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RESEARCH ARTICLE

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Towards resource-efficient forests: Mixing species changes crown biomass allocation and improves growth efficiency

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Societal Impact Statement

Forests worldwide face significant challenges due to climate change, impacting their health and productivity. In this study, we examined how European beech and Scots pine influence each other's phenology and growth in mixed forests. Our findings indicate that mixing these complementary tree species can increase resource efficiency within forest ecosystems. By leveraging informed species selection, this research highlights the potential for developing knowledge-based, resource-efficient forests. These insights are invaluable for policymakers and forest managers in designing forests that are not only productive but also sustainable and adaptable to evolving environmental conditions.

Summary

- We investigated the effects of interspecific neighbors on crown morphology and growth efficiency in European temperate forests, specifically focusing on European beech (*Fagus sylvatica* L.) and Scots pine (*Pinus sylvestris* L.). Our goal was to determine whether the previously reported overyielding in this mixture is primarily due to improved space-use efficiency and packing density or enhanced resource-use efficiency.
- Our methodology involved a detailed analysis of 128 individual felled trees. We assessed the effect of intraspecific and interspecific neighbors on stem volume growth, the allometric relationships of tree crowns and their components, and the allocation of branch and leaf biomass along the trees' vertical structure.
- Our findings demonstrate that interspecific neighbors significantly influence the allometric relationships of tree crowns, especially altering the vertical biomass distribution in European beech. Additionally, we found that interspecific neighbors can significantly enhance the growth efficiency of European beech but not for Scots pine.
- This research provides valuable insights for enhancing forest growth models and guiding forest management practices. By understanding the critical role of crown biomass allocation and growth efficiency in mixed-species stands, policymakers

and forest managers can design forests that are both productive and adaptable to changing environmental conditions. This study emphasizes the importance of species interactions in forest dynamics and bridges theoretical concepts with practical applications.

KEYWORDS
allometric relationships, European beech (*Fagus sylvatica*), growth efficiency, overyielding, plant–plant interactions, scots pine (*Pinus sylvestris*), temperate mixed forests

1 | INTRODUCTION

Recent studies have highlighted a key phenomenon in forestry: Mixed-species stands often demonstrate superior productivity, known as overyielding, compared with homogenous, mono-specific stands (Jactel et al., 2018; Liang et al., 2016). A primary explanation for the higher productivity is the increased stand density (Pretzsch & Biber, 2016; Williams et al., 2017), resulting in greater crown coverage (Pretzsch, 2014) and higher leaf area (Peng et al., 2017) when different tree species are mixed. Higher packing density at the stand level suggests better space or area use efficiency (Pretzsch & Schütze, 2005), possibly caused by different tree shade tolerances and crown shapes leading to spatial niche separation (von Felten & Schmid, 2008) or temporal asynchrony (Jucker et al., 2015; del Río et al., 2022, 2021, 2017). At same stand densities, these factors might lessen interspecific competition compared with intraspecific competition (Forrester, 2017; Metz et al., 2020; Pretzsch, 2022a). Based on the idea that it is predominantly the effect of packing density that increases growth in mixed stands, the benefits of mixing different tree species would be most pronounced at higher stand densities (Brunner & Forrester, 2020; Condés et al., 2013). In contrast, mixed stands characterized by lower stand density due to a specific management strategy or inherit ecological traits may show lower or no increased yield in temperate forests (Garber & Maguire, 2004; del Río et al., 2016).

Supplementary to the effect of higher packing density on growth in mixed stands linked to niche complementarity, other factors play a role in these environments. Vandermeer (1992) suggested that two tree species growing together might interact in ways that positively affect one another. Examples of this facilitation include atmospheric nitrogen fixation (Kelty, 1992; Kou-Giesbrecht & Menge, 2021) and water uptake (hydraulic lift) (Dawson, 1993; Zapater et al., 2011), where one species augments the nitrogen or water supply for the other. Another hypothesis posits that interspecies interactions enhance resource use efficiency (Forrester, 2014; Vandermeer, 1992), increasing growth efficiency (i.e., growth per unit leaf area or leaf mass). Interspecific neighbors may improve crown light efficiency, leading to enhanced growth (Forrester, 2014; Kelty, 1992; Pretzsch et al., 2013). Such benefits may materialize irrespective of stand density (trees ha^{-1}) (Pretzsch & Schütze, 2021). Low stand densities may nullify the density effect but not impede efficiency gains (Brunner & Forrester, 2020). Forrester et al. (2013) showed that efficiency effects can be amplified by density, making complementarity more pronounced at high stand densities. Further, complementarity could allow higher stand densities, with both factors reinforcing each other. Nevertheless, hardly any studies have analyzed the effect of interspecific neighbors on growth efficiency, including leaf biomass measurements (but see Guillemot et al. (2020) in tropical species mixtures). A more detailed understanding of how interspecific neighbors affect tree growth efficiency, that is, whether overyielding is mainly an effect of higher space-use-efficiency and packing density or a higher efficiency of resource use (e.g., water, light, and nutrient), may improve the knowledge-based design of resource-efficient forest ecosystems (Pretzsch, 2022b).

Tree allometry, the scaling relationships between the size of a tree component and the tree as a whole, is fundamental in understanding tree dynamics and species interactions (Forrester et al., 2018; del Río et al., 2019). Although general allometric scaling laws exist (e.g., Enquist et al., 2007; West et al., 1997), significant variation occurs both between and within species (Duursma et al., 2010; Mäkelä & Valentine, 2006). This variability is influenced by ontogeny, environmental conditions, and competitive interactions (Lines et al., 2012; Poorter et al., 2015; Pretzsch et al., 2012). The response of tree allometry responds to competition varies greatly between species and depended largely on the composition of competing species (Forrester, Tachauer, et al., 2017; Thorpe et al., 2010). However, differences in tree crown allometry between mixed and mono-specific stands are not well-understood. Numerous studies have explored tree crown allometry, comparing trees with intraspecific and interspecific neighbors focusing on traits like crown length and width (Pretzsch, 2019), crown profile (e.g., Cattaneo et al., 2020), crown eccentricity (Pretzsch, 2014), crown sinuosity (e.g., Kunz et al., 2019), and the number and angle of branches (Bayer et al., 2013). Despite these studies, there remains a gap in research specifically comparing crown biomass allocation patterns in temperate mixed forests between trees with interspecific and intraspecific neighbors.

Understanding how species mixing modifies canopy packing density (how closely trees are spaced in a forest), resource use efficiency, or both is crucial for developing individual tree simulation models. A common model structure uses a potential tree growth rate under optimal conditions, modified by factors such as tree size, competition, and site conditions (potential-modifier approach) (Weiskittel et al., 2011). If interspecific neighbors affect growth efficiency, potential-modifier growth models need adjustments for mixed-species stands (Condés et al., 2023). Changes in stand density would also require modifications to competition indices for trees with interspecific or intraspecific neighbors. Recent studies on European tree species mixtures emphasize the need for simulation models tailored to mixed-species stands (Pretzsch, 2022b). These models should recalibrate both potential growth and competition modifiers. This study aims to deepen our understanding of how tree neighbor composition (interspecific or intraspecific), biomass distribution within tree crowns, and tree growth efficiency are interconnected. We focus on a common tree species mixture in European temperate forests: European beech (*Fagus sylvatica* L.) and Scots pine (*Pinus sylvestris* L.), where overyielding has been previously reported (Pretzsch et al., 2015).

