biomass}_{(\text{stem section})} = \text{FW}_{(\text{stem section})} * \frac{\text{SDW}_{(\text{stem section})}}{\text{SFW}_{(\text{stem section})}} \quad (1.3)$$

$$\text{AGB} = (\text{Biomass}_{\text{SB}} + \text{Biomass}_{\text{SM}} + \text{Biomass}_{\text{ST}}) + \text{Biomass}_{\text{branches}} + \text{Biomass}_{\text{foliage}} \quad (1.4)$$

where $\text{FW}_{(\text{stem section})}$ is 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.

3.4. Competition metrics

Based on the approach outlined by Ahmed et al. (2024) and Pretzsch (2022), the influence zone was delineated as a radius equal to 25 % of the target tree's height (see Figure 4 for more information).

In Studies II and III, different approaches were employed to quantify tree competition because of the varying specific objectives and stand characteristics of each study. Both methods are based on distance-independent CIs but differ in how neighboring trees are defined and in how the basal area is aggregated to estimate competitive pressure. To evaluate the competitive environment of individual trees, neighboring trees within a defined influence zone were identified for each target tree. Each method for Study II and Study III assumes that tree height provides a reliable indicator of the spatial extent of competition. The following sections describe each approach in detail: the neighborhood basal area (NBA) in Study II and the basal area of larger trees (BAL) in Study III.

3.4.1. Neighborhood basal area (NBA) (Study II)

In Study II, tree competition was quantified using the neighborhood basal area (NBA). This distance-independent metric aggregates the basal area of all neighboring trees within a fixed competition radius around each target tree irrespective of the relative size of neighboring trees. This index is widely used due to its simplicity and interpretability (Burkhart and Tomé, 2012; Dahlhausen et al., 2017). NBA was calculated using the Equation (1.5):

$$NBA_i = \sum_{j=1}^{n_i} \left(\frac{\pi * {d_j}^2}{4}\right) \quad (1.5)$$

where NBA_i = total neighborhood basal area (m^2) for the i^{th} target tree, d_j = diameter (cm) of the j^{th} tree and n_i = total number of neighboring trees within R.

For simplicity and consistency, the NBA is hereafter referred to as the competition index (CI) in the results, discussion and conclusion parts of the thesis. Furthermore, total competition was divided into intraspecific competition and interspecific competition:

1. Intraspecific competition: This represents the contribution of competition from neighboring trees of the same species as the target tree. Equation (1.6) was used to estimate the basal area of all conspecific trees larger than the target tree.

$$CI_{intra,i} = \sum_{j=1}^{n} \left(\frac{\pi * {d_j}^2}{4}\right), \ where\ species_j = species_i \quad (1.6)$$

2. Interspecific competition: This accounts for competition exerted by neighboring trees of different species. Additionally, Equation (1.7) was used to estimate the basal area of all heterospecific neighbors larger than the target tree.

$$CI_{inter,i} = \sum_{j=1}^{n} \left(\frac{\pi * {d_j}^2}{4}\right), \ where\ species_j \neq species_i \quad (1.7)$$

Furthermore, the total competition experienced by a tree, as quantified by the CI, is the sum of its intraspecific and interspecific components, as indicated in Equation (1.8).

$$CI_i = CI_{intra,i} + CI_{inter,i} \quad (1.8)$$

To assess and examine the separate effects of intra- and interspecific competition on AGB, we used the best-fitting statistical model for each species. Prior to modeling, both CI_{intra} and CI_{inter} were log-transformed to approximate normality, an assumption required for linear modeling. As some of the competition index values were zero, a constant of 1 was added before transformation (i.e., $\log(\mathrm{CI}_{\mathrm{intra}} + 1)$ and $\log(\mathrm{CI}_{\mathrm{inter}} + 1)$) to prevent undefined logarithmic results. After the regression coefficients were calculated on a log scale, they were translated back to their original form using the exponential function exp(w) to capture effects within the same species, and exp(z) to reflect interactions between different species. This transformation formed the basis for the refined competition model, as expressed in Equation (1.9). These adjusted competition variables were integrated into earlier model frameworks to evaluate their impact on biomass distribution.

$$\log(\mathrm{CI}) = \mathrm{w} * \log(\mathrm{CI}_{\mathrm{intra}} + 1) + \mathrm{z} * \log(\mathrm{CI}_{\mathrm{inter}} + 1) \qquad (1.9)$$

w and z denote the coefficients corresponding to the intra- and interspecific competition indices, respectively.

3.4.2. Basal area of larger trees (BAL) (Study III)

Study III used the basal area of larger trees (BAL) index as a competition index to quantify tree competition. Unlike NBA, which includes all neighbors, the BAL index reflects the total competitive pressure exerted on a target tree by larger neighbors (in DBH) within the influence zone. Specifically, it is calculated as the cumulative basal area of neighboring trees with a DBH greater than that of the target tree. The BAL index is commonly used in distance-independent tree growth models (Wykoff et al., 1982) and is calculated as per Equation (2.0).

$$BAL_i = \sum_{j=1}^{n} \left(\frac{\pi * {d_j}^2}{4}\right), \ where\ d_j > d_i \qquad (2.0)$$

where BAL_i = total CI of the target tree i; n = number of neighboring trees with a DBH larger than that of the target tree; d_j = DBH of a neighboring tree j; and d_i = DBH of the target tree. Similarly, BAL is hereafter referred to as CI in the results, discussion and conclusion sections of the thesis.

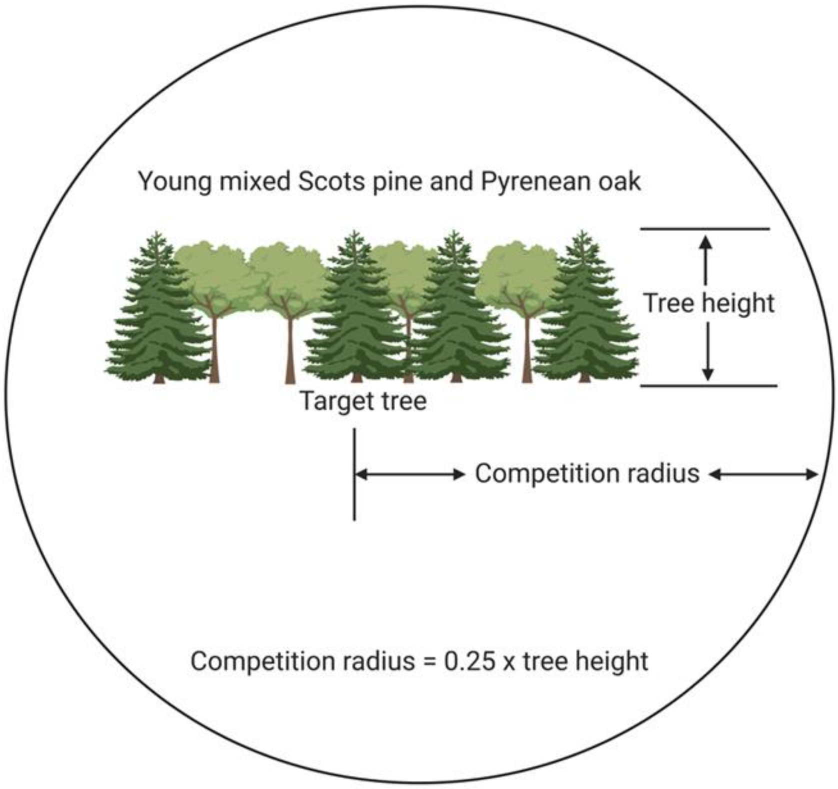

Figure 4. Conceptual representation (not to scale) of the zone of influence used to identify competing trees within a fixed competition radius. The competition radius is defined as 25% of the target tree's height, with surrounding trees considered competitors if they fall within the radius.

3.5. Data analysis

3.5.1. Data assumptions and preliminary checks

Before model fitting, the dataset underwent thorough preliminary checks for common data assumptions to ensure the validity of the subsequent statistical analyses. These checks included evaluations of normality, homogeneity of variance, independence and linearity. Residual normality was assessed using the Shapiro–Wilk test, homogeneity of variance using the Studentized Breusch–Pagan test, and residual autocorrelation using the Durbin–Watson test. Multicollinearity was performed through correlation matrices and variance inflation factor

(VIF) analysis, particularly involving these predictors (e.g., structural attributes such as DBH, tree height, crown base height, and crown length).

A threshold value greater than 5 was considered indicative of problematic multicollinearity. Additionally, an analysis was conducted to visually evaluate model performance by plotting predicted versus observed values, predicted versus residual values, and Q–Q plots of the residuals. These checks were performed to ensure the statistical validity and reliability of the regression models. All analyses were conducted in R software version 4.3.1 (R Core Team, 2023), with data visualization carried out using the "ggplot2" package (Wickham, 2016). Variance inflation factor (VIF) values were calculated using the "car" package (Fox et al., 2012). The following sections provide a detailed statistical analysis for studies I, II, and III.

3.5.2. Biomass growth patterns in mixed and monoculture stands (Study I)

3.5.2.1. Assessing differences in aboveground biomass

To determine whether significant differences in AGB exist between mixed and monospecific stands, analysis of covariance (ANCOVA) was applied. DBH was included as a covariate to account for differences in tree size among stands. Before ANCOVA, a Spearman correlation test was performed to analyze the relationships among AGB, DBH, and HT. This correlation test helped determine the strength of the relationship between AGB and tree structural attributes, providing a basis for including DBH in subsequent regression models.

ANCOVA was then used to assess significant variations in AGB and its components (stem, thick branches, thin branches, and foliage) between monospecific and mixed stands. In cases where the assumption of homogeneity of regression slopes was violated, the Johnson–Neyman procedure, implemented in the R package ‘JNplots’ (Toyama, 2024), was used to identify specific regions where significant differences occurred.

