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RESEARCH ARTICLE

Tree species diversity drives above-ground carbon sequestration through light-related trait shifts

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Abstract

1. Functional traits can vary in response to tree species mixing, which in turn might influence biomass production and, consequently, carbon (C) sequestration in diverse forests. However, evidence for consistent broad-scale patterns in tree trait responses, particularly regarding trait identity and their contribution to above-ground biomass outcomes, remains limited.
2. Using data from even-aged forest stands in 11 tree diversity experiments in Europe and Brazil, encompassing 40 tree species, we estimated the influence of species mixing on above-ground biomass components (woody, litterfall and understory biomass), as well as effects of mixing on plasticity-driven changes in species- and community-level functional traits.
3. At the community level, specific leaf area (SLA) and leaf area index (LAI) were higher in mixtures than expected values based on monocultures, while leaf nitrogen per area decreased, and leaf nitrogen per mass remained stable. SLA increases were primarily due to the response of less dominant tree species. Woody and litterfall biomass increased in mixtures, whereas understory biomass remained unchanged. At the species level, diversity-driven plastic changes were observed

For affiliations refer to page 15.

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in multiple traits, but only SLA showed a consistent shift across species. Tree diversity effects on above-ground biomass were influenced by both functional diversity and diversity-driven trait shifts, where increased SLA and LAI enhanced woody biomass accumulation, while higher LAI in diverse stands reduced understory biomass.

4. Together, these results show that tree species mixing alters canopy structure and light-related traits, with shifts in SLA and LAI constituting key pathways through which mixed forests accumulate more woody biomass.

KEYWORDS
biodiversity–productivity relationships, biomass accumulation, ecosystem functioning, intraspecific trait variability, leaf traits, mixed-species forestry, structural equation modelling, TreeDivNet

1 | INTRODUCTION

Approximately 30% of the world's forest area is dedicated to the production of woody biomass (FAO, 2020). Management regimes in these production forests aim to maximise the quantity, quality and predictability of wood products for materials and energy. In their most intensive form, production forests are planted as even-aged monocultures. This approach is favoured for ease of management and consistent product supply, but the resultant homogenisation and simplification of forests carry costs in terms of reduced habitat provision for biodiversity, increased susceptibility to disturbances (Jactel et al., 2017), and a limited breadth of ecosystem service (ES) provision (Felton et al., 2016; Lindenmayer & Franklin, 2002).

One promising approach for diversifying production forests involves transitioning from monoculture forests to mixed-species stands (Depauw et al., 2024; Messier et al., 2021). Mixing tree species has been found to improve carbon (C) storage (Augusto & Boča, 2022; Chen et al., 2018; Warner et al., 2023; Werner et al., 2025), which has implications for climate change mitigation. Forest diversification has therefore gained increasing attention as a means to deliver more resilient and sustainable wood production, as well as increased wood production (Paquette & Messier, 2011; Messier et al., 2021; Blondeel et al., 2024; Jensen et al., 2025). To ensure that this transition successfully delivers enhanced ES provision and climate change mitigation, it is necessary to understand the mechanisms of biomass accumulation and C storage in mixed-species plantations. Forest biomass accumulates in different components, including above-ground woody biomass, litter deposition and understory biomass, as well as belowground root biomass and soil C stocks (Pan et al., 2024). Differences in biomass accumulation between these components can have significant ecological implications, for example for food webs, habitat provision and the length of C residence time (Bloom et al., 2016; Gregor et al., 2024; Litton et al., 2007). In this study, we investigated the effects of tree species mixing on woody biomass, litterfall biomass and understory biomass, providing a representation of a substantial majority of the above-ground C pool.

The ecological functions of forest stands, including their biomass accumulation rates, are strongly influenced by their functional identity (Grime, 1998), which is determined by the combined functional traits of the trees within the stand. Functional traits encompass morphological, chemical, physiological and phenological characteristics that determine plant functioning, often positioning species along trade-off gradients such as resource acquisition versus conservation (Díaz et al., 2004, 2022; Poorter et al., 2009; Violle et al., 2007; Wright et al., 2004). These traits differ between species, as well as within species (i.e. intraspecific trait variation) and can respond to both neighbouring trees and environmental conditions (Belluau & Shipley, 2018; Castro Sánchez-Bermejo et al., 2024, 2025; Rozendaal et al., 2006; Westerband et al., 2021). Consequently, the functional identity of a mixed stand may not just be the product of the functional traits of each species in monoculture, but also the result of differential trait expression in response to mixing. This provides a basis for integrating two non-exclusive trait-based hypotheses in biodiversity–ecosystem functioning theory: ecosystem functioning may be shaped both by the traits of dominant species (mass-ratio effects; Grime, 1998) and by trait-mediated complementarity among species arising from resource partitioning or facilitation (Tilman et al., 1996). By focusing on how species mixing alters community-level trait expression, this study explicitly links these mechanisms through trait-mediated pathways, rather than treating dominance and complementarity as independent explanations of diversity effects. Viewed in this way, functional diversity is expected to influence biomass accumulation primarily by shaping community-level trait expression, rather than acting independently of traits. Given that stand functional identity underpins stand productivity and functioning, such trait-mediated shifts arising from species interactions are expected to play a key role in determining biomass accumulation in mixed stands.

One possible mechanism underlying shifts in functional traits between mixed stands and monocultures is the higher functional diversity of mixed stands, which arises from interspecific differences in trait values (Guillemot et al., 2020; Williams et al., 2020). Functional diversity represents the diversity of functionality present in a community and is measured in terms of trait differences between species (Tilman, 2001). Compared to taxonomic diversity metrics, it better captures ecological similarities and differences between species, and often better explains diversity effects (Cadotte et al., 2011). Functional diversity, along with increased canopy packing and structural complexity in mixed-species stands, has been associated with enhanced biomass accumulation (Williams et al., 2017; Ray et al., 2023), primarily through more efficient use of canopy space (Pretzsch, 2014). Greater functional diversity also indicates greater differences in the conditions experienced by each species in the stand, possibly inducing intraspecific variation in functional traits through plastic responses to local neighbourhood conditions. For instance, smaller trees next to taller trees will experience increased shading compared to a monoculture, while the taller trees will experience increased light availability, differences in environmental conditions that could underpin functional trait shifts. For example, smaller trees in mixed stands may develop their upper crowns to compete with more dominant trees, whereas dominant trees may invest more in their lower crowns, which are already well-positioned to capture light (Guisasola et al., 2015). Conversely, increased canopy cover may limit light penetration to the understory, thereby suppressing understory biomass production. In denser or more stratified canopies, specific leaf area (SLA) and leaf nitrogen (N) content may increase in response to shading (Coble & Cavaleri, 2015; Keenan & Niinemets, 2016). Together, higher functional diversity and the resulting niche complementarity may promote more complete resource use, with both interspecific trait differences and intraspecific trait plasticity contributing to enhanced biomass accumulation in mixed stands (Wright et al., 2010; Hao et al., 2020).