We relied on 128 felled trees across Europe, including 64 European beech and 64 Scots pine. Half were surrounded by intraspecific neighbors (same species) and half by interspecific neighbors (different species). Our methodology examined individual tree characteristics in terms of their allometric relationships, branch and leaf biomass variation along the vertical stem axis, and stem volume growth efficiency. We hypothesized that (H I) Crown allometric relationships will differ between trees with interspecific and intraspecific neighbors; (H II) Branch and leaf biomass allocation along the vertical stem axis will vary based on neighbor composition; and (H III) Trees with interspecific neighbors will exhibit greater stem volume growth given the same leaf mass.

Furthermore, we discuss the implications of crown biomass allocation patterns and growth efficiency in temperate forest mixtures for forest modeling and management.

2 | MATERIAL AND METHODS

Six Scots pine – European beech triplets (Pretzsch et al., 2015) were sampled and selected across Europe (Figure 1b). The term "triplet" refers to a group of three nearby forest stands, all within 1 km of each other. Each group includes one stand with only European beech, one with only Scots pine, and a third stand with a mix of both species (see Figure 1a). These plots were established in mature, even-aged, and fully stocked stands devoid of any indications of recent thinning interventions to represent stands close to maximum stand densities (Pretzsch et al., 2015). The southernmost triplet is in Spain, and the northernmost triplet is situated in Lithuania. They spread across a large proportion of the overlapping area of the distributions of Scots pine and European beech (Figure 1b). We selected these triplets to ensure a representative sampling of mixed-species and mono-specific stands across different regions where Scots pine and European beech coexist.

Climatic characteristics for all six triplets were obtained from the CRU-TS 4.01 gridded observation-based dataset, spanning the period from 1901 to 2017 (Harris et al., 2020). The triplets were dispersed along a gradient that fluctuated from 6.8°C to 10.3°C in mean annual temperature, from 558 to 788 in annual precipitation, and from an elevation of 20 to 1290 m a.s.l. (Figure 1c and Table S1). More detail about the climatic and edaphic conditions of each triplet is provided in Table S1. For a more comprehensive insight into field measurements and main stand characteristics see Table S2 and refer to Pretzsch et al. (2015).

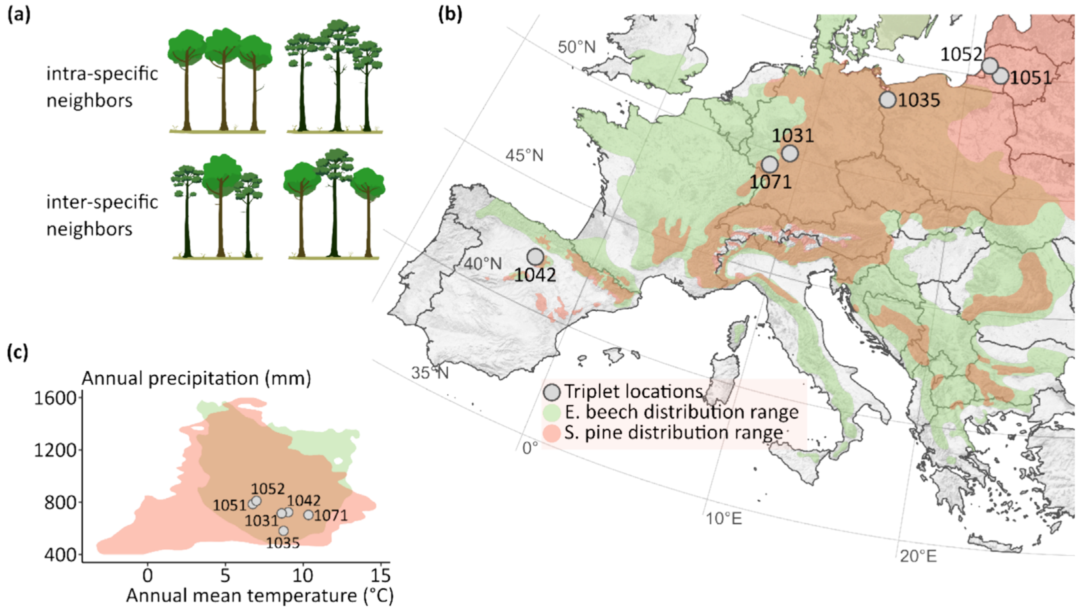

FIGURE 1 Representation of the study design (a), locations of the six triplets under study in relation to the current distribution of European beech (*Fagus sylvatica* L.) and Scots pine (*Pinus sylvestris* L.) (b) and their position within the climate-space of European beech and Scots pine (c). Colored areas in (b) and (c) refer to forest field observations of European beech (green) and Scots pine (red) in Europe. Geographic data on field observations of European beech and Scots pine were obtained from Mauri et al. (2017), while climate data were extracted from the CRU-TS 4.01 gridded observation-based dataset (Harris et al., 2020).

2.1 | Tree sampling

In our study, we selected 20 dominant trees from each triplet, ensuring an equal number of European beech and Scots pine. This selection process involved identifying five trees of each species surrounded by neighbors of the same species (intraspecific neighbors) in the monospecific plots and another five trees of each species that were surrounded by the other species (interspecific neighbors) in the mixed-species plots. These trees were accurately measured and then felled for further detailed examinations. For triplet 1042 in Spain, we selected seven dominant trees for each species, considering both types of neighboring relationships, resulting in 28 trees for this triplet. Overall, this method led to the inclusion of 128 trees in our study, with an equal split of 64 European beech and 64 Scots pine, allowing for a comprehensive and balanced analysis of both species. To avoid cutting down trees in the plots, we took the sampled trees from the buffer zone around each plot, which was similar to the plot itself. Trees within this buffer zone mirrored comparable dimensions and growth conditions to those found in the more central sectors of our experimental plots. In our selection process, we paid close attention to factors such as tree size and competitive situation to ensure that trees with both interspecific and intraspecific neighbors were growing in comparable conditions. This careful consideration allows us to attribute any observed differences in structural properties specifically to the influence of the interspecific neighbors, rather than to variations in local stand basal area or tree size.

2.2 | Measurements and metrics

2.2.1 | Tree variables

To illustrate and examine the impact of interspecific neighbors on tree morphology and growth, we focused on the following tree characteristics:

dbh: measured individual stem diameter at a height of 1.30 m above ground level using diameter-measuring tapes (cm).

h,hcb: measured individual tree height, h (m), and height to crown base, hcb (m), using a Vertex hypsometer (Haglöf Sweden AB, Långsele, Sweden). The height to crown base was defined by the position of the lowest still living primary branch.

ba,v: individual tree basal area, ba (m^2), and stem volume, v (m^3), were deduced and reconstructed through tree ring width measurements (captured from four cardinal directions) of six to nine stem disks per tree, sampled at specific intervals: stem base, 1.3 m, crown base height, and subsequent divisions of the total tree height by six. Disk extraction continued as long as the stem diameter exceeded 7 cm. The segmentation of the stem into volumetric units was executed by employing paraboloid frustums for the lower and middle stem sections and a cone for the apex. Finally, Smalian's formula (Husch et al., 2002) was applied for volume calculation: $\mathrm{v} = (\mathrm{ba}_1 + \mathrm{ba}_2)/2 \times \mathrm{L}$. Here ba_1 and ba_2 are the basal areas of the small and the large ends of the stem section in m^2, respectively. L denotes the length of the stem section. Note that stem volumes in both species refer exclusively to the volume of the stem main axis, without accounting for the branches.