3.5.2.2. Development of biomass estimation models

The biomass estimation models tested in this study were based on the general power–law allometric equation (Enquist and Niklas, 2002), which describes how tree dimensions scale with biomass, as presented in Equation (2.1).

$$Y = \beta_0 X^{\beta 1} * \varepsilon \quad (2.1)$$

where Y = aboveground dry biomass, X = tree dimension variable (e.g., DBH or HT), and ε = an error term assumed to be multiplicative. β_0 and β_1 = model parameters or fitted coefficients. Furthermore, two complementary statistical frameworks were applied. The first strategy involves taking the natural logarithms of both sides of Equation (2.2), thereby converting the power-law model into a linear form as follows:

$$\log Y = \log\beta_0 + \beta_1 \log X + \varepsilon \quad (2.2)$$

log-transformed regression models were applied to linearize the power–law relationships and to correct for heteroscedasticity observed in the biomass residuals. It also introduces an additive error term that is approximately homoscedastic. The second strategy retained the original, untransformed equation with a multiplicative (log-normal) error structure and fitted it by non-linear least squares. This also included an additive-error variant on the natural scale, which is shown in Equation (2.3).

$$Y = \beta_0 X^{\beta 1} + \varepsilon \quad (2.3)$$

Before the models were fit, ANCOVA was used to test whether biomass–dimension relationships differed between stand types (monospecific vs. mixed). Whenever the test revealed a significant stand-type effect, separate equations were calibrated for each stand; when no such effect was detected, a single species-specific model was applied to both stand types. Two primary modeling approaches were employed for AGB: log-transformed regression models and nonlinear mixed-effects (NLME) modeling. These methods were selected to address different modeling needs and to provide a robust comparison of the predictive performance of AGB estimates across all forest types.

First, log-transformed regression models were applied to linearize the power-law relationships and to correct for heteroscedasticity observed in the biomass data. Second, NLME models were designed to account for hierarchical data structure, specifically the variation among plots, by treating the plot variable as a random effect, whereas DBH and tree height were included as fixed predictors (Chave et al., 2005; Forrester et al., 2017). The NLME models use biomass data directly without transformation, accommodating the inherent heterogeneity in modeling tree biomass. The NLME models incorporated 'plot-level random effects' to account for spatial variability and were fitted using the 'nlme' package in R (Pinheiro and Bates, 2017). Importantly, both modeling frameworks utilized an identical set of predictor equations, offering a consistent basis for comparison among model types. These models included different predictor structures, as shown in Equations (2.4)–(3.1).

$$\log(\text{AGB}) = \beta_0 + \beta_1 \log(\text{DBH}) \quad (2.4)$$

$$\log(\text{AGB}) = \beta_0 + \beta_1 \log(\text{HT}) \quad (2.5)$$

$$\log(\text{AGB}) = \beta_0 + \beta_1 \log(\text{DBH})^2 + \beta_2 \log(\text{HT}) \quad (2.6)$$

$$\log(\text{AGB}) = \beta_0 + \beta_1 \log(\text{DBH}^2\text{HT}) \quad (2.7)$$

$$\log(\text{AGB}) = \beta_0 + \beta_1 \log(\text{DBH}) \quad (2.8)$$

$$\log(\text{AGB}) = \beta_0 + \beta_1 \log(\text{HT}) \quad (2.9)$$

$$\log(\text{AGB}) = \beta_0 + \beta_1 \log(\text{DBH})^2 + \beta_2 \log(\text{HT}) \quad (3.0)$$

$$\log(\text{AGB}) = \beta_0 + \beta_1 \log(\text{DBH}^2\text{HT}) \quad (3.1)$$

Finally, following the approach of Baskerville (1972), the correction of back-transformation bias introduced by log-transformation, a correction factor (CF) was multiplied by antilogged (back-transformed) predictions as computed by Equation (5.1).

$$CF = exp\left(\frac{SEE^2}{2}\right) \quad (3.2)$$

where SEE is the standard error of the estimate.

3.5.2.3. Estimating biomass component allocation using Dirichlet regression

To assess how biomass was distributed among tree components (stems, thick branches, thin branches, and foliage), Dirichlet regression was applied (Douma and Weedon, 2019). This statistical technique, implemented in the 'DirichReg' package (Maier, 2014) was appropriate for compositional data because it ensures that biomass component predictions sum to the total AGB. Moreover, the predicted component proportions were converted into actual biomass values (in kilograms) by multiplying each predicted proportion by the corresponding tree's observed AGB.

3.5.2.4. Performance assessment of biomass estimation models

The AGB and its components for the biomass estimation models were evaluated using statistical criteria for model selection and predictive performance (Equations (3.3)–(3.6)). The Akaike information criterion (AIC) was used to assess model fit, with lower AIC values indicating better performance. The root mean square error (RMSE) was used to measure the difference between observed and predicted biomass values in kilograms, providing an estimate of model accuracy.

Furnival's index (FI), as shown in Equation (3.7), was used to compare the performance of the nonlinear mixed-effects (NLME) and logarithmic models. When comparing models with different error structures or transformations, the FI is a universal goodness-of-fit criterion that takes into consideration both the variance of the residuals and the transformation applied to the dependent variable (Furnival, 1961). Because it allows a direct comparison of models on a similar scale, this index is particularly suitable when the models being compared employ different forms of the dependent variable (e.g., log-transformed vs. untransformed biomass).

$$\mathrm{AIC} = -2\ln(\mathrm{L}) + 2\mathrm{p} \tag{3.3}$$

$$\mathrm{RMSE} = \sqrt{\frac{\sum_{i=1}^{n}(y_i - \hat{y}_i))^2}{n-p}} \tag{3.4}$$

$$\mathrm{Bias} = \frac{\sum_{i=1}^{n}(y_i - \hat{y}_i)}{n} \tag{3.5}$$

$$\mathrm{Bias}\ (\%) = 100 \times \frac{\mathrm{Bias}}{\overline{\mathrm{Y}}}\,\% \tag{3.6}$$

$$\mathrm{FI} = \frac{1}{[f'(Y)]}\sqrt{\mathrm{MSE}} \tag{3.7}$$

where n represents the total number of trees, y_i and $\hat{y}_i$ represent the observed and predicted values of AGB or the component, respectively, p represents the number of parameters in the equation, and $\overline{Y}$ represents the mean aboveground or component biomass. L represents the maximum likelihood of the equation. Additionally, f'(Y) represents the derivative of the dependent variable with respect to biomass, and MSE denotes the mean square error of the fitted equation. The square bracket symbol ([]) represents the geometric mean.

3.5.2.5. Comparative performance evaluation of the developed biomass models

As part of the comparative analysis, the models developed in this study, designated Model I, was compared to Models II and III, two existing models commonly used in Spanish forest biomass studies. Therefore, the following models were considered: the model proposed by Ruiz-Peinado et al. (2011) for Scots pine, designated Model II, and Balboa-Murias et al. (2006) for pedunculate oak (*Quercus robur*), both of which were derived from seemingly unrelated regression (SUR) techniques. Since there are no species-specific biomass models for sessile oak in the Spanish context, the pedunculate oak model was used as a proxy. Given the significant physical and ecological similarities between pedunculate oak and sessile oak, this substitution is justified.

Model III, on the other hand, is based on a more recent model developed by Menéndez-Miguélez et al. (2021) in the case of Scots pine and sessile oak (these authors incorporated only stem biomass and crown ratio estimations, also fitted with SUR). Models II and III were developed using monospecific stand data. However, the dataset used for the development of Model I included observations from monospecific and mixed stands. Nevertheless, the evaluation of model performance and accuracy was conducted through two statistical measures: (i) bias percentage, calculated as the mean relative difference between observed and predicted component weights and (ii) RMSE.

3.5.3. Influence of competition on biomass models (Study II)

3.5.3.1. Influence of competition on biomass

This study assessed the influence of competition on AGB models in Study II. Several logarithmic models were tested, including those with and without competition factors (Equations (3.8)–(4.5)). This method was used to address the exponential growth patterns with which the competitor trees and their associated AGB behave. By converting these exponential relationships into linear relationships, we effectively address the problem of heteroscedasticity in residuals that are common 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, the study adopted and adapted four commonly used biomass estimation models as a baseline (Equations (3.8), (4.0), (4.2), and (4.4)) from Chave et al. (2005) and Sun et al. (2024). This study then included neighborhood competition factors in the four baseline models, resulting in four additional models (Equations (3.9), (4.1), (4.3), and (4.5)). A total of eight models were constructed to observe how competition influences biomass prediction. A likelihood ratio test (LRT) was used to establish whether competition terms introduced a meaningful difference compared with baseline models, primarily by testing those equations that included the same tree size variables (see Supplementary Tables S1 and S2 in Study I).

$$\log(\mathrm{AGB}) = \mathrm{a} + \mathrm{b} * \log(\mathrm{DBH}) + \varepsilon \tag{3.8}$$

$$\log(\mathrm{AGB}) = \mathrm{a} + \mathrm{b} * \log(\mathrm{DBH}) + \mathrm{c} * \log(\mathrm{NBA}) + \varepsilon \tag{3.9}$$

$$\log(\mathrm{AGB}) = \mathrm{a} + \mathrm{b} * \log(\mathrm{DBH}) + \mathrm{c} * \log(\mathrm{HT}) + \varepsilon \tag{4.0}$$

$$\log(\mathrm{AGB}) = \mathrm{a} + \mathrm{b} * \log(\mathrm{DBH}) + \mathrm{c} * \log(\mathrm{HT}) + \mathrm{d} * \log(\mathrm{NBA}) + \varepsilon \tag{4.1}$$

$$\log(\mathrm{AGB}) = \mathrm{a} + \mathrm{b} * \log(\mathrm{DBH}^2 * \mathrm{HT}) + \varepsilon \tag{4.2}$$

$$\log(\mathrm{AGB}) = \mathrm{a} + \mathrm{b} * \log(\mathrm{DBH}^2 * \mathrm{HT}) + \mathrm{c} * \log(\mathrm{NBA}) + \varepsilon \tag{4.3}$$

$$\log(\mathrm{AGB}) = \mathrm{a} + \mathrm{b} * \log(\mathrm{HT}) + \varepsilon \tag{4.4}$$

$$\log(\mathrm{AGB}) = \mathrm{a} + \mathrm{b} * \log(\mathrm{HT}) + \mathrm{c} * \log(\mathrm{NBA}) + \varepsilon \tag{4.5}$$

In this context, log () represents the natural logarithm, whereas a, b, and c denote the model coefficients. The term ε accounts for the error component in the model.