Not all tree species in mixed stands fare equally; some species will experience lower resource availability in a mixed stand than in a monoculture (e.g. a short species shaded by a taller one), while others will experience greater resource availability (e.g. the taller species). Consequently, some species will become dominant and over-represented in a mixed stand, in terms of having greater biomass. Because dominant species exert a disproportionate effect on stand functional identity and ecosystem functioning (Grime, 1998), the identification of shifts in trait expression along a dominance hierarchy is particularly consequential. In this study, we examined the role of dominance by comparing how tree species diversity influenced trait shifts when stand functional identity is calculated using biomass-weighted species traits versus when it is calculated solely from the proportional representation of species planted in mixtures. Although biomass-weighted and unweighted trait means are widely used, previous studies have not, to our knowledge, contrasted diversity-driven trait shifts derived from these two approaches. This comparison allowed us to evaluate whether diversity-driven trait shifts are motivated mainly by dominant species, by less dominant species, or by contributions from all species in the mixture.

To understand the direct and indirect effects of tree species diversity on functional traits and above-ground biomass accumulation, we assembled data from 11 tree diversity experiments spanning 40 tree species and varieties, conducted across 10 study sites in Europe and one in Brazil. These experiments, comprising both even-aged monocultures and mixtures, represent relatively young forest stands (5–15 years) and permit robust comparisons of functional traits and above-ground biomass components across broad environmental conditions that are generally homogenous within sites but differ between them (Kambach et al., 2019; Leuschner et al., 2009). This broad geographic and ecological scope also enabled us to examine whether shifts in functional trait expression in mixtures could explain observed patterns of above-ground biomass accumulation. While previous studies have explored diversity effects on trait expression and variability, these have largely focused on single experiments (Castro Sánchez-Bermejo et al., 2024; Davrinche & Haider, 2021; Serrano-León et al., 2022), through meta-analyses (Felix et al., 2023), or by using trait data derived from plant trait databases (Zheng et al., 2024). By analysing traits at both the species and community levels, we are able to assess whether diversity-driven plastic responses of individual species translate into changes in community functional identity that are relevant for ecosystem functioning. To our knowledge, this is the first study to explicitly link diversity-driven changes in functional traits to above-ground biomass components across multiple, aligned tree diversity experiments.

We hypothesised that:

(H1) Above-ground woody and litterfall biomass increase in response to tree species mixing, while understory biomass decreases.

(H2) Functional diversity in mixed stands drives shifts in species functional trait expression in mixed stands, leading to different community-level trait means than predicted from the component monocultures.

(H3) Functional diversity as well as community-level trait shifts are associated with changes in above-ground biomass components.

(H4) Species-level responses to species mixing in woody biomass production and functional traits differ both in their general patterns (intraspecific variation) and in their overall magnitude (net difference).

2 | MATERIALS AND METHODS

2.1 | Study sites

The study included 11 sites selected based on data availability for the functional traits and biomass components of interest. These sites are geographically distributed across six European countries and one site in Brazil (Table 1; Figure 1). All sites are part of TreeDivNet, a global network of tree diversity experiments (Paquette et al., 2018; Verheyen et al., 2016), and further details about each study site can be found on the website (www.treedivnet.ugent.be). At each site, trees were planted in equal proportions per species per plot (i.e. admixtures), and species pools consisted of tree species that were deemed to suit local growing conditions. While the experimental designs varied in plot structure and size, each tree species within a site was represented across all species richness levels specific to that site. Comparisons

TABLE 1 Study site characteristics for all tree diversity experiments included in this study. Mean annual temperature (MAT) and mean annual precipitation (MAP) were derived from http://www.worldclim.org/current.

Study site	Country	Planting year	Plot size [m^2]	Planting density [trees ha^{-1}]	Soil type	MAT [°C]	MAP [mm]	Former land-use	Richness gradient
B-Tree	Austria	2013	170–300	12,500	Chernozem	9.7	624	Pasture	1, 2, 4
BIOTREE Kaltenborn-Species	Germany	2004	5952	2500–5000	Arenosol	7.4	693	Pasture	1, 2, 4
ECOLINK Uppsala	Sweden	2014	92	15,625	Cambisol	5.8	551	Crop	1, 2, 3, 4
FORBIO Gedinne	Belgium	2010	1575–1764	4444	Cambisol	8.3	1060	Plantation	1, 2, 4
FORBIO Hechtel-Eksel	Belgium	2012	1296	4444	Podzol	10.1	713	Plantation	1, 2, 4
FORBIO Zedelgem	Belgium	2009	1764	4444	Cambisol	9.5	816	Crop	1, 2, 4
IDENT Freiburg	Germany	2013	13	49,438	Cambisol	10.5	841	Pasture	1, 2, 6
IDENT Macomer	Italy	2014	10	62,500	Regosols	13.9	879	Plantation	1, 2, 4
MataDIV	Brazil	2019	460	1887	Ferrasol	19.3	1314	Plantation	1, 3, 6
MyDiv	Germany	2015	121	10,000	Chernozem	8.9	493	Crop	1, 2, 4
ORPHEE	France	2008	400	2500	Podzol	12.6	1000	Plantation	1, 2, 4

between plots differing in diversity were always made within consistent management conditions (usually unfertilised and without irrigation; see Methods S1 for site-specific details). As a whole, our experiments span a range of 40 unique species across multiple environmental gradients, enhancing the generalisability of our findings, at least in temperate regions. While many TreeDivNet member experiments, as well as many of the experiments featured in this study, are located in temperate regions, the inclusion of data from the tropical MataDIV experiment in Brazil expands the biogeographical robustness and generalisability of our results. Although methodologies occasionally differed among study sites, protocols were applied consistently within each site. Since our analyses focused on within-site variability and included site as a random effect, these differences do not significantly impact the main conclusions (see Methods S1–S3 for site-specific details).