cr,cd: mean crown radius, cr (m), and crown diameter, cd (m), derived from crown radius measurements taken from eight subcardinal directions (N, NW, …, NE) using the vertical sighting methodology (Preuhsler, 1979). This involved designating the crown radius as the distance from the center of the stem to the boundary of the crown (Röhle, 1986). The mean crown radius should be perceived as the quadratic mean, represented by the formula $\mathrm{cr} = \sqrt{\mathrm{r}_{\mathrm{N}}^2 + \mathrm{r}_{\mathrm{NW}}^2 + \ldots + \mathrm{r}_{\mathrm{NE}}^2/8}$, ensuring an unbiased conversion between crown radius and crown projection area.

cpa: crown projection area, $\mathrm{cpa} = \mathrm{cr}^2 \times \pi$, which expresses the area occupied by a tree (m^2).

cl: crown length (m), $\mathrm{cl} = \mathrm{h} - \mathrm{hcb}$.

cv: crown volumes (m^3) were calculated assuming a half-elliptical crown shape with a length equal to the crown length and a diameter equal to the crown diameter (Forrester et al., 2018).

cratio: ratio of crown length (m) and tree height (m), $\mathrm{cr} = \mathrm{cl}/\mathrm{h}$

cd/d: ratio of crown diameter (m) and stem diameter (cm) as an indicator for the crown extension.

h/d: ratio of tree height (m) and stem diameter (cm) as an indicator for mechanical tree stability.

locBA: local stand basal area $(\mathrm{m}^2\mathrm{ha}^{-1})$ was appraised via angle count samplings using a factor of 4 $\mathrm{m}^2\mathrm{ha}^{-1}$ with a mirror relascope (Relaskope-Technik, Salzburg), observed from the eastern and western aspects of the trees. To measure the competitive pressure on the central tree, we included all surrounding trees in our analysis but intentionally excluded the central tree from the locBA calculation.

paiv: the periodic annual volume increment $(\mathrm{m}^3\mathrm{year}^{-1})$, occurring between two successive surveys, was determined via the following calculation: $\mathrm{paiv} = (\mathrm{v}_2 - \mathrm{v}_1)/(\mathrm{t}_2 - \mathrm{t}_1)$. Here $\mathrm{t}_2 - \mathrm{t}_1$ is the number of growing seasons elapsed between two subsequent surveys, with v_1 and v_2 being the tree volume at surveys 1 and 2, respectively. To investigate the relationship between stem volume growth and leaf mass, as well as potential divergences between trees in interspecific and intraspecific surroundings, we used the paiv of the last 3 years for Scots pine. The choice of 3 years was made as Scots pine needles typically remain on the tree for about 2 to 4 years (Jalkanen et al., 1994; Pensa & Jalkanen, 1999). Due to the annual deciduous nature of European beech, only the growth data from the last year were considered for this species.

2.2.2 | Branch mass, leaf mass, and crown packing density

After the trees were felled, both the distance from the top to the base, bh, and the diameter, bd, for all living branches per tree were measured. Furthermore, the tree crowns were segregated into four uniform horizontal sections, evenly dispersed along the length of the crown. From each of these horizontal partitions, a subsample of four representative branches was cut per tree. To enable comprehensive evaluations of branch mass (branchM) and leaf mass (leafM), living foliage was separated from branch wood, and both samples were subjected to oven drying until a constant weight was achieved at 55°C. Missing branch and leaf masses from unsampled branches were projected using the branch diameter, bd, via a nonlinear mixed-effect power model

$$branchM_{ijkl} = (a_0 + b_i + b_{ij} + b_{ijk}) \times bd_{ijkl}^{(a_1 + c_i + c_{ij} + c_{ijk})} + \varepsilon_{ijkl} \tag{1}$$

$$leafM_{ijkl} = (a_0 + b_i + b_{ij} + b_{ijk}) \times bd_{ijkl}^{(a_1 + c_i + c_{ij} + c_{ijk})} + \varepsilon_{ijkl} \tag{2}$$

The indexes i, j, k, and l correspond to the level's triplet, plot, tree, and branch on the tree, in respective order. To consider the dependence caused by grouping of the data, random effects b and c were implemented at the triplet, plot, and tree level. All random effects were assumed to be normally distributed with expectation mean of 0. With ε_{ijkl}, we denoted the additive error term. To account for heteroscedasticity in the residuals, we applied a power-type variance function with branch diameter as a predictor prior to parameter estimation.

By employing tree-level predictions derived from models 1 and 2, inclusive of the random effects, we aggregated the branch and leaf masses, yielding the estimates of variables total leaf mass, *totLeafM*, and total branch mass, *totBranchM*, for each individual tree. Parameters used for the up-scale process are presented as Tables S3 and S4. Proceeding from this, we calculated crown packing density metrics as follows:

branchM/cv: ratio of total branch mass (kg) and tree crown volume (m^3).

leafM/cv: ratio of total leaf mass (kg) and tree crown volume (m^3).

leafM/branchM: ratio of total leaf mass (kg) and total branch mass (kg).

A description of the main tree characteristics is presented in Table 1. Their averaged characteristics were consistent with previous publications describing the triplets from the stand level (Heym et al., 2017).

2.3 | Statistical analyses

2.3.1 | Tree allometric relationships (H I)

In our study of tree allometric relationships, we postulated that these allometric relationships were distinct to each species and were influenced by factors such as tree size (measured by tree diameter or tree height), the local stand basal area, and their two-way interaction. We used linear mixed-effect models to investigate whether crown allometric relationships change depending on whether trees have interspecific or intraspecific neighbors (H I) as follows:

$$\begin{aligned} \ln(y_{ijk}) = {} & a_0 + a_1 \times \ln(x_{ijk}) + a_2 \times locBA_{ijk} + a_3 \times comp_{ijk} + a_4 \times \ln(x_{ijk}) \\ & \times locBA_{ijk} + a_5 \times \ln(x_{ijk}) \times comp_{ijk} + a_6 \times locBA_{ijk} \times comp_{ijk} + b_i \\ & + b_{ij} + \varepsilon_{ijk} \end{aligned} \tag{3}$$

where y represents the crown or biomass variables considered (see Table 1). The independent variable x was either tree height, h, or tree diameter, *dbh*. Further independent variables were the local stand basal area, *locBA*, whether trees had interspecific or intraspecific neighbors, *comp*, and all their two-way interactions. The indexes i, j, and k refer to the levels triplet, plot, and tree, respectively. $a_0,\ldots,a_6$ were fixed regression coefficients, b_i and b_{ij} were normally distributed triplet and plot random effects with mean zero and unknown unrestricted variance–covariance matrix, and ε_{ijk} was a residual error with mean zero and unknown variance of σ^2. The random effects are independent across triplets and plots, and residual errors are independent across observations.