To examine the separate effects of intra- and interspecific competition on AGB, we used the best-fitting model for each species and extended it to include distinct competition indices. The competition indices were log-transformed to satisfy the assumption of normality in linear regression. Because some index values were zero, a constant of one was added before transformation (i.e., $\log(\mathrm{CI}_{\mathrm{intra}} + 1)$ and $\log(\mathrm{CI}_{\mathrm{inter}} + 1)$) to avoid undefined values. After the regression coefficients were estimated on the log scale, the outputs were back-transformed using the exponential function: exp(w) for intraspecific effects and exp(z) for interspecific competition effects. The adapted competition model can be expressed in Equation (4.6).

$$\log(\mathrm{NBA}) = \mathrm{w} * \log(\mathrm{CI}_{\mathrm{intra}} + 1) + \mathrm{z} * \log(\mathrm{CI}_{\mathrm{inter}} + 1) \tag{4.6}$$

where w and z represent the coefficients for the intra- and interspecific competition indices, respectively. These competition-adjusted variables were incorporated into the previously described model structures to assess their influence on biomass allocation.

Because biomass models were developed using logarithmic transformations, predictions needed to be back-transformed to kilograms. This can introduce a slight underestimation bias. This was corrected by applying a correction factor (CF) as defined in Equation (3.2).

3.5.3.2. Model evaluation metrics

We assessed model performance using four widely accepted statistical criteria: The Akaike information criterion (AIC), root mean square error (RMSE), adjusted R-squared (Adj. R^2), and model efficiency (MEF). These formulations are provided in Equations (4.7)–(4.9), whereas the AIC formula was introduced earlier (Equation (3.3)).

$$RMSE = \frac{\sum_{i=1}^{n}(y_i - \hat{y}_i)^2}{n-p} \quad (4.7)$$

where n = the number of target trees, y_i and $\hat{y}_i$ = the observed and predicted values, respectively, and p = the number of parameters in the equation.

$$Adj.R^2 = 1 - \frac{\sum_{i=1}^{n}(y_i - \hat{y}_i)^2}{\sum_{i=1}^{n}(y_i - \bar{y}_i)^2} * \frac{n-1}{n-p} \quad (4.8)$$

where $\bar{y}_i$ = the mean of the observed value.

$$MEF = 1 - \frac{\sum_{i=1}^{n}(y_i - \hat{y}_i)^2}{\sum_{i=1}^{n}(y_i - \bar{y}_i)^2} \quad (4.9)$$

This is a measurement of the model's predictive power, in the sense that MEF = 1 would equate to perfect prediction, and MEF = 0 would equate to the model doing no better than the mean.

3.5.4. Effects of competition on tree structure and biomass (Study III)

This section describes the statistical framework employed to assess the relationships between competition and various structural attributes and biomass allocation patterns in young mixed stands of Scots pine and Pyrenean oak. Finally, this thesis explored the use of structural equation modeling (SEM) to assess the indirect pathways through which competition may influence biomass allocation, offering deeper insight into species-specific adaptive responses within mixed-species forest dynamics. These are outlined in the following sections.

3.5.4.1. Allometric relationship analysis

To examine how BAL influences the allometric relationships between diameter at breast height (DBH) and structural attributes, an analysis of variance (ANOVA) was conducted. This approach facilitated the assessment of interaction terms between competition and species, providing insights into the impact of competition on allometric scaling relationships. Additionally, analysis of covariance (ANCOVA) was employed to integrate multiple covariates, both continuous and categorical, addressing common issues such as nonlinearity and heteroscedasticity in ecological datasets (Akritas and Van Keilegom, 2001; Wilcox, 2005). Log transformation was applied to all variables to enhance the effectiveness of analyzing allometric relationships. The log-transformed relationships were modeled using the following equation:

$$\log(\mathrm{Y}) = \beta_0 + \beta_1 * \log(\mathrm{X}) + \beta_2 * \log(\mathrm{Z}) + \beta_3 * (\log(\mathrm{X}) * \log(\mathrm{Z})) + \beta_4 * \mathrm{Species} + \varepsilon \qquad (5.0)$$

where Y represents the dependent variable (e.g., tree height, crown base height, or crown length), X is the DBH (independent variable), Z represents competition, β_{0-4} denotes the regression coefficient, and ε is the error term for the residuals. The significant interaction terms (β_3) indicated that competition influenced allometric relationships. In cases where the interaction effect was not significant, the model was refitted without the interaction term. The species variable was included in the model (Equation (5.0)) as a categorical predictor. Additionally, model validity was assessed through diagnostic checks: residuals plotted against fitted values did not indicate heteroscedasticity, and Q–Q plots demonstrated that the residuals followed a normal distribution (see Supplementary Figures S1 and S2 in Study III for further details).

3.5.4.2. Biomass allocation analysis

To investigate the influence of competition on the biomass relationships among different biomass components, ANCOVA was applied using the same methodology as in the allometric analysis. In this instance, the variables represent biomass components instead of structural attributes.

3.5.4.3. Structural equation modeling (SEM)

While competition did not directly impact all aspects of biomass allocation, it was hypothesized that structural attributes such as DBH, tree height, crown base height (CBH), and crown length (CL) may act as mediators, indirectly influencing biomass allocation. Given the limited sample sizes for individual species, species-specific SEM analyses were not feasible. Figure 5 presents the conceptual framework employed to develop the structural equation model (SEM) used to explore both direct and indirect effects among key variables. SEM was performed using the "lavaan" package (Rosseel, 2012).

All continuous variables, including biomass components and structural attributes, were standardized to have a mean of zero and a standard deviation of one to facilitate meaningful coefficient comparisons and improve model interpretability, following the approach of Mensah et al. (2023). A multicollinearity assessment using a correlation matrix and variance inflation factor (VIF) analysis led to the exclusion of CL due to redundancy, as it exhibited a strong correlation with tree height ($R = 0.78$). Five candidate SEMs were tested (see Supplementary Material Table S1 in Study III) to ensure robust results, and the best-fitting model was selected based on the AIC and Bayesian information criterion (BIC) rankings (Burnham and Anderson, 2002; Garrido et al., 2022).

This selection process minimized model complexity and prevented overfitting. Model fit was evaluated using multiple standard goodness-of-fit indices including: the chi-square test (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 final SEM was used to assess the indirect pathways through which competition influences biomass allocation. Residual correlations between biomass components were modeled to account for unexplained shared variance, a standard SEM practice that improves model fit.

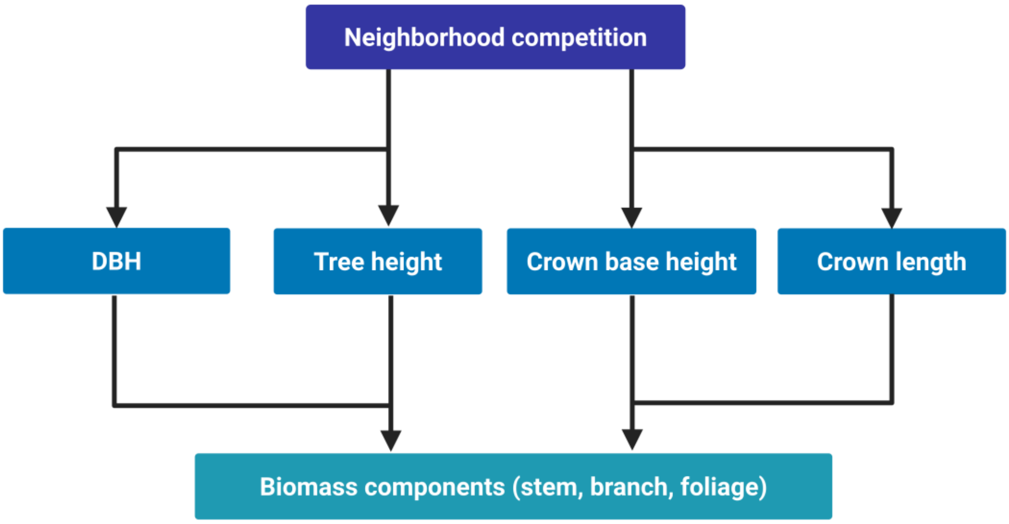

Figure 5. The conceptual diagram illustrates the indirect effect of competition on biomass allocation through various tree structural attributes, including DBH, tree height, crown base height, and crown length. These attributes function as mediators, channeling the influence of competition on the distribution of biomass among tree components. The arrows in the diagram represent the directional pathways of influence from competition, through the structural attributes, to the biomass components.

4. RESULTS

Below are the results obtained in each of the studies included in this thesis.

4.1. Descriptive (Study I)

4.1.1. Differences in biomass distribution across forest compositions

We analyzed the biomass distribution across different forest types, including mixed Scots pine–sessile oak stands, monospecific Scots pine stands, and monospecific sessile oak stands. In the monospecific Scots pine stands, the allocation of aboveground dry biomass (AGB) was distributed as follows: stems accounted for 80.9 %, thick branches accounted for 10.0 %, thin branches accounted for 5.8 %, and needles accounted for 3.3 % of the mean AGB. The biomass proportions in mixed pine–oak stands shifted slightly, with stems contributing 85.9 %, thick branches contributing 7.6 %, thin branches contributing 3.9 %, and needles contributing 2.6 % of the mean AGB.

For pure sessile oak stands, the distribution of aboveground biomass was notably stem-dominant, with 90.8 % allocated to stems, 7.6 % to thick branches, and 1.6 % to thin branches. The mixed sessile oak stands, on the other hand, exhibited a different pattern, with stems representing 82.0 % of the aboveground biomass, thick branches representing 13.8 %, and thin branches representing 4.2 % (refer to Table 2 in Study I). As expected, we observed positive correlations between AGB and DBH across both mixed and pure stands of Scots pine and sessile oak trees. A moderately positive relationship was also noted between AGB and tree height for Scots pine. In contrast, the correlation between AGB and tree height was stronger in mixed stands than in monospecific stands for oak trees (refer to Supplementary Table S1 of Study III).

4.1.2. Comparison of AGB and tree components

The ANCOVA indicated no statistically significant interaction effects for Scots pine trees when comparing trees growing in mixed and monospecific stands across AGB and its components including AGB, stems, thick branches, thin branches, and needle biomass (see Figure 6). In contrast, sessile oak trees presented notable differences. A significant interaction effect was observed for AGB and stem biomass but not for thick branches or thin branches. This suggests distinct growth patterns between mixed and monoculture settings. Specifically, the differences in AGB between mixed and monospecific sessile oak trees were driven primarily by substantial variations in stem biomass.