2.2 | Assessment of above-ground plant biomass components

To estimate the above-ground C pool, we calculated woody biomass (11 sites), litterfall biomass (10 sites) and understory biomass (8 sites) (Table 2; Table S1). Woody biomass for individual trees was estimated using allometric equations, incorporating both stem and branch biomass, based on tree diameter measurements (see Table S3 for a list of equations and Figure S1 for an illustration). For each study site, equations were selected to best fit the range of tree sizes, species, locations, and measurement heights; either root collar diameter or diameter at breast height. Individual tree biomass values were then aggregated at the species and plot levels and subsequently scaled to biomass per hectare. Litterfall biomass represents the dry weight of leaf litter collected per hectare over the course of a year for each plot using litter traps, further information can be found in Table S4.2. Litter traps were placed to ensure equal representation of species within each plot. Collected samples were dried at 70°C to a constant weight before being weighed. Understory biomass represents the aggregated dry weight of grasses, herbs, ferns and shrubs per hectare for each plot. Percentage cover of the major morphological groups was assessed non-destructively and converted to dry weight per hectare using allometric equations based on shoot length and ground cover in the PhytoCalc model (Heinrichs et al., 2010).

2.3 | Functional traits

While many traits could potentially serve as functional traits to explain diversity effects in tree mixtures, only a few have well-established links to ecological functions, supported by data from multiple experiments. The traits analysed in this study included those related to resource acquisition, which is key to plant growth and competition, and thus may be especially sensitive to species mixing. Alongside individual species traits, we also included leaf area index (LAI), which can be considered a community (plot) level trait

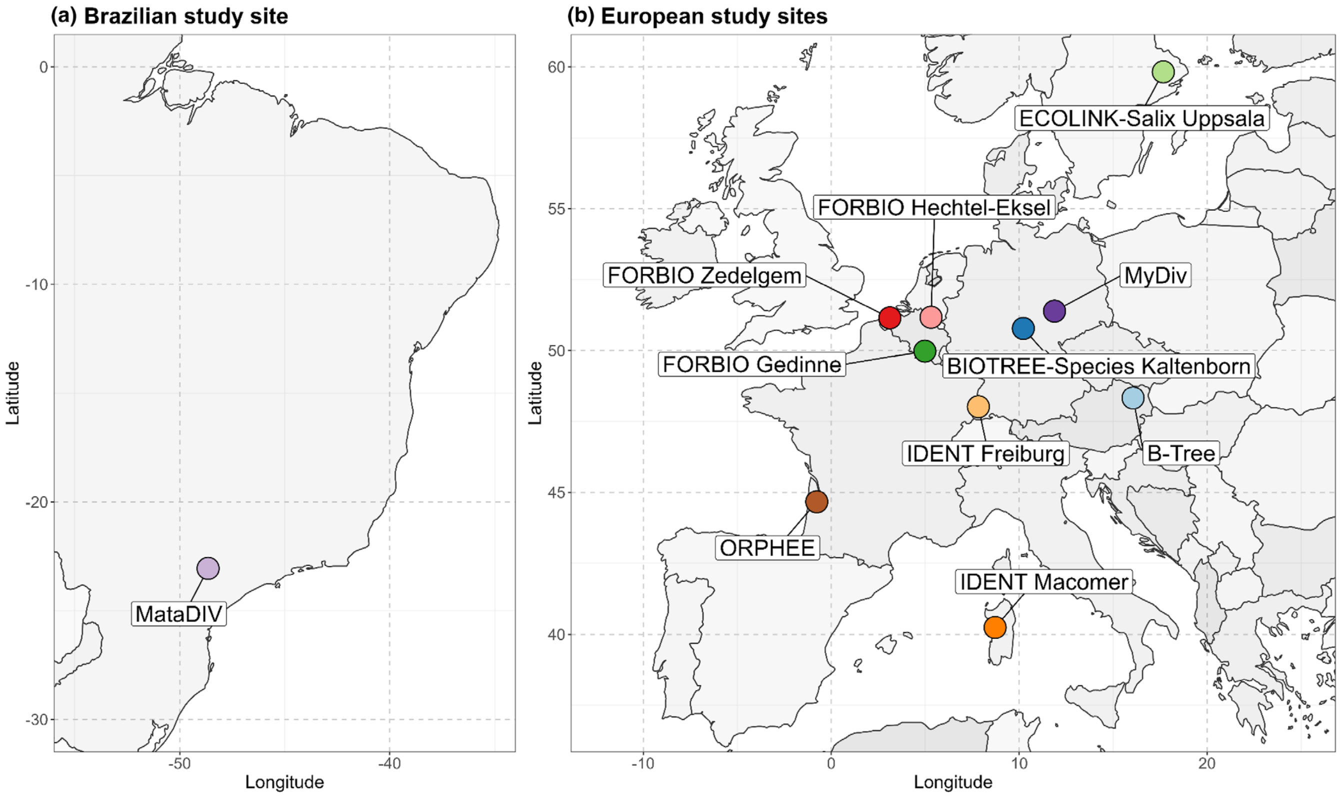

FIGURE 1 Map of study sites in (a) Brazil and (b) Europe.

that indicates stand light interception. LAI is commonly interpreted as a trait influencing light interception and, consequently, productivity (Reich, 2012; Sterck & Schieving, 2011; Yan et al., 2023). Although LAI is sometimes interpreted to reflect tree- or stand-level biomass, Parker (2020) showed that the relationship between LAI and productivity is often weak or even absent in tree stands, supporting the use of LAI as a functional trait rather than solely as a productivity proxy. Species-level traits included SLA, which reflects, among other things, the trade-off between resource acquisition and leaf longevity (Díaz et al., 2016), and stoichiometric ratios of leaf elements, such as C per N unit (leaf C:N) and N per phosphorus (P) unit (leaf N:P), which indicate plant adaptation to variable element needs over space and time (Alonso & Herrera, 2001, 2003). Maximum tree height is commonly used as a functional trait, often interpreted in the context of competitive strategies (Maynard et al., 2022; Wright et al., 2010). In this study, however, we use the average annual height increment since planting as a proxy for the same functional interpretation. We chose height increment rather than maximum height because on-site measurements capture growth expressed under the local environmental conditions of the experiments. As such, height increment reflects interspecific differences in realised growth strategies during early developmental stages, rather than long-term potential growth represented by maximum height. Additionally, we assessed wood density (WD), a predictor of growth strategies and C storage capacity, as well as leaf nutrient contents as indicators of plant nutrient use efficiency: leaf P content (LPC) and LNC, the latter expressed both per unit area (LNCA) and per unit mass (LNCM), each capturing distinct ecological implications (Westoby et al., 2013; Wright et al., 2004). LNCM primarily reflects biomass economy and is more strongly linked to biomass allocation for C fixation, aligning closely with species' relative growth rates (Poorter et al., 1990; Reich et al., 1992). In contrast, LNCA is the LNCM divided by SLA and is more closely tied to functional surface processes such as light interception and CO$_2$ diffusion (Hikosaka, 2004). Empirical evidence shows that LNCA is positively associated with photosynthetic capacity but negatively associated with photosynthetic nitrogen-use efficiency, suggesting a trade-off between maximal flux and efficiency (Lambers et al., 2008).