2.3.2 | Biomass allocation along the vertical stem axis (H II)

In order to test whether there is similarity or difference in how branch and leaf biomass is distributed along the vertical stem in trees with interspecific or intraspecific neighbors, we defined relative tree heights (tree top = 0, forest floor = 1). Following this, the relative tree heights were segregated into intervals of 5% with an ensuing accumulation of the branch and foliar masses within these sections. For each species, we used a piecewise linear function to explore possible differences in how branch and leaf biomass is distributed along the vertical stem of trees with either interspecific or intraspecific neighbors. The piecewise linear function presupposes the augmentation of branch or leaf mass, y, progresses in a linear manner concomitant with the increment of relative height interval until it reaches a maximum at point c, subsequently maintaining this maximum. The expression for the nonlinear mixed-effects model can be delineated as follows:

$$y_{ijkl} = a \times z_{ijk} + \varepsilon_{ijkl} \tag{4}$$

with

$$z_{ijk} = Min(relative\,height\,interval_{ijkl}, c)$$
$$a_{ijk} = a_0 + a_1 \times dbh_{ijk} + a_2 \times locBA_{ijk} + a_3 \times comp_{ijk} + d_i + d_{ij} + d_{ijk}$$
$$c_{ijk} = c_0 + c_1 \times dbh_{ijk} + c_2 \times locBA_{ijk} + c_3 \times comp_{ijk} + e_i + e_{ij} + e_{ijk}$$

where y and the relative height interval were the response and predictor variables correspondingly, a controls the steepness of curve, while c indicates the point after which the curve perpetually retains its apex.

TABLE 1 Tree characteristics for the analyzed Scots pine (*Pinus sylvestris* L.) and European beech (*Fagus sylvatica* L.) trees with interspecific and intraspecific neighbors.

Variables' and metrics' names	Abbreviation	Unit	European beech Intraspecific ($N = 32$)	European beech Interspecific ($N = 32$)	Scots pine Intraspecific ($N = 32$)	Scots pine Interspecific ($N = 32$)
(i) Stem and crown size						
Tree age	*a*	years	62 (49–80)	62 (49–80)	75 (46–145)	75 (46–145)
Stem diameter at 1.3 m	*dbh*	cm	20.7 (12.1–33.1)	20.2 (11.1–29.0)	25.1 (15.8–37.4)	24.8 (15.5–43.5)
Tree height	*h*	m	25.0 (18.7–31.2)	23.3 (16.9–30.3)	26.2 (19.3–33.4)	26.2 (19.1–36.0)
Ratio of tree height and tree diameter	*h*/*d*	m/cm	1.24 (0.88–1.78)	1.19 (0.87–1.52)	1.07 (0.85–1.26)	1.10 (0.83–1.31)
Height to crown base	*hcb*	m	15.1 (6.7–23.3)	10.4 (4.0–17.1)	18.3 (13.7–24.2)	19.8 (15.2–27.1)
Living crown length	*cl*	m	10.0 (4.7–17.7)	12.9 (5.3–21.4)	7.8 (4.3–13.6)	6.3 (3.9–10.1)
Crown diameter	*cd*	m	5.3 (3.3–7.2)	6.5 (4.2–9.8)	4.4 (2.4–6.6)	4.1 (2.6–7.9)
Crown projection area	*cpa*	m^2	22.6 (8.5–40.9)	34.5 (13.8–75.0)	16.1 (4.6–34.5)	14.8 (5.5–48.5)
Crown volume	*cv*	m^3	159.4 (40.8–397.8)	314.6 (58.1–428.7)	91.1 (15.9–283.5)	70.9 (17.4–287.9)
Ratio of crown length and tree height	*cratio*	./.	0.40 (0.25–0.66)	0.55 (0.29–0.84)	0.30 (0.21–0.46)	0.24 (0.15–0.32)
Ratio of crown diameter and stem diameter	*cd*/*d*	m/cm	0.26 (0.17–0.36)	0.33 (0.22–0.47)	0.18 (0.13–0.22)	0.17 (0.11–0.26)
(ii) Branch and leaf mass						
Total branch mass	*totBranchM*	kg	26.93 (77.27–69.67)	34.68 (7.34–95.61)	20.36 (6.04–44.98)	12.72 (5.50–27.81)
Total leaf mass	*totleafM*	kg	2.03 (0.75–4.29)	2.56 (0.81–6.76)	6.60 (2.61–15.97)	4.91 (2.27–9.56)
Ratio of total branch mass and crown volume	*branchM* : cv	kg/m^3	0.17 (0.9–0.31)	0.12 (0.03–0.23)	0.30 (0.09–0.70)	0.26 (0.06–0.66)
Ratio of total leaf mass and crown volume	*leafM* : cv	kg/m^3	0.014 (0.008–0.029)	0.009 (0.003–0.023)	0.103 (0.030–0.295)	0.117 (0.019–0.311)
Ratio of total leaf mass and total branch mass	*leafM* : *branchM*	./.	0.086 (0.043–0.161)	0.085 (0.025–0.280)	0.347 (0.149–0.665)	0.409 (0.166–0.613)
(iii) Current growth rate						
Periodic annual mean stem volume growth	*paiv*	$m^3 year^{-1}$	0.007 (0.002–0.014)	0.010 (0.004–0.016)	0.012 (0.004–0.022)	0.010 (0.005–0.022)
(iv) Competitive status						
Local stand basal area	*locBA*	$m^2 ha^{-1}$	43 (31–56)	40 (30–51)	30 (21–44)	32 (24–48)

Note: The table presents the mean values of each characteristic, with the corresponding minimum and maximum values shown in brackets. Note that differences in tree age, diameter, height, and local stand basal area between trees with interspecific and intraspecific neighbors were tested using linear mixed-effects models (see Table S5).

In this model, the indexes *i*, *j*, *k*, and *l* depict the i^{th} triplet, the j^{th} plot within triplet *i*, the k^{th} tree of plot *j* nested within triplet *i*, and the l^{th} observation of tree *k* embedded in plot *j* in triplet *i*. To account for the grouped structure, random effects d_i, d_{ij}, d_{ijk} e_i, e_{ij}, and e_{jik} were implemented at the level of triplet, plot, and tree in alignment with the standard assumptions of mixed-effects models (e.g., Mehtätalo & Lappi, 2020). To determine if the branch and leaf biomass allocation along the vertical stem axis varies with tree diameter, *dbh*, local stand basal area, *locBA*, and between trees with interspecific or intraspecific neighbors, we included *dbh*, *locBA*, and the type of neighbors (interspecific or intraspecific), *comp*, as fixed effects in the submodels of a_{ijk} and c_{ijk}. Finally, ε_{ijkl} represents independently and identically distributed errors ($\varepsilon_{ijkl} \sim N(0,\sigma^2)$).

2.3.3 | Growth efficiency of trees with interspecific and intraspecific neighbors (H III).

We applied linear mixed-effect models to address whether interspecific neighbors can lead to an enhanced tree growth efficiency (H III). In this context, it would mean that for identical leaf mass, the stem volume growth of trees with interspecific neighbors would be higher compared with trees with intraspecific neighbors. The respective models were as follows:

$$\ln(\mathrm{paiv}_{ijk}) = a_0 + a_1 \times \ln(\mathrm{totLeafM}) + a_2 \times \mathrm{locBA} + a_3 \times \mathrm{comp} + a_4 \times \ln(\mathrm{totLeafM}) \times \mathrm{locBA} + a_5 \times \ln(totLeafM) \times comp + a_6 \times locBA \times comp + b_i + b_{ij} + \varepsilon_{ijk} \quad (5)$$

This model was used to delineate the periodic annual stem volume increment, *paiv*, as a function of the total leaf mass, *totLeafM*, the local stand basal area, *locBA*, whether trees had interspecific or intraspecific neighbors, *comp*, and all their two-way interactions. The indexes *i*, *j*, and *k* represented the i^{th} triplet, the j^{th} plot in triplet i, and the k^{th} tree of plot j in triplet i. Assumptions about random effects and uncorrelated remaining errors, ε_{ijk}, are as before in model 3.