The Johnson–Neyman technique identified specific DBH ranges where slope differences between mixed and monoculture stands were significant. For the DBH ranges of 11.0–26.9 cm (for AGB) and 12.6–33.5 cm (stem biomass), no significant slope differences were detected. Interestingly, for small values in the diametric range (mainly dominated trees), sessile oak trees in mixed stands presented significantly lower AGB than those in monospecific stands. However, for the greatest values of the diametric range (mainly dominant trees), the AGB of sessile oak trees in mixed stands surpassed that of their monoculture counterparts (see Figure 6).

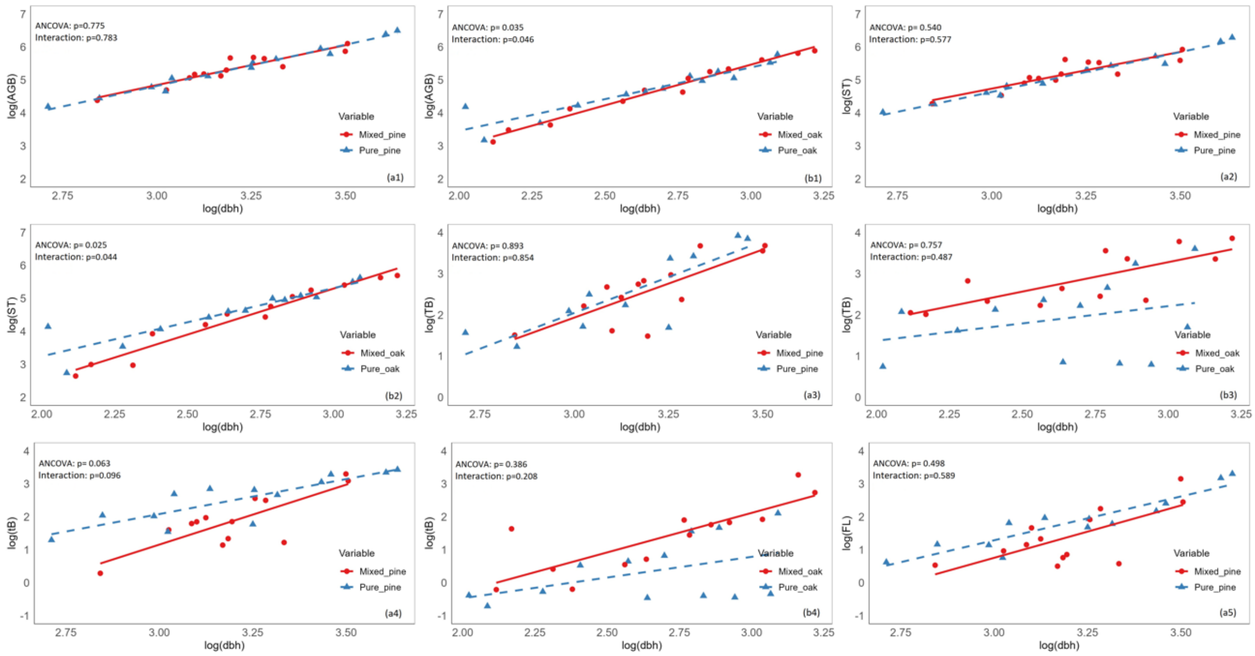

Figure 6. Relationships between log-transformed aboveground biomass (AGB) components and log (DBH) in mixed and monospecific/pure stands of Scots pine and sessile oak. Each panel shows the results of ANCOVA assessing the interaction effects between stand type and DBH for different biomass components: AGB (a1, b1), stem biomass (a2, b2), thick branches (a3, b3), thin branches (a4, b4), and foliage biomass (a5). Red circles and solid lines represent mixed stands; blue triangles and dashed lines represent monospecific stands.

4.1.3. Predicting aboveground biomass (AGB)

For Scots pine trees, the logarithmic model represented by Equation (2.6), which incorporates both DBH and tree height as predictors, emerged as the best-fit model for estimating AGB. This model demonstrated the highest goodness-of-fit among all tested equations (Table 2). For oak trees, the optimal model varied depending on forest composition. In the monospecific oak stands, Equation (2.6) was also the most effective, as it relies on both the DBH and tree height. However, in mixed oak stands, Equation (2.4), which uses only the DBH as a predictor, showed superior performance. Further analysis using nonlinear mixed-effects (NLME) models revealed that Equation (3.0), which incorporates both DBH and height, produced the lowest AIC value for Scots pine trees (Table 3). Similarly, Equation (3.0) was the best performer for monospecific oak stands, whereas for mixed oak trees, Equation (2.8), which depends exclusively on DBH, provided the lowest AIC value. Detailed evaluations using Furnival's index (FI) supported the superiority of the NLME models over the logarithmic models. Equations (3.0), (3.0), and (2.8) resulted in the lowest FI values for Scots pine (0.033), pure oak (0.300), and mixed oak (0.075), respectively. Additionally, no signs of heteroscedasticity were detected in the models, further supporting their robustness for AGB estimation.

Table 2. Weighted regression results for the analyzed forest stands: estimated coefficients, standard errors, and goodness-of-fit statistics of the AGB prediction models.

Equation	Parameter	Scots pine						Pure sessile oak						Mixed sessile oak					
		Estimate	SE	AIC	RMSE	FI	CF	Estimate	SE	AIC	RMSE	FI	CF	Estimate	SE	AIC	RMSE	FI	CF
2.4	β0	-2.601	0.394	-23.251	0.138	0.186	1.074	-0.397	0.623	8.094	0.262	0.266	1.153	-1.948	0.306	**-10.056**	0.130	0.146	1.074
	β1	2.477	0.123					1.926	0.234					2.471	0.113				
2.5	β0	-2.561	2.121	39.988	0.465	0.341	1.274	0.319	1.557	26.585	0.534	0.453	1.337	-5.227	1.732	21.288	0.436	0.185	1.267
	β1	2.742	0.736					1.612	0.572					3.569	0.622				
2.6	β0	-3.873	0.552	**-29.560**	0.118	0.114	1.064	0.587	0.599	**2.450**	0.195	0.350	1.118	-1.894	0.636	-8.068	0.130	0.290	1.077
	β1	1.144	0.062					1.369	0.170					1.246	0.124				
	β2	0.651	0.221					-1.155	0.408					-0.040	0.408				
2.7	β0	-4.543	0.448	-27.759	0.126	0.178	1.068	-0.605	0.893	14.890	0.341	0.881	1.203	-3.156	0.461	-3.856	0.166	0.423	1.094
	β1	1.064	0.048					0.662	0.111					0.963	0.056				

SE = standard error, AIC = Akaike information criterion, RMSE = root mean square error, FI = Furnival index, CF = log-bias correction factor. The values in bold indicate the best model for each species type, based on the AIC. All regression terms were significant at $p < 0.05$.

Table 3. Weighted regression results of the Scots pine, pure sessile oak, and mixed sessile oak stands: coefficient estimates, standard errors, and goodness-of-fit statistics for the AGB prediction models.

Equation	Parameter	Scots pine					Pure sessile oak					Mixed sessile oak				
		Estimate	SE	AIC	RMSE	FI	Estimate	SE	AIC	RMSE	FI	Estimate	SE	AIC	RMSE	FI
2.8	β0	0.073	0.029	259.363	35.982	0.028	0.124	0.054	123.371	16.888	0.150	0.126	0.044	**114.358**	13.39	0.075
	β1	2.483	0.124				2.513	0.141				2.515	0.119			
2.9	β0	0.094	0.198	326.659	118.176	0.008	0.069	0.180	150.576	54.674	0.249	0.003	0.005	146.368	54.906	0.018
	β1	2.710	0.729				2.717	0.907				3.843	0.698			
3.0	β0	0.022	0.012				0.047	0.021				0.199	0.101			
	β1	1.142	0.063	**251.940**	30.198	0.033	1.048	0.079	**119.602**	16.962	0.300	1.295	0.126	115.487	19.786	0.051
	β2	0.646	0.225				0.764	0.243				-0.233	0.383			
3.1	β0	0.011	0.005	253.499	32.288	0.031	0.032	0.012	119.974	17.771	0.334	0.016	0.008	119.868	13.068	0.077
	β1	1.063	0.05				0.996	0.040				1.079	0.058			

SE = standard error; AIC = Akaike information criterion; RMSE = root-mean-square error; FI = Furnival index. Within each species type, the entries in bold indicate the model with the smallest AIC value. All the coefficients are statistically significant at the 5 % level ($p < 0.05$).

4.1.4. Estimation of biomass proportions using Dirichlet regression

The parameter estimates and model performance of the Dirichlet regression models are summarized in Table 5 of Study I. These models revealed changes in biomass proportions along the DBH and tree height gradients for Scots pine, monospecific oak, and mixed oak stands, as shown in Figure 7. For Scots pine trees, increases in DBH were associated with a decline in stem biomass proportions, whereas the proportions of thick branches, thin branches, and foliage increased. However, as the tree height increased, the trend reversed, with the stem biomass proportions increasing and those of the other components decreasing (Figure 7a, b).

For both mixed and monospecific oak stands, stem biomass proportions increased with DBH and height, whereas the proportions of thick and thin branches decreased (Figure 7c–f). Among the tested equations (Equations (2.8)–(3.1)), Equation (3.0), which included both DBH and height as independent variables showed the lowest AIC value for Scots pine (Table 5). For oak species, Equation (2.9), which relies solely on height, was the best-performing model in both monospecific and mixed stands. The model predicted that, on average, stems contributed 81.99 % of the AGB of Scots pine, followed by thick branches (8.70 %), thin branches (5.61 %), and needles (3.69 %). For pure sessile oak, stems accounted for 83.34 % of the AGB, with thick and thin branches contributing 11.36 % and 5.30 %, respectively. In mixed sessile oak stands, stems represented 74.00 % of the AGB, whereas thick branches and thin branches accounted for 19.27 % and 6.74 %, respectively. As shown in Table 5, the Dirichlet regression model provided unbiased and precise estimations of biomass proportions.