In this paper, SLA, LAI, LNCM, LNCA, LPCM, WD, leaf C:N, leaf N:P and annual height increment were considered as functional traits (Table 2). These traits were measured across experiments at the level of individual trees per species per plot, with the exception of LAI, which was measured at the plot level. The measured traits were subsequently aggregated to the appropriate resolution depending on the requirements of each analysis, as described in the relevant analysis sections. SLA (cm^2 g^{-1}) was estimated at most sites by dividing the scanned area of fresh individual leaves, obtained using a flatbed scanner and analysed with ImageJ (Collins, 2007), by their dry weight. Leaves were dried at 70°C until achieving a constant weight, and then weighed. An exception was made in MyDiv, where leaf spectroscopy was used in tandem with classical methods to predict SLA values and leaf nutrient concentrations (see Castro Sánchez-Bermejo et al. (2024) for details). LAI, representing the ratio of leaf area per ground area (m^2 m^{-2}), was measured at the plot level

TABLE 2 Acronyms, units and descriptions for study variables.

Variable	Acronym	Unit	Description
Woody biomass		$\mathrm{Mg\,ha^{-1}}$	Dry weight of stems and branches, calculated using allometric equations.
Litterfall biomass		$\mathrm{Mg\,ha^{-1}\,year^{-1}}$	Dry weight of leaf litter per hectare collected over a year.
Understory biomass		$\mathrm{Mg\,ha^{-1}}$	Dry weight of understory plants per hectare for each plot.
Specific leaf area	SLA	$\mathrm{cm^2\,g^{-1}}$	Leaf area per unit of dry mass.
Leaf area index	LAI	$\mathrm{m^2\,m^{-2}}$	Total canopy area per ground area.
Leaf nitrogen per mass	LNCM	%	Nitrogen content in leaves expressed per unit dry mass.
Leaf nitrogen per area	LNCA	$\mathrm{g\,m^{-2}}$	Nitrogen content in leaves expressed per unit area.
Leaf phosphorus per mass	LPCM	%	Phosphorus content in leaves expressed per unit dry mass.
Leaf carbon-to-nitrogen ratio	Leaf C:N	Ratio	Ratio of carbon to nitrogen content in leaves.
Leaf nitrogen-to-phosphorus ratio	Leaf N:P	Ratio	Ratio of nitrogen to phosphorus content in leaves.
Wood density	WD	$\mathrm{kg\,m^{-3}}$	Dry mass per volume of wood.
Height increment		$\mathrm{m\,year^{-1}}$	Average annual height growth.
Functional dispersion (as measure of functional diversity)	FDis	Unitless	Mean absolute deviation from each centroid in trait space.
Community weighted mean	$\mathrm{Trait_{CWM}}$	Same as trait	Mean trait values at the community level, weighted by species basal area proportion to account for dominance.
Net diversity effect	$\mathrm{NDE_{variable}}$	Ratio	Measure of diversity effects in each community, calculated as the ratio of observed (from mixed stands) to expected value (based on observations in pure stands) mixture values. Values above 1 indicate a positive diversity effect, below; negative.

using various methods in the different study sites (Table S4.1). All LAI measurements were taken at maximum foliar biomass for each study site, based solely on the trees within each plot. Fresh leaves, dried at 70°C until constant weight, were used to derive LNCM (%) and LPCM (%) by grinding samples (Retsch GmbH, Haan, Germany) for elemental analyses (for details see Methods S3). Ground plant material was acid-digested, and P concentrations were quantified photometrically.

Wood densities at species-per-plot level were estimated on wood increment cores as described in Serrano-León et al. (2025). Increment cores were scanned at the HECTOR XCT scanner of the Ghent University Centre for X-ray tomography (UGCT; http://www.ugct.ugent.be) following De Mil et al. (2016). Three-dimensional images of each core were reconstructed using Octopus reconstruction software (Vlassenbroeck et al., 2007) and converted to WD estimates using specific densitometry toolboxes (De Mil et al., 2016; De Mil & Van den Bulcke, 2023; Van den Bulcke et al., 2014). An exception to this methodology was at MyDiv, where wood densities were estimated by water displacement. Height increment was estimated at both species-per-plot and plot level as the total height of each individual tree divided by the age of the experiment. At FORBIO Gedinne, a representative subsample of approximately half of the trees measured for diameter was also measured for height. At ECOLINK Uppsala, tree heights were estimated using variety-specific, diameter-based allometric equations, which were fitted to each shoot and then aggregated at the stool level (Hoeber et al., 2018; Methods S2 and S3; Figure S2).

2.4 | Community weighted means, expected mixture values and net diversity effects

To characterise community-level trait expression, we calculated two complementary types of community means that differ in whether species' relative dominance is accounted for. Basal area–weighted community means (CWMs) account for differences in species' realised dominance, whereas unweighted community means treat all species equally, independent of dominance.

Because dominance weights require measurements at the species-per-plot level, CWMs were calculated only for values measured at this level (SLA, LNCM, LNCA, LPCM, leaf C:N, leaf N:P and WD). Variables quantified directly at the plot level (biomass components, LAI and height increment) were analysed using plot-level values only and not as CWMs. Basal area was used to account for species dominance, with species' trait values weighted by their proportional basal area within each plot (Table 2), as basal area serves as a reliable proxy for plant biomass (Lövenstein & Berliner, 1993) while avoiding the additional assumptions required by allometric equations.

To disentangle whether differences between monoculture and mixture values were driven by more or less dominant species in mixtures (i.e. a higher or lower basal area) or by an average shift across all species in mixtures, we compared observed mixture values with expected mixture values calculated using both weighted and unweighted community means. Expected mixture values were calculated by first aggregating values to the plot level, then weighting the

TABLE 3 Interpretation guide to results in Figure 3.

	Weighted: Observed≠expected	Weighted: Observed≈expected
Unweighted: Observed≠expected	All species contribute to the diversity effect	Less dominant species are driving the diversity effect
Unweighted: Observed≈expected	More dominant species are driving the diversity effect	No diversity effect

monoculture values for each species by their respective basal area in each mixture (Dawud et al., 2016):

$$\text{Weighted expected mixture values} = \sum_{i=1}^{s} p_{ij} \times t_{ij} \tag{1}$$

$$\text{Unweighted expected mixture values} = \frac{1}{s} \sum_{i=1}^{s} t_{ij} \tag{2}$$

where s is the number of species in the plot, p_{ij} is the proportion of the total plot basal area contributed by species i in study site j and t_{ij} is the trait value of species i in monoculture in study site j. See Table 3 for an interpretation of the differences between these approaches.