When fitting models 3–5, nonsignificant interactions were removed, and the models were refitted. Still, if the interaction was significant, the contributing main effects were kept in the model even when not significant, following the marginality principle (Weisberg, 2005). Note that all predictor variables in models 3–5 were standardized to facilitate the models' interpretability and allow for direct comparison between regression coefficients (Schielzeth, 2010). To account for the climatic gradient among the triplets, we included triplet as a random effect in our statistical models. This approach allowed us to control for site-specific variability, ensuring that our findings reflect the influence of interspecific and intraspecific interactions on crown biomass allocation and growth efficiency, independent of climatic differences among the triplets. All models were fitted for each species separately, and modeling results were evaluated with the basic fit statistics: AIC, BIC, and -2Log likelihood. For the candidate models, residual plots of the dependent variable over each independent variable were carefully examined to ensure a good model fit by using the fixed effect parameters. In no case, the plots suggested a violation of variance homogeneity. Likewise, the approximate normality of errors was verified by making normal q-q plots of the residuals. All data processing and analyses were conducted using the statistical software R version 4.0.5 (R Core Team, 2022), explicitly employing the packages nlme (Pinheiro et al., 2022; Pinheiro & Bates, 2000), *lmfor* (Mehtätalo & Kansanen, 2022), *lme4* (Bates et al., 2015) in combination with the package lmerTest (Kuznetsova et al., 2017), and *tidyverse* (Wickham et al., 2019).

3 | RESULTS

3.1 | Effects of tree species composition on tree allometry (H I)

Our linear mixed-effect models provide evidence that interspecific neighbors modulate tree allometry. For European beech, we found a significant effect ($p < 0.05$) of interspecific neighbors on the corresponding allometric relationship in 7 out of the 10 allometric relationships under study (Figure 2 and Table S6). In the case of Scots pine, a significant effect ($p < 0.05$) of interspecific neighbors was found in half of the 10 allometric relationships (Figure 2 and Table S6).

European beech demonstrated significantly lower height to crown base ratios ($-25 \pm 7\%$) coupled with a higher crown length to tree height ratios ($+27 \pm 6\%$) when growing next to interspecific neighbors, whereas Scots pine showed higher height to crown base ratios ($+8 \pm 3\%$) and lower crown length to tree height ratios ($-20 \pm 5\%$) (Figure 2a,b). While European beech showed significantly wider crowns ($+37 \pm 8\%$) and lower tree heights at equivalent diameters ($-5 \pm 2\%$) when surrounded by interspecific neighbors, Scots pine had narrower crowns and higher tree heights, though this effect was not statistically significant (Figure 2c–e and Table S6).

Regarding branch and leaf masses, European beech with interspecific neighbors showed no statistically significant differences in total branch masses (Figure 2f and Table S6) and total leaf mass ($p = 0.0615$) (Figure 2g) compared with European beech with intraspecific neighbors. There was a reduced proportion of both total branch and leaf masses relative to crown volume ($-47 \pm 11\%$ less dense crowns) (Figure 2h,i). The ratio of total leaf mass to total branch mass was not different between European beech with both interspecific and intraspecific neighbors (Figure 2j). In contrast, we found that Scots pine exhibited significantly diminished total branch ($-34 \pm 8\%$) and leaf masses ($-20 \pm 8\%$) when growing next to interspecific neighbors (Figure 2f,g). The ratios between total branch or leaf mass and crown volume showed no significant disparity between trees with either interspecific or intraspecific neighbors (Figure 2h,i). However, the ratio of total leaf mass to total branch mass was significantly higher for Scots pine with interspecific neighbors (branches with $+13 \pm 6\%$ more needle mass) (Figure 2j). For a graphical representation of the respective response variable in relation to tree dimension and the effect of interspecific neighbors, see Figures S1–S10.

The local stand basal area had a negligible effect on allometric relationships for Scots pine, except for a reduced total branch mass in instances of increased local stand densities (Figure 2f). In contrast, the impact was considerably more marked for European beech. Growing in increased local stand densities, European beech showed reduced crown lengths and crown projection areas (Figure 2a–c) and narrowed crowns for a given diameter (Figure 2e), which consequently led to a reduction in total branch and leaf masses (Figure 2f,g). In every allometric