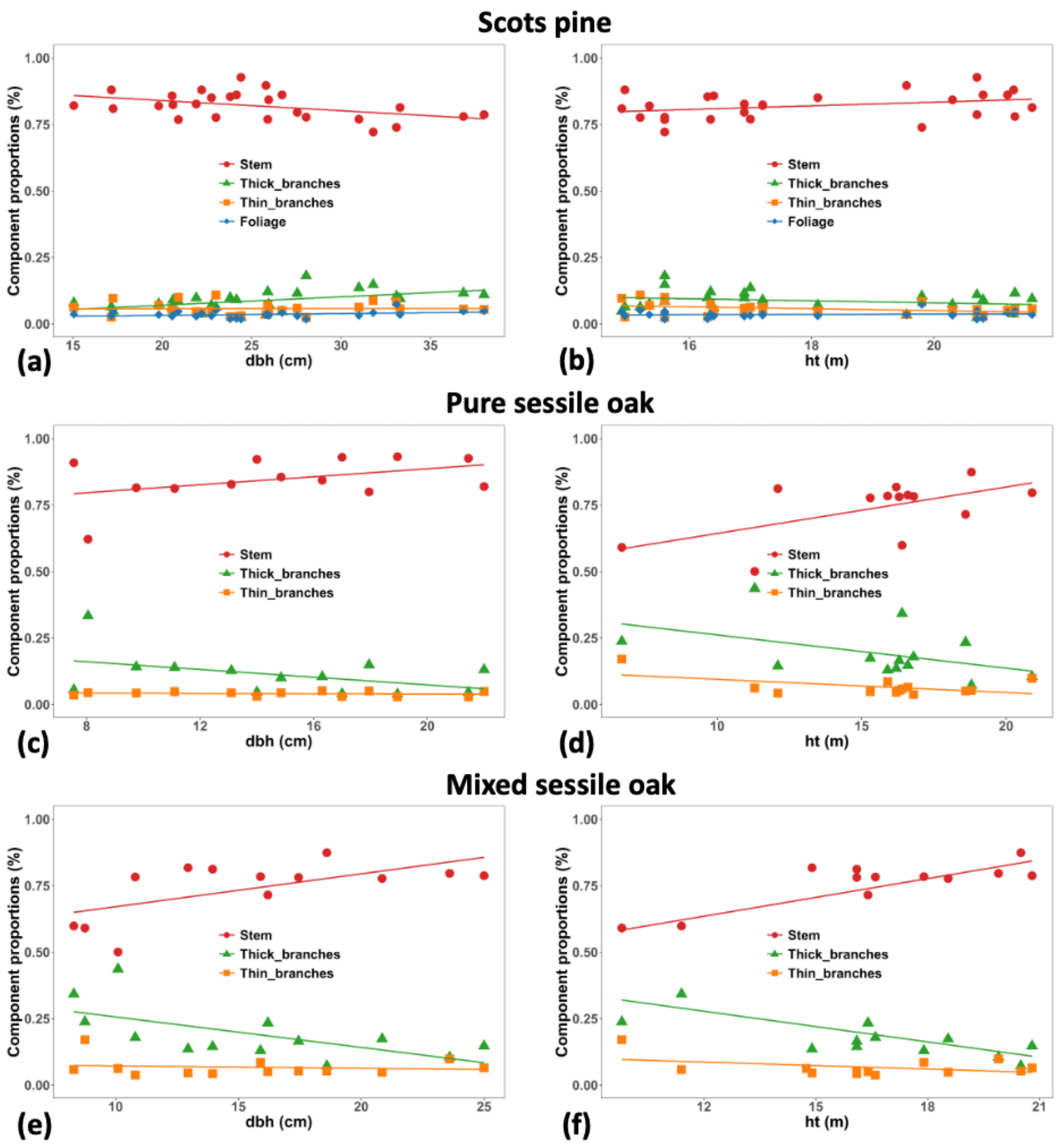

Figure 7. Trends in the predicted biomass component proportions for Scots pine (a, b), pure sessile oak (c, d), and mixed sessile oak (e, f) as functions of diameter at breast height and tree height. The dots, triangles, and squares are the observed values for the stem, thick, and thin branch biomass proportions, respectively, whereas the diamond shapes indicate foliage (only Scots pine).

4.1.5. Comparative performance of new versus established biomass models

In this study, the results revealed differences in predictive performance across Model I for the newly developed biomass models, Model II for the models by Ruiz-Peinado et al. (2011) for Scots pine and Balboa-Murias et al. (2006) for pedunculate oak and Model III for the models by Menéndez-Miguélez et al. (2021). The current models demonstrated superior predictive performance across all the AGB components (stem, crown, and total biomass) for both the Scots pine and sessile oak species, as illustrated in Figure 4 of Study I. Model I resulted in minor overestimations of AGB and crown biomass and slight underestimations of stem biomass. However, Models II and III exhibited greater biases, with Model II showing the highest RMSE values, particularly for AGB and crown components. In contrast, Model I had significantly lower RMSE values, underscoring its ability to capture the variability in mixed oak biomass. The application of the models developed in the monospecific stands to the mixed stands resulted in greater bias and RMSE values than did the application of the models to the pure stands when applied to pure stands. Overall, the results confirmed that Model I outperformed previously established models in terms of accuracy and predictive reliability for estimating AGB, stem biomass, and crown components across Scots pine and Pyrenean oak (Figure 4a–f in Study I). This highlights the influence of mixed-stand data in Model I's development compared with the monospecific focus of the reference models.

4.2. Biomass modeling and the role of competition in young mixed stands (Study II)

4.2.1. Assessing biomass prediction models for Scots pine and Pyrenean oak in mixed stands

We evaluated eight different models to determine the most effective combination of predictor variables for estimating AGB in young mixed stands of Scots pine and Pyrenean oak and tested whether the inclusion of competition conditions improved the fit statistics. The results are summarized in Tables 4 (Scots pine) and 5 (Pyrenean oak). For Scots pine, Equation (4.3) emerged as the best-fit model, demonstrating the highest performance based on fit statistics, with AIC = 45.931, RMSE = 0.353, adjusted R^2 = 0.789, and MEF = 0.803. Importantly, the chosen CI (neighborhood basal area, NBA) was statistically significant in three of the four models tested ($p < 0.05$), except for Equation (3.8). These findings highlight the importance of incorporating competition variables into biomass prediction to improve estimations.

In Equation (4.3), the inclusion of DBH, HT, and NBA as predictors significantly enhanced the model's predictive capacity. Compared with the other models, Equation (6.1) reduced the RMSE by 14%, increased the adjusted R^2 by 12%, and improved MEF by 15%. Supplementary Table S3 in Study II provides a detailed comparison of the statistical performance of the evaluated models.

In contrast, for Pyrenean oak, the inclusion of the CI variable did not yield any significant improvement in model performance, as its effect was not statistically significant in any of the tested models ($p > 0.05$). Among the evaluated models, Equation (3.8), which included only DBH, showed the best predictive performance. This model had an AIC of -12.980, an RMSE of 0.196, an adjusted $R^2 = 0.850$, and MEF = 0.854. Although Equation (3.9) slightly outperformed Equation (3.8) in some regression metrics, the NBA remained statistically insignificant ($p > 0.05$). A comprehensive comparison of these models is provided in Supplementary Table S3 of Study II.

Table 4. 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.

Equation	Coefficient	Estimate	SE	p-value	AIC	RMSE	Adj. R^2	MEF	CF
5.6	a	-1.510	0.403	0.001 ***	54.842	0.416	0.622	0.630	1.095
	b	1.889	0.221	$7.68 \cdot e^{-11}$ ***					
5.7	a	-2.119	0.695	0.004 **	52.619	0.411	0.623	0.640	1.095
	b	1.971	0.233	$1.30 \cdot e^{-10}$ ***					
	c	-0.107	0.100	0.288 ns					
5.8	a	-1.893	0.474	$3.00 \cdot e^{-04}$ ***	54.549	0.406	0.632	0.649	1.092
	b	1.617	0.285	$1.14 \cdot e^{-06}$ ***					
	c	0.510	0.344	0.146 ns					
5.9	a	-4.698	1.003	$3.06 \cdot e^{-05}$ ***	47.073	0.365	0.695	0.715	1.076
	b	1.433	0.266	$3.22 \cdot e^{-06}$ ***					
	c	1.396	0.424	0.002 **					
	d	-0.377	0.122	0.004 **					
6.0	a	-1.997	0.445	$5.25 \cdot e^{-05}$ ***	53.020	0.408	0.637	0.645	1.091
	b	0.732	0.083	$3.18 \cdot e^{-11}$ ***					
6.1	a	**-3.824**	**0.757**	**$8.98 \cdot e^{-06}$ *** **	**45.931**	**0.353**	**0.789**	**0.803**	**1.077**
	b	**0.850**	**0.087**	**$2.16 \cdot e^{-12}$ *** **					
	c	**-0.280**	**0.097**	**0.006 ** **					
6.2	a	-1.137	0.598	0.064 ns	78.198	0.540	0.364	0.379	1.165
	b	1.770	0.346	$6.81 \cdot e^{-06}$ ***					
6.3	a	-5.150	1.290	$3.00 \cdot e^{-04}$ ***	69.150	0.477	0.491	0.514	1.130
	b	2.800	0.432	$7.99 \cdot e^{-08}$ ***					
	c	-0.524	0.153	0.002 **					

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 species.

Table 5. 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.

Equation No.	Coefficient	Estimate	SE	p-value	AIC	RMSE	Adj. R^2	MEF	CF
5.6	a	**-1.046**	**0.228**	**$3.89 \cdot e^{-05}$ *****	**-12.980**	**0.196**	**0.850**	**0.854**	**1.020**
	b	**1.857**	**0.117**	**$2.00 \cdot e^{-16}$ *****					
5.7	a	-0.643	0.357	0.079 ns	-13.192	0.191	0.854	0.861	1.020
	b	1.806	0.121	$2.00 \cdot e^{-16}$ ***					
	c	0.076	0.052	0.153 ns					
5.8	a	-0.914	0.474	0.005 **	-11.401	0.195	0.848	0.855	1.021
	b	1.944	0.285	$1.42 \cdot e^{-13}$ ***					
	c	-0.153	0.344	0.533 ns					
5.9	a	-0.323	0.461	0.488 ns	-12.478	0.188	0.855	0.865	1.020
	b	1.948	0.178	$9.18 \cdot e^{-14}$ ***					
	c	-0.271	0.248	0.282 ns					
	d	0.092	0.054	0.096 ns					
6.0	a	-1.494	0.298	$9.54 \cdot e^{-06}$ ***	-1.674	0.222	0.808	0.812	1.026
	b	0.693	0.051	$2.00 \cdot e^{-16}$ ***					
6.1	a	-1.231	0.461	0.011 *	-0.273	0.221	0.826	0.814	1.026
	b	0.680	0.054	$9.27 \cdot e^{-16}$ ***					
	c	0.046	0.061	0.457 ns					
6.2	a	-1.037	0.594	0.088 ns	45.811	0.377	0.447	0.460	1.077
	b	1.828	0.302	$3.12 \cdot e^{-07}$ ***					
6.3	a	-0.496	0.903	0.586 ns	47.137	0.374	0.542	0.468	1.078
	b	1.725	0.330	$5.19 \cdot e^{-06}$ ***					
	c	0.084	0.106	0.430 ns					

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 the Pyrenean oak species.