To evaluate diversity effects as a response to species mixing, we calculated the net diversity effect for each given variable ($\text{NDE}_{\text{variable}}$) as the ratio of observed to expected mixture values for each variable per plot (Dawud et al., 2016; Scherer-Lorenzen et al., 2007; Wardle & Nicholson, 1996). NDE calculations were weighted by the basal area proportion per tree species per plot for traits derived from species-level means (i.e. for SLA, LNCM, LNCA, leaf C:N ratio, leaf N:P ratio, LPCM, WD; Equation 3), see Figure S3 for comparisons between weighted and unweighted NDE per variable and study site:

$$\text{Weighted NDE} = \frac{\text{Weighted observed mixture value}}{\text{Weighted expected mixture values}} \tag{3}$$

Meanwhile, variables derived from plot-level means remained unweighted (i.e. woody biomass, litterfall biomass, understory biomass, LAI and height increment; Equation 4):

$$\text{Unweighted NDE} = \frac{\text{Unweighted observed mixture value}}{\text{Unweighted expected mixture values}} \tag{4}$$

NDE values greater than 1 indicate a positive diversity effect for the corresponding variable, whereas an NDE below 1 reflects a negative effect.

2.5 | Functional diversity and standardisations

To assess the functional diversity of each stand, particularly given that tree species richness levels varied across study sites (Table 1), functional diversity was represented by functional dispersion (FDis) and was calculated at the plot level following Laliberté and Legendre (2010) (Table 2). To calculate FDis, which represents the mean distance of species to the community centroid in multivariate trait space, we required trait values for every species present in each plot across all experiments. Because species-specific trait measurements were not always available from the mixed-species plots, we relied primarily on data derived from measurements taken in monoculture plots at each study site ($n=283$; Table S2). When site-specific measurements were missing, we supplemented these values with information from literature and trait databases ($n=17$; Table S2). This use of monoculture- and database-derived trait values was restricted to the calculation of FDis; all other trait- and biomass-related analyses relied exclusively on measured values. All comparative analyses were further restricted to cases where both monoculture and mixture data were available. The database values were derived from the TRY database (Kattge et al., 2011) and the global WD database (Chave et al., 2009; Zanne, 2009). The traits considered included SLA, WD, LAI, LNCM and height increment (Table S2; Figure S4). FDis was calculated to reflect the planting designs of the mixtures, assigning equal weighting to each species within a plot (Figure S5), thereby serving as a proxy for species richness. This approach offered a more consistent and ecologically meaningful measure of tree diversity than species richness and created a more continuous gradient across sites (Table S2; Figure S6). To facilitate comparisons across variables and experiments, community-level values were standardised within each site before analysis by computing *z*-scores (subtracting the mean and dividing by the standard deviation).

2.6 | Data analyses

All analyses were conducted using R (R Core Team, 2022). To evaluate the effects of species mixing on above-ground biomass components and functional trait expression at the community level (i.e. shifts of trait expressions) (H1 and H2), we compared observed mixture values against expected mixture values (i.e. using values from monocultures of each species). These comparisons were conducted using mixed effects models, with an indicator variable denoting observed or expected mixture values included as a fixed effect and fitted using the *lmer* function from the *lme4* package (Bates et al., 2003). Random effects of site, and block nested within site for blocked sites, were included to account for the hierarchical nature of the data. This approach was applied to mixture values both weighted and unweighted by species dominance. Additionally, to determine whether the effects of species mixing could be attributed to the functional diversity of a stand (H1 and H2), we tested the influence of FDis on NDE values using mixed effects regression models, also with random effects of site and block nested within site to account for the hierarchical nature of the data.

To evaluate whether shifts of trait expression in mixtures influenced biomass changes and whether functional diversity acted as a key driver within mixtures (H3), we implemented a structural equation model (SEM) using the package *piecewiseSEM* (Lefcheck, 2016) alongside *lme4*. As SEMs require complete data coverage across all variables, the analysis was restricted to study sites with full datasets (i.e. B-Tree, ECOLINK Uppsala, FORBIO Gedinne, FORBIO Hechtel-Eksel, FORBIO Zedelgem, IDENT Macomer). This model incorporated functional diversity (FDis) alongside diversity effects on SLA (NDE_{SLA}), LAI (NDE_{LAI}) and LNCM (NDE_{LNCM}), as well as on above-ground biomass components: woody biomass ($NDE_{woody\ biomass}$), litterfall biomass ($NDE_{litterfall\ biomass}$) and understory biomass ($NDE_{understory\ biomass}$). Each individual model in the SEM used the random effects structure of site and block nested within site to account for the hierarchical nature of the data. Model fit was evaluated using Fisher's C statistic and its associated p-value. We assessed variable independence and included non-directional correlations between variables when they improved model fit, as determined by tests of directed separation ($p < 0.05$ indicating a violation of independence assumptions). Since the NDE is a ratio-based metric derived from comparisons with corresponding monocultures, it can only be calculated for mixture plots. Consequently, our analysis included exclusively mixed stands, allowing us to investigate species interactions within these systems.

To assess species-level responses in trait expression and intraspecific variation to species mixing (H4), we calculated, for each species within each site, the $\log_{10}$-transformed ratio between trait values in mixtures and monocultures (i.e. $\log_{10}$[value in mixture/value in monoculture]). Net differences were defined as the mean of these $\log_{10}$ differences, thereby representing systematic shifts in trait expression due to mixing. Intraspecific variation was quantified as the mean absolute deviation from the 1:1 line (i.e. from zero in $\log_{10}$ space), capturing the magnitude of species-level responses to mixture regardless of direction. Net differences were tested against zero using fixed effects one-sample t-tests to evaluate whether traits showed consistent directional shifts in response to being grown in mixture. To express these $\log_{10}$-based estimates as percentages for interpretation in the figures, we calculated percentage values using the formula: $(10^{\Delta} - 1) \times 100$, where Δ is the mean $\log_{10}$ difference.

3 | RESULTS

Across all study sites, the mean biomass values for mixed-species communities were 40.2 Mg ha^{-1} for woody biomass, 4.1 Mg ha^{-1} $year^{-1}$ for litterfall biomass, and 0.5 Mg ha^{-1} for understory biomass. In contrast, monocultures exhibited mean biomass values of 31.2 Mg ha^{-1} for woody biomass, 3.4 Mg ha^{-1} $year^{-1}$ for litterfall biomass, and 0.5 Mg ha^{-1} for understory biomass. Comparing observed values in species mixtures to expected mixture values derived from pure stands for above-ground biomass components at the community level, we found that observed values in species mixtures exceeded expected mixture values (i.e. overyielding) for woody biomass (z-score difference = 0.39, $p < 0.001$) and for litterfall biomass (z-score difference = 0.53, $p < 0.001$) (Figure 2; Table S5). No significant differences were detected between observed and expected mixture values for understory biomass ($p > 0.05$).