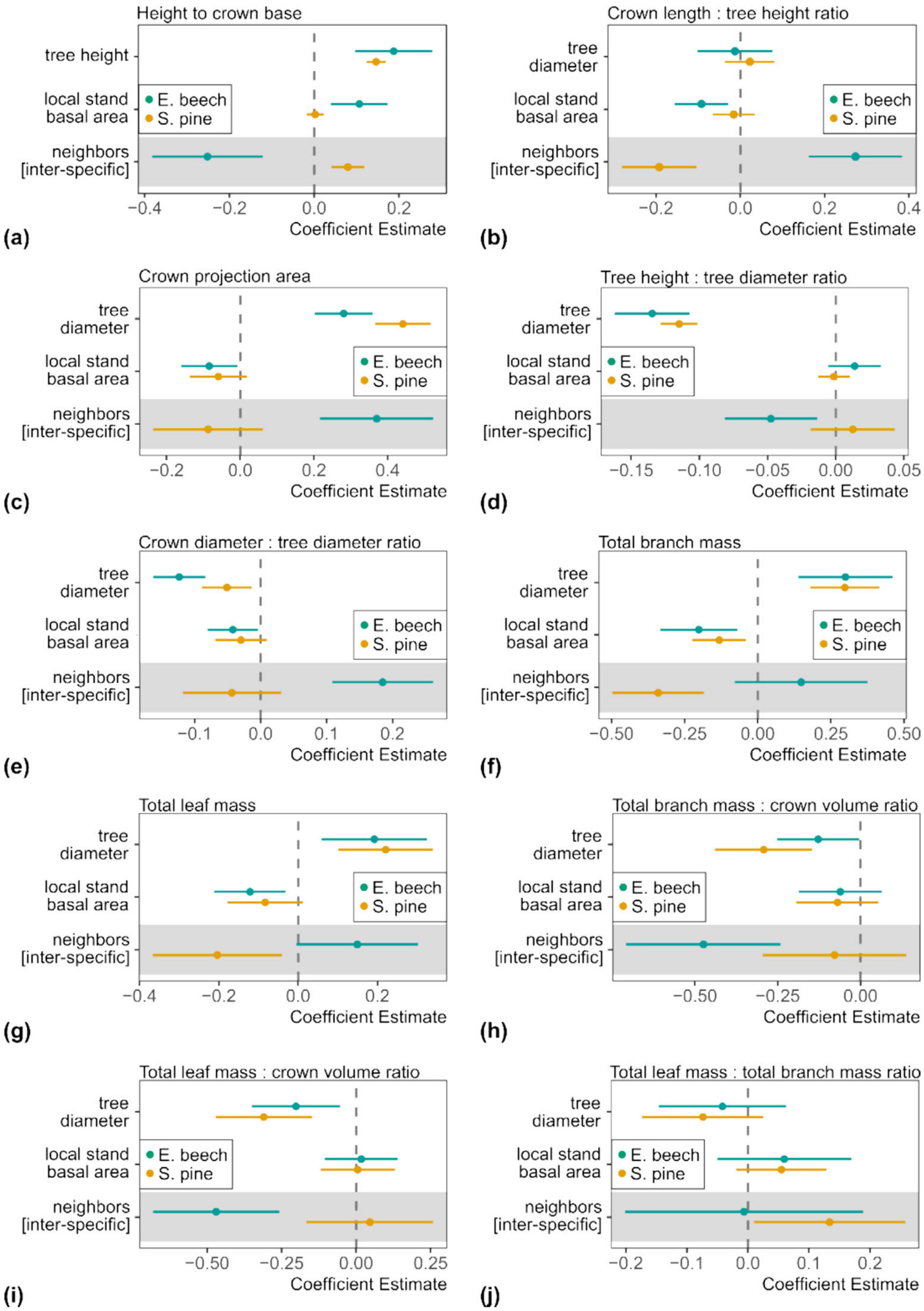

FIGURE 2 Dot-Whisker plots of the fit results of the tree allometry models (Equation (3)) for European beech (*Fagus sylvatica* L.; E. beech) (green) and scots pine (*Pinus sylvestris* L.; S. pine) (orange). The coefficient estimates with 95% confidence intervals of the fixed effects are shown. Since our objective was to reveal potential differences in the allometric relationships between trees grown next to interpecific and intraspecific neighbors, the coefficient estimates of the fixed effect neighbors were highlighted with a gray bar and referred to intraspecific neighbors (vertical dashed gray line). See Table 1 for the variables and metrics' description (a–j) and Table S6 for the complete model summaries.

relationship we examined, there was no significant interaction found between tree diameter, the local stand basal area, and whether trees were surrounded by intraspecific or interspecific neighbors.

3.2 | Crown biomass allocation along the vertical stem axis (H II)

Our modeling results indicate that crown biomass allocation patterns of European beech and Scots pine changed when growing next to interspecific neighbors. For European beech, we found that the point from which biomasses remain at maximum was 10% lower when growing next to interspecific neighbors than when growing next to intraspecific neighbors for both branch and leaf mass, as indicated by the positive c_3 parameter in Tables S7 and S8 (Figure 3a,c). A significant negative effect ($p < .05$) of local stand basal area on the parameter c was identified for both branch and leaf mass allocation. Additionally, a significant negative effect of tree dimension on the parameter c was found for European beech branch mass (Table S7). The steepness of the curves (parameter a) to the apex c was

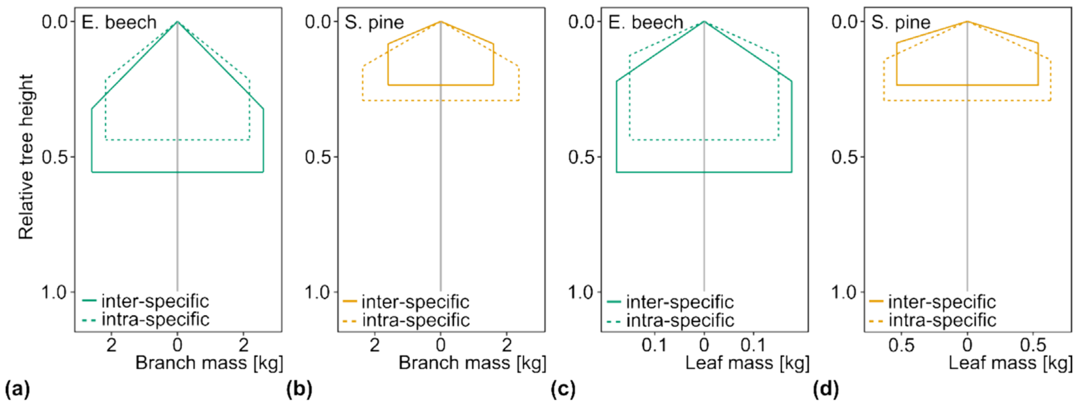

FIGURE 3 Visualization of the allocation of branch mass (a, b) and leaf mass (c, d) along the vertical stem axis (vertical gray line) for European beech (*Fagus sylvatica* L.; E. beech) (green; a, c) and Scots pine (*Pinus sylvestris* L.; S. pine) (orange; b, d). Lines: model predictions for trees with interspecific neighbors (solid lines) or intraspecific neighbors (dashed lines) and mean tree diameter and local stand basal area. The predictions are based on the fixed effects of the fitted Equation (4) (see Tables S7 and S8). Height to crown base was estimated based on the fixed effects of the fitted Equation (3) (see Table S6). Note that the *x*-axis and *y*-axis are reversed due to visualization reasons.

significantly influenced by tree dimension (positive) and the composition of neighbors for both branch and leaf mass allocation (Tables S7 and S8). The curve's steepness was significantly flatter for European beech with interspecific neighbors compared with those with intraspecific neighbors (cf. Figure 3a,c).

For Scots pine with interspecific neighbors, we found that the point at which biomass plateau was elevated by 10% for branch mass and by 6% for leaf mass compared with Scots pine with intraspecific neighbors (parameter c_3 in Tables S7 and S8) (Figure 3b,d). Tree stem diameter (leaf mass, Table S8) and local stand basal area (branch mass, Table S7) had negative effects on the parameter c ($p < .05$). A significant effect of stem diameter (positive) and composition of neighbors on the steepness of the curve (parameter a) was found for both branch and leaf mass allocation (Tables S7 and S8). The steepness was significantly flatter for Scots pine with intraspecific neighbors than for those with interspecific neighbors (cf. Figure 3b,d).

3.3 | Interspecific neighbors can increase growth efficiency (H III)

Our findings indicate that European beech demonstrates enhanced growth efficiency when growing next to interspecific neighbors. Given a consistent leaf mass and competition level, European beech neighboring Scots pine experienced a 14% rise in stem volume increment (parameter $a_3 = 0.144$) compared with European beech neighbored by their conspecifics (Table 2). In contrast, when Scots pine was interspersed with European beech, we found a neutral effect ($p = 0.844$) on its growth efficiency, with no notable augmentation.

The total leaf mass of a tree had a substantial influence on the periodic annual stem volume increment for both species (Table 2), insomuch that trees with higher total leaf masses demonstrated significantly higher stem volume growth (Figure 4). Additionally, a higher local stand basal area reduced the volume growth of European beech significantly and had an almost significant ($p = 0.0662$) reduction effect on Scots pine volume growth (Table 2). For European beech, the significant effect of the interaction between total leaf mass and local stand basal area (parameter a_4) indicates that the negative effect of local stand basal area on the trees' growth was mitigated by higher total leaf masses.

4 | DISCUSSION

Our findings emphasize the significant influence of the composition of neighbors on tree allometry of European beech and Scots pine. Compared with trees that were neighboring trees of the same species (e.g., European beech surrounded by European beech), both species showed modified allometric characteristics when they were neighboring trees of the other species (e.g., European beech surrounded by Scots pine); while European beech had broader and longer crowns with increased leaf mass, Scots pine had shorter crowns with a lower branch and leaf mass. Interestingly, these changes in tree size allometry occurred with changes in crown biomass partitioning. Highlighting the potential benefits of interactions between different species, our findings indicate that European beech surrounded by Scots pine demonstrated enhanced growth efficiency in terms of stem volume growth per unit leaf mass. However, it is important to note that this benefit was observed specifically for European beech. The growth efficiency of Scots pine did not vary significantly, regardless of whether it was surrounded by its own species or European beech.