4.2.2. Influence of intra- and interspecific competition on AGB

The effects of intra- and interspecific competition on the AGB of Scots pine and Pyrenean oak were assessed using logarithmic regression models, and the results are presented in Table 6. For Scots pine, intraspecific competition was associated with a marginal decrease in AGB (estimated coefficient = -12.995), but this effect was not statistically significant (p-value = 0.055). Intraspecific competition accounted for 8.44 % of the variance in AGB. Interspecific competition, on the other hand, resulted in a significant reduction in AGB, with an estimated coefficient of -34.049 (p-value = 0.003), explaining 7.09 % of the variance. This highlights the more pronounced effect of interspecific competition than intraspecific competition on the AGB of Scots pine. For Pyrenean oak, intraspecific competition had a positive but statistically insignificant effect on AGB (estimated coefficient = 5.063, p = 0.091), contributing to 10.93% of the variance. Similarly, interspecific competition had a slight positive effect (estimated coefficient = 2.593) but was not statistically significant (p = 0.467), accounting for only 0.72 % of the variance in AGB. Figure 8 shows the varying responses of these species to competitive interactions.

Table 6. 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. Coefficients (a, b, w, z) represent the model's intercept and the effects of the predictors. Statistical significance is indicated by *** ($p < 0.001$), ** ($p < 0.01$), and ns (not significant).

Species	Model	Coefficient	Estimate	SE	p-value	AIC	RMSE	Adj. R^2	MEF	CF
Scots pine	6.1 with CI_{intra} and CI_{inter}	a	-2.104	0.438	$2.11 \cdot e^{-05}$ ***	47.051	0.365	0.695	0.716	1.050
		b	0.815	0.089	$1.62 \cdot e^{-11}$ ***					
		w	-12.995	6.565	0.055 ns					
		z	-34.049	10.939	0.003 **					
Pyrenean oak	5.6 with CI_{intra} and CI_{inter}	a	-0.987	0.236	$1.46 \cdot e^{-04}$ ***	-12.153	0.189	0.854	0.864	1.020
		b	1.782	0.125	$2.00 \cdot e^{-16}$ ***					
		w	5.063	2.927	0.091 ns					
		z	2.593	3.529	0.467 ns					

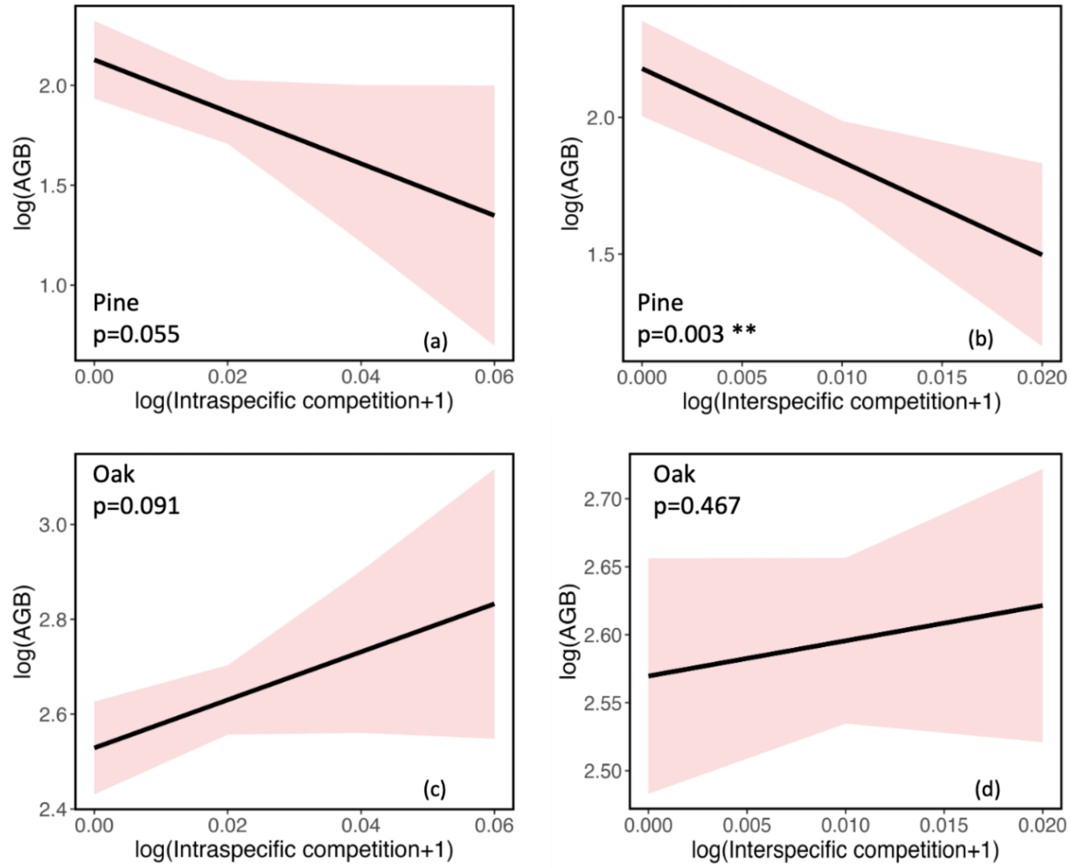

Figure. 8. Relationships between aboveground biomass (AGB) and intraspecific and interspecific competition for Scots pine and Pyrenean oak. (a) and (c) show the influence of intraspecific competition on the AGB of Scots pine and Pyrenean oak, respectively, whereas (b) and (d) show the corresponding effects of interspecific competition. Shaded regions represent 95% confidence intervals. Statistically significant relationships are denoted by $^{**}p < 0.01$.

4.3. Effects of competition on allometry and biomass allocation (Study III)

4.3.1. Effects of competition on allometric relationships

4.3.1.1. Allometric relationship between DBH and tree height

The ANCOVA results ($R^2 = 0.74$) revealed that both DBH (parameter estimate = 1.018, $p < 0.001$) and BAL (parameter estimate = 0.562, $p < 0.001$) had significant effects on tree height. Furthermore, a significant interaction was observed between DBH and competition (parameter estimate = -0.228, $p < 0.001$), indicating that the strength of the relationship between DBH and tree height weakens as competition increases. These findings revealed that competition significantly modifies the allometric relationship between DBH and tree height for both Scots pine and Pyrenean oak. Additionally, a significant difference was observed between the two species (parameter estimate = -0.142, $p < 0.001$), with Scots pine trees consistently exhibiting shorter tree heights compared to Pyrenean oak trees at the same DBH (Figure 4a of Study III). This result highlights distinct species-specific allometric patterns in response to competition.

4.3.1.2. Allometric relationship between DBH and crown base height

The analysis of the relationships between DBH and CBH (Adj. $R^2 = 0.31$) revealed significant effects of both DBH (parameter estimate = 1.380, $p < 0.01$) and competition (parameter estimate = 0.934, $p < 0.01$). Additionally, a significant interaction was detected between DBH and BAL (parameter estimate = -0.380, $p < 0.05$), suggesting that competition modulates the relationship by reducing the influence of DBH on CBH. Unlike the relationship with tree height, no significant species-specific differences were observed in the DBH–CBH relationship ($p > 0.05$), indicating that both species adjust their crown base height similarly in response to competitive environments. (Figure 4b of Study III)

4.3.1.3. Allometric relationship between DBH and crown length

The relationship between DBH and CL was also investigated, and after removing the nonsignificant interaction term, the model (Adj. $R^2 = 0.65$) showed independent effects of both DBH (parameter estimate = 0.498, $p < 0.001$) and the CI (parameter estimate = 0.070, $p < 0.05$) (Table 7). These results indicate that competition influences CL independently of DBH, suggesting that larger trees develop longer crown lengths despite competitive pressures. Furthermore, significant species-specific differences (parameter estimate = -0.282, $p < 0.001$) were found, with Scots pine exhibiting shorter crown lengths than Pyrenean oak (Figure 4c of Study III).

Table 7. 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	$2.46 \times {}^{-6}$	***
	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)	–	–	–	–	–

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 ($p \geq 0.05$).

4.3.2. Competition and biomass allocation patterns

4.3.2.1. Biomass allocation between stems and branches

ANCOVA (Adj. $R^2 = 0.70$) revealed that BAL (competition) had no significant effect ($p > 0.05$) on the allocation of biomass between stems and branches (Table 8). These findings suggest that competitive intensity does not alter branch–stem partitioning in either Scots pine or Pyrenean oak. However, significant species-specific differences ($p < 0.05$) were observed, with Scots pine consistently allocating more biomass to branches compared to Pyrenean oak (Figure 5a of Study III). These results imply that inherent species traits drive the observed allocation patterns, which remain stable across varying levels of competition.

4.3.2.2. Biomass allocation between foliage and stems

In contrast to branch-stem allocation, the relationship between foliage and stem biomass was significantly affected by competition (Adj. $R^2 = 0.75$, $p < 0.001$; Table 8). This finding indicates that competition influences resource allocation strategies related to foliage and stems. Additionally, significant species-specific differences ($p < 0.001$) were identified, with Pyrenean oak allocating a greater proportion of biomass to stems, whereas Scots pine allocated relatively more biomass to foliage. The species-specific difference was significant ($p < 0.001$), indicating that the magnitude of allocation shifts differed between the two species (Figure 5b of Study III).

4.3.2.3. Biomass allocation between branches and foliage

As shown in Table 8, competition did not significantly influence the biomass allocated to branches and foliage (Adj. $R^2 = 0.62$, $p > 0.05$). This suggests that competition does not alter the branch-foliage allocation pattern in either species. However, significant species-specific differences ($p < 0.001$) were observed, with Scots pine allocating more biomass to foliage compared to Pyrenean oak (refer to Figure 5c of Study III). These findings underscore the stability of branch-foliage allocation under competitive pressure and highlight species-specific adaptations in biomass distribution.