For functional traits at community level, expected and observed mixture values were calculated for weighted (by each species' proportional contribution to the total basal area in the plot) and unweighted data (Figure 3; Table S6). Observed values in mixtures were higher than expected values for LAI (z-score difference = 0.34, $p < 0.001$), but lower than both unweighted and weighted expected values for LNCA (unweighted z-score difference = −0.59, $p < 0.001$; weighted z-score difference = −0.29, $p = 0.008$). In contrast, SLA showed a different pattern: while observed SLA values were significantly higher than expected values (z-score difference = 0.51, $p < 0.001$) using unweighted data, they did not differ significantly when using weighted data. No significant differences were detected between observed and expected mixture values for height increment, LNCM, LPCM, C:N, N:P, or WD, neither for weighted or unweighted data.

FDis was positively correlated with the NDE of woody biomass (regression coefficient $\beta = 0.27$, $p < 0.001$) and litterfall biomass ($\beta = 0.15$, $p = 0.014$; Figure 4). Among functional traits, FDis was positively related to the NDE of leaf C:N ($\beta = 0.09$, $p = 0.001$) and WD ($\beta = 0.09$, $p < 0.001$). No significant relationships with FDis were detected for the NDEs of understory biomass, SLA, LAI, LNCM, LNCA, LPCM, leaf N:P, or height increment.

Individual species varied in the magnitude of their responses to species mixing, with certain traits exhibiting greater intraspecific variation to mixing than others (Figure 5). On average, species-level woody biomass did not differ significantly between mixed stands and monocultures, exhibiting an intraspecific variation of 55%. SLA increased by an average of 7% in mixed stands compared to monocultures ($p = 0.004$), with an intraspecific variation of 13%. In contrast, neither LNCM nor LNCA showed significant net differences between mixed and monoculture stands, though their intraspecific variation in response to mixing was 9% and 15%, respectively.

In the SEM (Figure 6), functional diversity showed a positive influence on $NDE_{woody\ biomass}$ (0.46, $p = 0.0003$). NDE_{SLA} and NDE_{LAI} both showed positive influences on $NDE_{woody\ biomass}$ (0.29, $p = 0.002$ and 0.48, $p < 0.0001$ respectively). Additionally, NDE_{LAI} showed a negative influence on $NDE_{understory\ biomass}$ (−0.37, $p = 0.0011$). NDE_{LNCM} positively influenced $NDE_{litterfall\ biomass}$ (0.42, $p = 0.0001$). All pathways in the model were direct, with no observed mediating effects through intermediate nodes. The marginal R^2 values, representing the proportion of variance explained by fixed effects, were 0.41 for $NDE_{woody\ biomass}$, 0.28 for $NDE_{litterfall\ biomass}$ and 0.22 for $NDE_{understory\ biomass}$. The SEM explained 41%, 28% and 22% of the variation in the diversity effect on woody biomass, litterfall biomass, and understory biomass, respectively. The SEM model provided an adequate fit to the data, as indicated by the Fisher's C statistic ($C = 11.5$, $p = 0.318$).

4 | DISCUSSION

Tree species interactions significantly influenced above-ground biomass accumulation and functional trait expression across 11 tree diversity experiments in different soil-climate contexts. Our findings

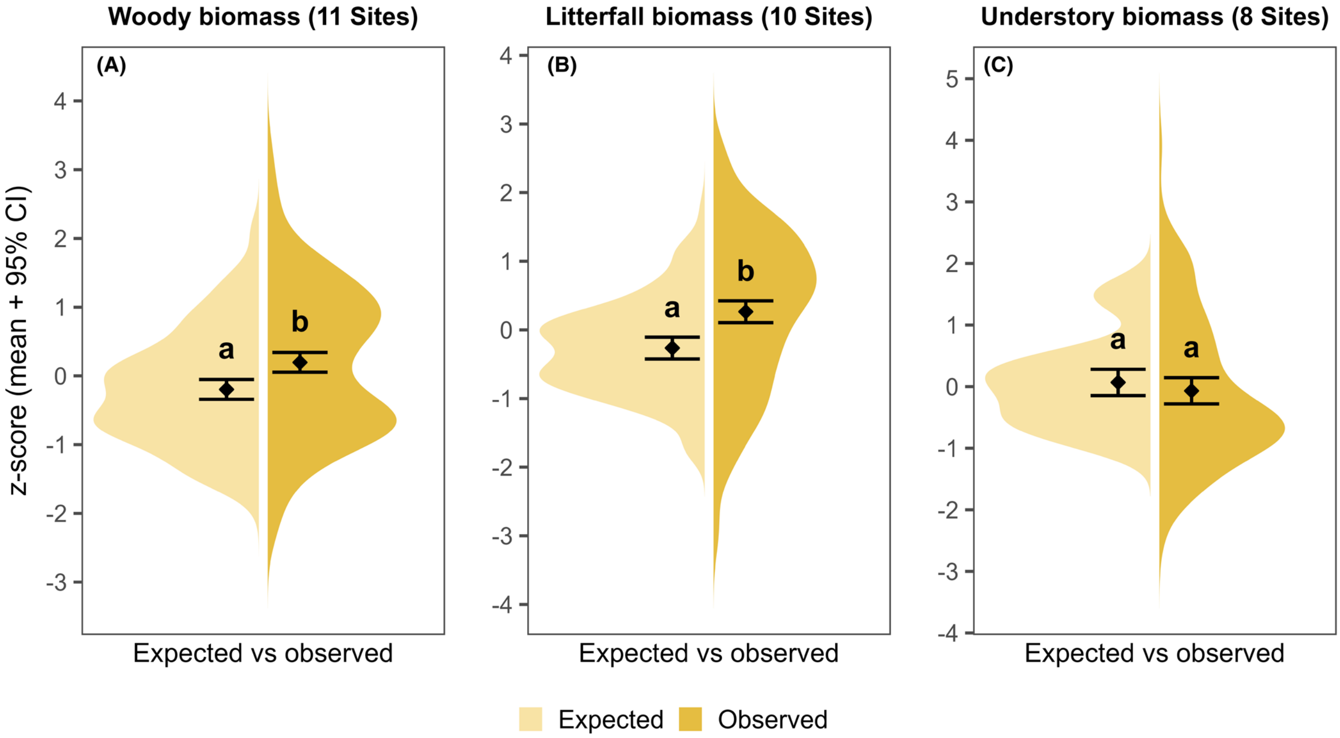

FIGURE 2 Relationships between expected (predicted from observations in pure stands; light beige) and observed (measured in mixed stands; dark beige) plot-level mixture values for three biomass components: (A) woody biomass, (B) litterfall biomass and (C) understory biomass. Split violin plots illustrate the kernel density distribution (*x*-axis) of *z*-scores within each study site for expected and observed mixture values. Positive *z*-scores indicate above-average values within study sites, while negative *z*-scores indicate below-average values within study sites. Points represent estimated marginal means, with error bars indicating corresponding confidence intervals. Different letters denote significant pairwise differences between expected and observed mixture values (a, b; $p < 0.05$).