4.1 | Allometric relationships of tree crown and vertical distribution of branch and leaf biomass

Our results align with earlier studies suggesting that tree allometry is significantly affected by the composition of the surrounding tree species (Barbeito et al., 2017; Guillemot et al., 2020; Kunz et al., 2019). In

TABLE 2 Parameter estimates of the total leaf mass and stem volume growth relationship models of European beech (*Fagus sylvatica* L.) and Scots pine (*Pinus sylvestris* L.) (Equation (5)).

Tree species	Fixed effect		Estimate	se	95% lb	95% ub	*p*-value
European beech			Fixed part				
		a_0	**−4.77**	0.0545	−4.89	−4.66	**<0.0001**
	Total leaf mass	a_1	**0.382**	0.0456	0.284	0.479	**<0.0001**
	Local stand basal area	a_2	**−0.114**	0.0433	−0.201	−0.0276	**0.0107**
	Neighbors (interspecific)	a_3	**0.144**	0.0705	0.00263	0.285	**0.0461**
	Total leaf mass: local stand basal area	a_4	**0.0814**	0.0312	0.0189	0.144	**0.0116**
			Random part and residual				
		var(b_i)	0.0404^2				
		var(b_{ij})	$1.37E\text{-}05^2$				
		σ2	0.261^2				
			Model fit				
	R^2 marginal		0.762				
	R^2 conditional		0.813				
Scots pine			Fixed part				
		a_0	**−4.58**	0.121	−4.87	−4.28	**<0.0001**
	Total leaf mass	a_1	**0.197**	0.0473	0.102	0.291	**0.0001**
	Locale stand basal area	a_2	−0.0777	0.0414	−0.161	0.00538	0.0662
	Neighbors (interspecific)	a_3	−0.0145	0.0737	−0.133	0.162	0.844
	Total leaf mass: local stand basal area	a_4	-	-	-	-	-
			Random part and residual				
		var(b_i)	0.268^2				
		var(b_{ij})	$8.64E\text{-}06^2$				
		σ^2	0.261^2				
			Model fit				
	R^2 marginal		0.492				
	R^2 conditional		0.656				

Note: Bold text within the table indicates statistically significant parameter estimates ($p < 0.05$). Dashes (–) within the table denote that the interaction term was not included in the model.

Abbreviations: lb, lower bound; se, standard error; ub, upper bound; var, variance.

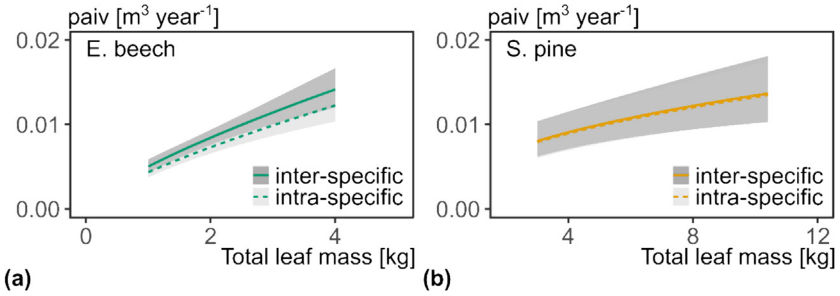

FIGURE 4 Effect of total leaf mass for trees with the mean local stand basal area and composition of neighbors on periodic annual stem volume growth, paiv, of European beech (*Fagus sylvatica* L.; E. beech) (a) and Scots pine (*Pinus sylvestris* L.; S. pine) (b). Lines with 95% confidence intervals: model predictions for trees with the mean local stand basal area and grown up next to interspecific (solid lines) and intraspecific (dashed lines) neighbors. The predictions are based on the fixed effects of the fitted Equation (5) (see Table 2).

proximity to interspecific neighbors, European beech showed notable enhancements in crown length, volume, total leaf mass, and branch mass, whereas Scots pine exhibited the opposite trend. This shift resulted in the maximum biomass point of European beech being 10% lower compared with its positioning when surrounded by intraspecific. Conversely, Scots pine showed an upward shift in biomass maximum when adjacent to European beech. These contrasting behaviors might be attributed to their distinct light acquisition strategies and growth patterns. European beech, adept at developing expansive crowns, likely sees this trait enhanced in the presence of light-demanding species like Scots pine (Ellenberg & Leuschner, 2010; Pretzsch et al., 2015). Scots pine, on the other hand, may respond to shading from European beech by prioritizing vertical growth, as evidenced by its upward biomass allocation in mixed stands (Gonzalez de Andres et al., 2018). These variations in crown morphology, coupled with differences in height between species, lead to more efficient crown packing and increased light absorption in mixtures compared with monocultures (Bauhus et al., 2004; Forrester & Albrecht, 2014).

We hypothesize that the crown relocation of Scots pine to the upper canopy in the mixed stand results from its light ecology. Scots pine benefits from full light exposition in the upper layer, whereas the light saturation of beech is optimal in the slightly shaded location in the middle canopy. As the light compensation point for Scots pine (27 $\mu\text{mol}\,\text{m}^{-2}\text{s}^{-1}$ for sun leaves at A_{max}, i.e., when light-saturated photosynthesis occurs under normal CO2 concentration) is much higher than that for European beech (13 $\mu\text{mol}\,\text{m}^{-2}\text{s}^{-1}$), the latter can penetrate and shorten the lower parts of the pine crowns (Ellenberg & Leuschner, 2010). This, along with the competition-driven acceleration of height growth, explains the upwards relocation of Scots pine crowns. The crown expansion of European beech in the middle crown layer and the downward shift of its center of gravity may result from the beneficial light conditions under the Scots pine crowns. Whereas light intensity under European beech canopies is only 1%–2% of above canopy light availability, it is 15%, that is, about tenfold, under Scots pine (Ellenberg & Leuschner, 2010). Thus, the light that penetrates the Scots pine canopies can be absorbed by European beech to increase the total light absorption of the mixtures compared with Scots pine monocultures.

The downward and upward shifts in the crowns of European beech and Scots pine, respectively, are likely adaptive responses to optimize light capture and reduce competitive stress, aligning with observations in various tree species mixtures (Cattaneo et al., 2020; Guillemot et al., 2020; Pretzsch et al., 2015). These changes in crown structure could significantly improve the growth and survival of European beech in the medium and lower canopy layers and reduce the crown length of Scots pine (Pretzsch et al., 2018).

Additionally, the dynamics of crown biomass allocation are strongly influenced by the admixed species identity. Our findings show a higher proportion of Scots pine crown volume in higher canopy tiers in mixtures with European beech. In contrast, mixtures involving Scots pine and Maritime pine (Pinus pinaster Ait.) displayed a contrasting pattern, with Maritime pine shifting its crown biomass upward, whereas Scots pine showed no changes (Cattaneo et al., 2020). This indicates that crown biomass allocation is not only species-specific but also closely linked to the characteristics of co-occurring species (Forrester, Benneter, et al., 2017).

The observed shifts in biomass distribution and crown architecture are perceived as quintessential mechanisms of crown complementarity (Kunz et al., 2019), which in turn explains the denser canopy space filling (Pretzsch, 2014) and contributes to the phenomenon of overyielding in mixed-species forests on the stand level (Guillemot et al., 2020). The modifications in crown structure within mixed-species stands thus appear to be a key strategy for optimizing light capture and enhancing growth and survival, driven by the specific composition of the forest stand. Moreover, it is important to acknowledge that many of these characteristics are not solely a response to species interactions but might also be optimized to balance carbon uptake through photosynthesis and carbon release through respiratory costs (Pretzsch & Dieler, 2012).