Table 8. 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}	***

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

4.3.3. Indirect effects of competition on biomass allocation

The structural equation model (SEM) provided strong support for the hypothesized relationships of a good fit to the study dataset ($\chi^2 = 2.831$, df = 3, p = 0.418, CFI = 1.000, TLI = 1.003, RMSEA = 0.000, SRMR = 0.029) as shown in Figure 6 of Study III. The results revealed that competition had a significant positive direct effect on tree height ($p < 0.001$). Additionally, competition indirectly influenced stem and branch biomass through its effect on tree height, with both indirect effects being statistically significant ($p < 0.001$). However, the indirect effect of competition on foliage biomass, mediated by tree height, was not statistically significant ($p > 0.05$). This suggests that foliage biomass allocation may be less responsive to competition when it is mediated through tree height.

SEM explained 61%, 19%, and 2% of the variance in stem, branch, and foliage biomass, respectively, indicating that competition and tree height explained a significant portion of the variation in stem and branch biomass but only a small portion of the foliage biomass variation. Significant residual correlations were observed among the biomass components, with strong relationships detected 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 ($R^2 = 0.38$, $p = 0.001$). These residual correlations suggest that neither competition nor tree height fully explains the shared variance between biomass components.

5. DISCUSSION

The findings of this thesis provide an integrated understanding of tree growth dynamics and aboveground biomass allocation, emphasizing how forest composition, species-specific traits, and competition interact to shape forest structure and function. Thus, this discussion highlights the relationships among forest composition, tree allometry, competition, and biomass distribution patterns by synthesizing results from three complementary studies. These findings are instrumental in understanding the ecological processes governing tree growth and the implications for forest management, particularly in mixed species stands. In the following sections, we discussed these findings in detail and their implications for ecological theory and sustainable forest management.

5.1. Biomass allocation and forest composition (Study I)

5.1.1. Biomass allometry and allocation in mixed versus monoculture stands

The findings revealed that Scots pine exhibited a consistent biomass growth pattern regardless of whether it was grown in mixed stands or pure stands. Conversely, the development of sessile oak – especially in terms of AGB and stem mass – varies considerably between mixed and monoculture settings. Earlier work (e.g., Pretzsch et al., 2020) suggested that sessile oak in mixed stands might develop broader crowns. However, the results suggest that a larger crown does not automatically translate to greater crown biomass. Both forest compositions yield comparable crown biomasses for sessile oak, which may be due to a lower proportion of woody tissue relative to crown area in mixed environments.

Additionally, rapid early growth in Scots pine might reduce interspecific competition for light in mixed stands, whereas in pure stands, competition within the species is equally influential. For sessile oak, the data indicate that smaller trees in mixed stands, those in the lower part of the DBH range, have lower AGB and stem mass than those in monocultures, likely due to intensified resource competition during the early growth phase. However, as these trees in mixed stands increase in size, those in the higher part of the DBH range, tend to catch up and sometimes even exceed their monoculture counterparts in terms of AGB and stem mass. This trend may reflect adaptive growth responses aimed at optimizing light capture when the light penetration of Scots pine canopies is limited. These observations are consistent with previous findings by Toïgo et al. (2015), who reported an overyielding effect in mature mixed oak–pine stands. Their work also highlighted the ability of sessile oak to adjust its growth and biomass allocation strategies in response to the competitive environment and stand composition.

5.1.2. Modeling aboveground biomass: Mixed versus monoculture equations

This study adds to the ongoing discussion on the best modeling approaches to account for data heterogeneity in biomass studies. We found that nonlinear mixed-effects (NLME) models with variance control fitting outperform traditional logarithmic regression models in terms of prediction accuracy and reduced bias. The NLME framework, which accommodates repeated measurements and correlations (e.g., plot effects), consistently produced more reliable estimates of AGB for both species. For

Scots pine and pure sessile oak, models incorporating both DBH and tree height yielded superior fit statistics. In contrast, for sessile oak in mixed stands, a simpler model based solely on DBH proved to be adequate. This outcome underscores the need for species- and stand-specific biomass equations, suggesting that a universal modeling approach may be insufficient, as observed in comparison with published models. These results agree with Bronisz and Mehtätalo (2020) in the idea that integrating tree height dataset can capture variations related to site quality and competitive dynamics while also emphasizing that oak dynamics in mixed stands might be better captured with less complex formulations.

5.1.3. Estimating tree components: Stem, branch, and foliage dynamics

When addressing the allocation of biomass into tree components, modeling proportions through Dirichlet regression was observed as an effective strategy to avoid extrapolation errors, which are commonly detected when estimates are made outside the fitting range. Although DBH, tree height, and biomass are interrelated, there is ongoing debate about the incremental value of including tree height in these equations. For Scots pine, combining DBH and tree height consistently improved AGB estimates, whereas for sessile oak trees in both mixed and pure stands, models based solely on tree height explained the variability in biomass allocation more effectively.

The analysis also revealed that as trees grow larger, there is a shift in allocation: the relative contribution of stem biomass decreases, whereas the proportion of biomass allocated to the crown (branches and needles) increases. This pattern likely reflects the trees' adjustment to increasing lateral competition, where emphasis shifts from vertical to canopy development. These insights support the idea that distinct management strategies might be required for different species and have practical implications for optimizing thinning and selection practices in mixed-species forests.

5.2. Modeling biomass estimation and the role of competition (Study II)

5.2.1. Role of independent variables in biomass estimation

The analysis revealed that the optimal biomass prediction model for young Scots pine trees integrates DBH, HT, and a CI. This combination notably enhances the estimation of AGB, echoing similar observations in earlier studies on young *Quercus robur* trees (e.g., Dahlhausen et al., 2017; Ehlers et al., 2022). In contrast, for Pyrenean oak, DBH alone was the most robust predictor of AGB, with neither tree height nor CI adding statistically significant explanatory power. This outcome reinforces earlier suggestions (e.g., Sileshi, 2014; Xiao and Ceulemans, 2004) that some species may be adequately characterized by simpler models based solely on DBH. These findings underscore the necessity for species-specific modeling strategies when estimating biomass in forests with mixed species.

5.2.2. Impact of neighborhood competition dynamics

This study further explored how local competition influences biomass estimates. In Scots pine, the inclusion of a neighborhood competition variable markedly improved the accuracy of biomass predictions, highlighting the importance of incorporating inter-tree interactions in modeling efforts. These results support previous work that emphasized competition as a key determinant of tree growth and biomass allocation, particularly for light-demanding species such as Scots pine (Chave et al., 2005; Forrester et al., 2017; Nong et al., 2019; Zhou et al., 2018).

Conversely, for Pyrenean oak, the findings suggest that neighborhood competition plays a much less critical role, as these trees appear relatively insensitive to competitive pressure in mixed stands. This observation aligns with previous studies (Ferrio et al., 2021; Lamonica et al., 2020), which suggest that Pyrenean oak is better adapted to coexist with other species, possibly due to the dominant influence of factors such as soil conditions, moisture availability, or disturbance regimes, which may outweigh direct competitive interactions. The difference in shade tolerance between the two species (Pyrenean oak tolerates a moderate degree of shadow compared with Scots pine during the initial growth stages) also supports this finding. Thus, these contrasting species responses underscore that the effects of competition on biomass allocation are highly species-specific.

5.2.3. Intra- and interspecific competition dynamics

Increasing attention in forest management has led to a closer look at how competition among and between species affects growth. In this study, we observed divergent responses: while Scots pine demonstrated a clear decline in biomass accumulation when exposed to interspecific competition – likely reflecting its vulnerability to resource shortages such as water and light – this was not the case for Pyrenean oak. Pyreanean oak trees presented a slight, although statistically nonsignificant, positive response to intraspecific competition, suggesting that these trees may benefit, at least in part, from mutual interactions under certain environmental conditions.

This difference could be attributed to contrasting ecological strategies: Scots pine tends to invest aggressively in tree height growth to secure light, increasing its sensitivity to neighboring interference, whereas Pyrenean oak's extensive rooting system and moderate shade tolerance enable it to maintain growth even when neighboring trees compete for resources. These findings are consistent with previous findings (de Tomás Marín et al., 2023; Ogaya and Penuelas, 2007) and highlight the complex interplay between facilitative and competitive processes that govern biomass accumulation in mixed-species forests.

5.3. Allometric relationships and indirect competition effects (Study III)

5.3.1. Effects of competition on allometric relationships

This study revealed that competitive pressure significantly altered the allometric scaling between DBH and key structural attributes, including tree height, CBH, and CL, in both Scots pine and Pyrenean oak (see Table 7 and Figure 4 of Study III). Notably, the strength of the DBH–tree height relationship decreases as competition intensifies, implying that trees under greater competitive stress may prioritize height growth differently, possibly due to limited light and nutrients. This observation is in line with previous research highlighting the plasticity of tree forms under competitive conditions (Chou et al., 2018; MacFarlane and Kane, 2017). Moreover, the fact that Scots pine tends to be shorter than Pyrenean oak for a given DBH in competitive environments points to species-specific growth strategies, which are likely linked to differences in physiological traits and root architecture.

Trees that are under greater competition have a larger CBH, which indicates a shift in the architecture of the crown that is likely aimed at increasing light capture. However, competition also appears to reduce the influence of DBH on CBH, i.e., in forests that are denser, CBH had a weaker relationship with DBH than other tree structural attributes. This pattern is in line with the idea that trees subjected to competitive stress invest more in vertical growth at the expense of crown development (Ulvcrona et al., 2007; Yamakawa et al., 2023).

Interestingly, while competition did not modify the interaction between DBH and CL, the competition term was associated with longer CL. This suggests that, in denser stands, trees might extend their crown length laterally as a compensatory mechanism to intercept more light – a phenomenon that aligns with earlier findings on crown plasticity in mixed-species environments (Antin et al., 2013; Pretzsch et al., 2012; Yang and Swenson, 2023). Additionally, the observation that Pyrenean oak trees develop longer crowns than Scots pine trees at the same DBH further highlights inherent differences in crown morphology between broadleaf and conifer species (Longuetaud et al., 2013).