demonstrate that tree species mixing can enhance both woody and litterfall biomass (H1) and therefore (short- to medium-term) carbon accumulation, while being associated with shifts in functional traits at both community and species levels (H2). Furthermore, changes in woody biomass, litterfall biomass and understory biomass in mixed stands were closely linked to shifts in SLA, LAI and LNCM, suggesting a mechanistic role of trait plasticity in biomass accumulation in mixtures (H3). As predicted (H4), the extent of intraspecific variation differed among species and trait types. However, while individual traits exhibited diversity-driven changes in intraspecific variation, average values across species remained relatively stable. This suggests that although some of the traits of certain species respond strongly to mixing, their influence on overall trait distributions may be moderated by broader community dynamics.

4.1 | Community trait shifts

Plant traits can shift in response to environmental conditions, with some species exhibiting greater plasticity under specific circumstances and others displaying a more generalised capacity for change (Nicotra et al., 2010). Accordingly, we found support for our second hypothesis (H2); that community functional trait means can shift in response to species mixing. Specifically, we revealed differences between observed and expected mixture values in SLA, LAI and LNCA. Notably, SLA changes were only detected when the community SLA was not weighted by species' proportion of basal area in the stand (i.e. dominance), which indicates that the SLA response to mixing may be primarily driven by less dominant species (Table 3). This pattern suggests that increased SLA in these species may be a response to shading by more dominant canopy species. Our results align with Serrano-León et al. (2022), who observed median shifts in SLA for oak when mixed with beech or spruce, and spruce when mixed with beech, highlighting the importance of neighbour species for trait shifts in leaf traits. Overall, substantial shifts in community trait expression indicate changes in functional identity and, consequently, in the stand's overall functioning, ultimately influencing the ecological role of a stand (Grime, 1998).

Our observation that LAI increased in mixed stands is consistent with previous research indicating that canopy cover increases in mixed stands, supporting the idea that greater crown height heterogeneity enhances canopy plasticity and space occupancy (Jucker et al., 2015; Martin-Blangy et al., 2023; Pretzsch, 2014). However, we found no correlation between the functional diversity of mixed stands and LAI, consistent with Hildebrand et al. (2021), who showed that branch trait dissimilarity, rather than overall functional diversity, drives crown complementarity. Furthermore, LNCA, but not LNCM,