4.2 | Interspecific neighbors can increase growth efficiency

Our study provides insights into the complex relationship between crown biomass allocation patterns and species interactions, a dynamic that has been widely theorized (Gargaglione et al., 2010; Kunz et al., 2019) but less often quantified with empirical data on leaf biomass. We demonstrate that European beech exhibited superior growth efficiency in terms of stem volume growth per unit leaf mass when growing next to Scots pine, highlighting a facilitative interaction potentially driven by altered crown biomass allocation patterns (Pretzsch & Schütze, 2021). The facilitation may be a result of improved light accessibility due to reduced self-shading, attributed to the decreased leaf mass per crown volume, and the development of broader crowns by European beech in mixed stands (Figure 2i), as well as diminished shading between adjacent crowns (Gspaltl et al., 2013). Scots pine's contribution to reduced intercrown shading could be a function of its crowns' higher light transparency compared with European beech (Ellenberg & Leuschner, 2010), lessening competitive pressure for light. Additionally, changes in the allometric relationships of Scots pine and European beech when growing in the surrounding of the other species are observed to decrease the overlap of their leaf areas (Forrester et al., 2018), potentially leading to lower competitive stress and enhanced light acquisition. This reasoning bolsters the argument that the effect of Scots pine admixture on European beech may be partly due to light interactions—a perspective that contrasts with Forrester et al. (2018). However, the enhanced growth efficiency of European beech in the presence of Scots pine may not only be due to improved light uptake but also to belowground interactions such as water uptake, where Scots pine can facilitate access to water for European beech during dry periods (Dawson, 1993; Polomski & Kuhn, 1998) and uplift of base cation, which enhances nutrient availability in the soil profile (Clarholm & Skyllberg, 2013). The interactions with soil microbiota (Gillespie et al., 2021) and the different nutrient cycling strategies between evergreen gymnosperms and deciduous angiosperms (Augusto et al., 2015) may also play a significant role in this positive interaction.

While studies have shown that European beech may have lower water use efficiency in mixed stands with Scots pine compared with pure stands (Conte et al., 2018; Gonzalez de Andres et al., 2018), it is important to consider the role of transpiration rates. These rates are a major factor in tree survival during droughts (Mas et al., 2024). Additionally, European beech shows increased nutrient uptake in mixed stands (Forey et al., 2016), which could lead to better growth conditions, including more efficient water usage (Magh et al., 2018). Enhanced canopy packing in mixed stands might also mitigate microclimate effects, particularly reducing heat stress and influencing water use dynamics (Aguirre et al., 2021; Wright et al., 2015). Thus, the observed positive effect on European beech in our study may depend on specific environmental interactions and conditions. Building on the "stress gradient hypothesis" (Michalet et al., 2014), earlier research indicates a transition from positive to negative effects on plant interactions as environmental conditions become drier and warmer (e.g., Ratcliffe et al., 2017). Both our findings and the results from other studies mentioned above together emphasize the complex nature of species interactions in temperate forest ecosystems. These interactions are shaped by a variety of factors, both above and below the ground, which play a key role in how crown biomass is allocated and in turn, influence the overall growth efficiency.

4.3 | Consequences for forest modeling and management

Our results are essential for individual tree modeling using potential-modifier approaches (Sharma & Brunner, 2017). They suggest that both potential growth and its reduction by local competition require an adjustment before models for monospecific stands can be successfully applied to mixed stands. The revealed allometric acclimation of crowns when growing in interspecific surroundings suggests that stand density, canopy packing, and competition operate differently and result in different growth rates in mixed compared with monospecific stands. The superior growth efficiency in the case of European beech means that the potential growth may be higher in mixed stands and the functions for predicting potential growth need adjustment. While differences in tree allometry (Del Río et al., 2019; Pretzsch, 2019), space occupation (Bayer et al., 2013), and packing density (Jucker et al., 2015) were addressed in many studies and have been incorporated into individual tree simulators already (Grote, 2002; Pearcy et al., 2005), our study advocates for a closer examination of potential growth modifications in such models (Condés et al., 2023). Notice that we found that the efficiency and growth of European beech can be by 14% higher with interspecific neighbors compared with those with intraspecific neighbors, ceteris paribus. This suggests an implementation of a higher potential tree growth in mixed compared with monospecific stands.

Empirical evidence suggests that European beech and Scots pine mixtures enhance stand-level gross growth by approximately 10% relative to mono-specific stands (Pretzsch et al., 2015, 2023), with our findings confirming a notable benefit for European beech in such mixed-species contexts. The higher gross overyielding on the stand level is attributed to better space-use and packing density, alongside temporal niche complementarity (Del Río et al., 2017; Pretzsch et al., 2015; Pretzsch & Biber, 2016). Nevertheless, without management interventions like thinning, it is critical to acknowledge that the benefits observed for European beech could potentially elevate the mortality risk for Scots pine (Aguadé et al., 2015; Searle et al., 2022). This, in turn, may trigger demixing processes and a reduction in the overall net overyielding (Pretzsch et al., 2023). This highlights the complexity of species interactions and underscores the necessity for prudent management practices to fully harness the potential of mixed stands. The consequences for silvicultural practices are substantial; while thinning plays a crucial role in harnessing the gross overyielding potential of mixed stands and mitigating demixing processes (Pretzsch et al., 2023), it may reduce the overdensity effect (Brunner & Forrester, 2020; Forrester et al., 2013). However, it may not mitigate the enhanced growth efficiency observed in the case of European beech. Silvicultural strategies should reflect these nuanced interspecific responses to mixing, optimizing thinning to leverage space-use efficiency and maintain beneficial species relationships over the stand's life cycle.

In the light of our findings, we must acknowledge that the limited sample size of 128 trees and the exclusive focus on European beech and Scots pine may not capture the full spectrum of interspecific dynamics. The absence of root biomass data is a further limitation, as belowground interactions can profoundly affect aboveground growth patterns and competition dynamics (Germon et al., 2020; Jacob et al., 2013; Ma et al., 2019; Richards et al., 2010). Expanding the scope of future studies to include a wider variety of species and site conditions, as well as accounting for root biomass, will be crucial to deepening our understanding of species interactions in mixed temperate forests. However, our results suggest that incorporating complementary tree species like Scots pine and European beech may pave the way for forest production systems that are potentially more resource-efficient in the face of adverse climate change conditions affecting forest growth (Hooper & Dukes, 2004 but see also Toïgo et al., 2015).

AUTHOR CONTRIBUTIONS

Hans Pretzsch and Miren del Río were responsible for project administration and funding acquisition; Hans Pretzsch, Miren del Río, Gediminas Brazaitis, and Enno Uhl conceived and designed the study; Kamil Bielak, Miren del Río, and Ricardo Ruiz-Peinado conducted and managed the experiments; and Torben Hilmers, Lauri Mehtätalo, and Gerhard Schmied analyzed the data. Torben Hilmers wrote the first draft and revised the manuscript according to the co-author's comments. All co-authors gave comments and revisions to the manuscript.

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CONFLICT OF INTEREST STATEMENT

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

DATA AVAILABILITY STATEMENT

The data that support the findings of this study are available from the corresponding author upon reasonable request.

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SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

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