5.3.2. Impact of competition on biomass allocation

The analysis revealed that competitive interactions selectively affect the distribution of biomass within young trees in mixed stands. Specifically, competition has a marked influence on the partitioning between foliage and stem biomass, whereas the relationships between branches and stem, or between branches and foliage, remain largely stable (Table 8). These stable patterns support the concept of allometric partitioning, which posits that biomass allocation is primarily a function of tree size rather than environmental fluctuations in the short term (Enquist and Niklas, 2002; Liu et al., 2021; Tsogtsaikhan et al., 2025). In this study, foliage allocation was especially sensitive to competition, underscoring the dynamic nature of resource distribution when light is a limiting factor. This aligns with optimal allocation theory, which suggests that trees will reallocate resources toward the organs that most limit growth under given conditions (McCarthy and Enquist, 2007).

Species-specific differences were also evident. Scots pine consistently invests more in branch and foliage biomass, perhaps as an adaptation to enhance light capture in crowded stands, whereas Pyrenean oak tends to allocate a greater proportion of biomass to its stem, possibly to secure a competitive advantage in belowground resource acquisition (Aldea et al., 2021). These differences highlight distinct adaptive strategies between the two species and suggest that the impact of competition on biomass allocation can vary substantially depending on species traits and developmental stages.

5.3.3. Indirect effects of competition on biomass allocation

Structural equation modeling (SEM) provides insights into the indirect pathways by which competition influences biomass allocation. The SEM results indicate that as competition increases, trees grow taller, and this increase in tree height contributes to a greater allocation of biomass to both stems and branches. This implies that morphological adaptation may lead to the support of taller statures and enhanced light capture. In contrast, foliage biomass appears to be less responsive to these indirect effects. This relative stability may reflect physiological constraints on leaf area expansion or the prioritization of structural growth under competition (Niinemets and Valladares, 2006).

The mediating effect of tree height underscores its role as a driver of biomass partitioning in a competitive environment – a finding that resonates with growth models (Dean et al., 2023; Yang et al., 2024). Moreover, the strong residual correlations among stem, branch, and foliage biomass suggest that other unmeasured factors (for example, soil fertility, which is often correlated with this allocation pattern or microclimate variation) may further modulate these allocation patterns, reinforcing the complex and multifaceted nature of tree responses to competition (Valor et al., 2024).

6. CONCLUSIONS

The key conclusions we can draw from the results of this thesis are as follows:

1. Biomass models have been developed for mature Scots pine (*Pinus sylvestris*) and sessile oak (*Quercus petraea*). During model development, we observed that sessile oak requires separate models for mixed and pure stands, whereas a single model can be applied to both mixed and pure stands for Scots pine.
2. The application of Dirichlet regression effectively captured species- and stand-specific patterns of AGB allocation in mature Scots pine and sessile oak. In Scots pine, increasing DBH led to reduced stem proportions and greater allocation to crown components, whereas sessile oak consistently increased stem biomass with size. The models that combined DBH and tree height performed best for Scots

pine, whereas height alone was sufficient for sessile oak. These results highlight how tree size and stand composition influence allocation strategies and support the use of proportion-based models for reliable biomass component estimation.

3. The new biomass models increase the accuracy of biomass estimation and support forest management, particularly concerning climate change. This differentiation in modeling requirements emphasizes the unique growth patterns and environmental interactions of each species. By improving biomass estimation, these models foster more effective forest management strategies, promote the sustainable use of forest resources and strengthen resilience against climate change impacts.
4. The incorporation of competition conditions improved the AGB prediction models for Scots pine, as evidenced by improved AIC, RMSE, and adjusted R^2 values, whereas for Pyrenean oak, DBH alone remained the best predictor.
5. Competition significantly alters the allometric relationships between DBH and tree structural attributes, with greater competition leading to a weakened DBH–tree height relationship and a reduced influence on crown base height, while simultaneously increasing crown length.
6. Biomass allocation patterns are differentially influenced by competition; although competition does not markedly affect branch-stem or branch-foliage allocation, it significantly alters foliage–stem partitioning. Pyrenean oak allocates more biomass to stems with the same foliage mass, and Scots pine allocates more biomass to branches and foliage with the same stem and branch masses, respectively.
7. Structural equation modeling demonstrated that competition indirectly enhances stem and branch biomass by increasing tree height, although foliage biomass appears to be less responsive to these competitive effects.
8. These findings highlight the necessity for forest management practices to be tailored to the unique responses of different species, ensuring that silvicultural interventions are species- and stand specific. This approach promotes sustainable forest growth and resilience, as it takes into account the specific needs and characteristics of each species. By doing so, forest managers can optimize the health and productivity of forest ecosystems.

7. CONCLUSIONES

Las principales conclusiones que podemos extraer de los resultados de esta tesis son las siguientes:

1. Se ha desarrollado un modelo de estimación de biomasa para árboles maduros de pino silvestre (*Pinus sylvestris*) y el roble albar (*Quercus petraea*). Durante el desarrollo de estos modelos, se observó que el roble albar requiere modelos separados para masas mixtas y puras, mientras que para el pino silvestre se puede aplicar un único modelo tanto en rodales mixtos como puros.
2. La aplicación de la regresión de Dirichlet capturó eficazmente los patrones específicos por especie y tipo de rodal en la asignación de biomasa aérea para los distintos compartimentos del árbol en rodales maduros de pino silvestre y roble albar. En el caso del pino silvestre, un aumento en el diámetro normal condujo a una menor proporción de biomasa en el fuste y una mayor asignación a los componentes de la copa, mientras que el roble albar incrementó consistentemente la biomasa del fuste con el tamaño del árbol. Los modelos que combinaron el diámetro normal y altura total fueron los más adecuados para el pino silvestre, mientras que la altura por sí sola fue suficiente para el roble albar. Estos resultados destacan cómo el tamaño del árbol y la composición del rodal influyen en las estrategias de asignación, y respaldan el uso de modelos basados en proporciones para estimaciones fiables de los componentes de biomasa.
3. Los nuevos modelos de ecuaciones de biomasa aumentan la precisión en la estimación de biomasa y apoyan la gestión forestal, especialmente en el contexto del cambio climático. Esta diferenciación en los requisitos de modelización resalta los patrones de crecimiento y las interacciones ambientales únicas de cada especie. Al mejorar la estimación de biomasa, estos modelos fomentan estrategias más eficaces de manejo forestal, promueven el uso sostenible de los recursos forestales y fortalecen la resiliencia frente a los impactos del cambio climático.
4. La incorporación de índices de competencia vecinal mejoró los modelos de predicción de biomasa aérea total (AGB) para el pino silvestre, como lo evidencian las mejoras en los valores de AIC, RMSE y R^2 ajustado, mientras que para el roble melojo, el diámetro normal (diámetro a la altura del pecho) siguió siendo el mejor predictor por sí solo.

5. La competencia altera significativamente las relaciones alométricas entre el diámetro normal y los atributos estructurales del árbol, ya que una mayor competencia debilita la relación entre el diámetro y la altura del árbol, reduce su influencia en la altura de la base de la copa y, al mismo tiempo, incrementa la longitud de la copa.
6. Los patrones de asignación de biomasa se ven influenciados de manera diferencial por la competencia; aunque la competencia no afecta notablemente la asignación entre ramas y fuste ni entre ramas y follaje, sí altera significativamente la partición entre follaje y fuste. El roble melojo asigna más biomasa al fuste, mientras que el pino silvestre asigna más biomasa a las ramas y al follaje para una misma cantidad de biomasa de fuste y de ramas respectivamente.
7. El modelado de ecuaciones estructurales demostró que la competencia incrementa indirectamente la biomasa del fuste y de las ramas al aumentar la altura del árbol, aunque la biomasa del follaje parece ser menos sensible a estos efectos competitivos.
8. Estos hallazgos resaltan la necesidad de adaptar las prácticas de manejo forestal a las respuestas específicas de cada especie, asegurando que las intervenciones silvícolas sean específicas tanto para la especie como para el tipo de rodal. Este enfoque favorece un crecimiento forestal sostenible y resiliente, ya que tiene en cuenta las necesidades y características particulares de cada especie. De este modo, los gestores forestales pueden optimizar la salud y productividad de los ecosistemas forestales.

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PEER-REVIEWED ARTICLES

Peer-reviewed article I

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.)

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Abstract

Mixed forests generally outperform monospecific forests in terms of productivity, stability, and resilience and are becoming increasingly important for sustainable forest management. However, accurate estimates of tree biomass allocation, as well as aboveground and component biomass in mixed forests, remain scarce. Our study addressed three different objectives to identify differences in biomass between mixed and monocultures and develop biomass models: (1) identification of biomass growth patterns in mixed and monoculture stands using analysis of covariance (ANCOVA), (2) investigation of the best fitting approach to modeling aboveground biomass using logarithmic regression and nonlinear mixed-effects models, and (3) fitting compartment biomass proportion models by Dirichlet regression, considering the additivity property. We analyzed 52 harvested trees from six plots within an experimental triplet in northern Spain, consisting of mixed and single-species stands of Scots pine (*Pinus sylvestris* L.) and sessile oak (*Quercus petraea* (Matt.) Liebl.). Moreover, diameter at breast height and tree height were used as covariate variables to determine the most accurate and unbiased models. The research findings showed that (i) allometric patterns of individual-tree biomass in mixed stands significantly differed from those in monospecific stands for sessile oak, while those in Scots pine did not change; (ii) nonlinear mixed-effect models demonstrated a better fit – indicated by lower Furnival index values – than logarithmic regression models in predicting aboveground biomass; and (iii) the fitted biomass equations provided good performance and accurate estimates of biomass component proportions compared to those of existing models. Consequently, our results offer a better understanding of biomass and carbon storage within mixed and monoculture forests in the context of climate change.

Keywords: Biomass equations, Dirichlet regression, Pine-oak mixed stand, Species mixture, Tree allometry

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

Keywords
Biomass models, Competition effect, Forest dynamics, Mixed-species stands, Model accuracy, Sustainable forest management, Tree characteristics

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

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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 traits (DBH, tree height, CBH, and CL relationships). Here, we destructively sampled 90 trees and applied ANCOVA to quantify the direct effects of competition on tree structural traits 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 (e.g., 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. Through SEM, the research further 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, the findings need to be interpreted with caution due to the single-site and limited sample size, which may restrict broader generalizability.

Keywords: Allometric scaling; Biomass partitioning; Competition dynamics; Resource allocation strategies; Structural equation modeling (SEM); Tree structural traits