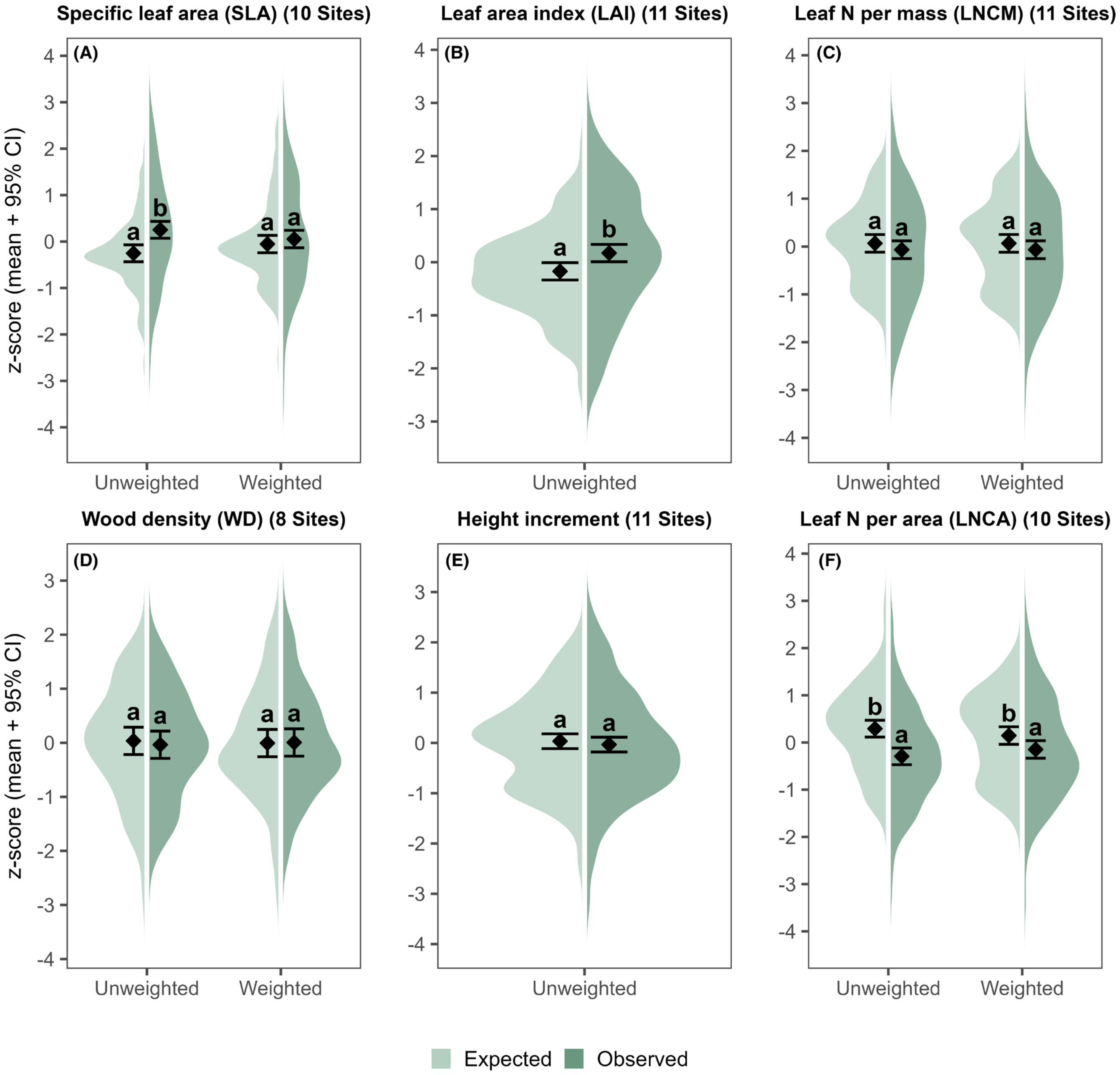

FIGURE 3 Relationships between expected (predicted from observations in pure stands; light green) and observed (measured in mixed stands; dark green) mixture values for six functional traits: (A) specific leaf area (SLA), (B) leaf area index (LAI), (C) leaf nitrogen content per mass (LNCM), (D) wood density (WD), (E) height increment and (F) leaf nitrogen content per area (LNCA). Trait values derived from species-per-plot-level measurements (SLA, LNCM, WD and LNCA) include both weighted and unweighted comparisons by species dominance. See Table 3 for an interpretation of the differences between these approaches. Split violin plots illustrate the kernel density distribution (*x*-axis) of *z*-scores within each study site for expected and observed mixture values. Positive *z*-scores indicate above-average values within study sites, while negative *z*-scores indicate below-average values within study sites. Points represent estimated marginal means, with error bars indicating corresponding confidence intervals. Different letters denote significant pairwise differences between expected and observed mixture values (a, b; $p < 0.05$). Illustrations of LPCM, leaf C:N and N:P ratios can be found in Figure S7.

decreased in response to mixing. Lower LNCA is associated with a reduced light-saturated rate of photosynthesis, but greater photosynthetic N-use efficiency, thus indicating a trade-off between efficiency and capacity (Lambers et al., 2008). In contrast, LNCM is more reflective of leaf construction costs (Wright et al., 2004). This discrepancy suggests that the observed reduction in LNCA in mixed stands may result from lower light availability in mixed stands (Keenan & Niinemets, 2016), possibly due to increased competition or crown complementarity (Williams et al., 2017), potentially promoting N-use efficiency at the expense of photosynthetic capacity.

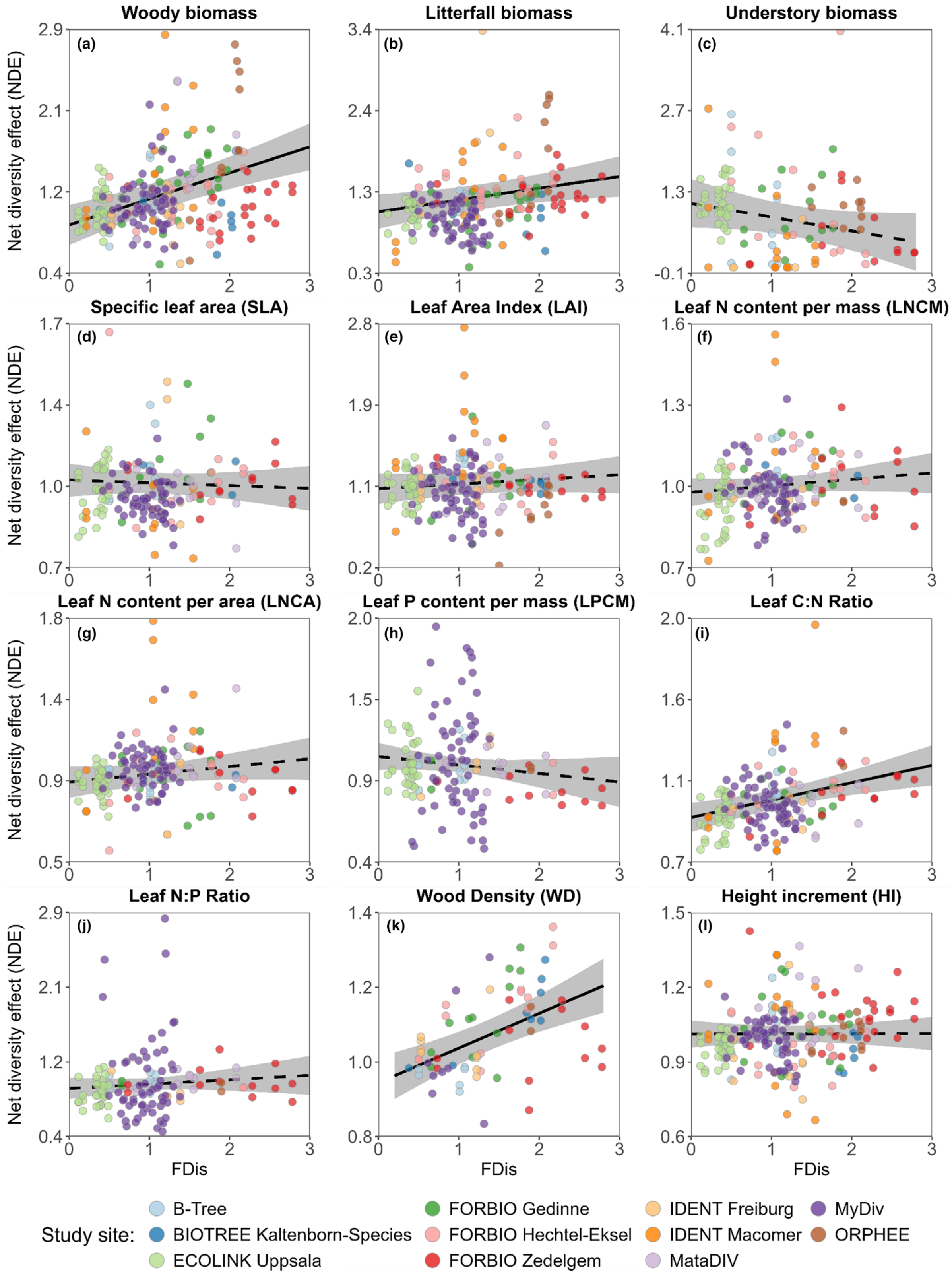

FIGURE 4 Relationships between functional diversity (FDis) and plot-level values of net diversity effect (NDE) for (a) woody biomass, (b) litterfall biomass, (c) understory biomass, (d) specific leaf area (SLA), (e) leaf area index (LAI), (f) leaf nitrogen content per mass (LNCM), (g) leaf nitrogen content per area (LNCA), (h) leaf phosphorus content per mass (LPCM), (i) leaf C:N ratio, (j) leaf N:P ratio, (k) wood density and (l) height increment. NDE values were weighted by the basal area proportion per tree species per plot for traits derived from species-level means (Equation 3), and unweighted otherwise (Equation 4). NDE values greater than 1 indicate a positive diversity effect for the corresponding variable. Values greater than 1 indicate a positive diversity effect for the corresponding variable. Solid black lines represent significant fitted regressions ($p < 0.05$); dashed lines represent non-significant ones. Shaded areas denote 95% confidence intervals. Colours indicate study site. Individual FDis values per plot per site can be found in Figure S6.

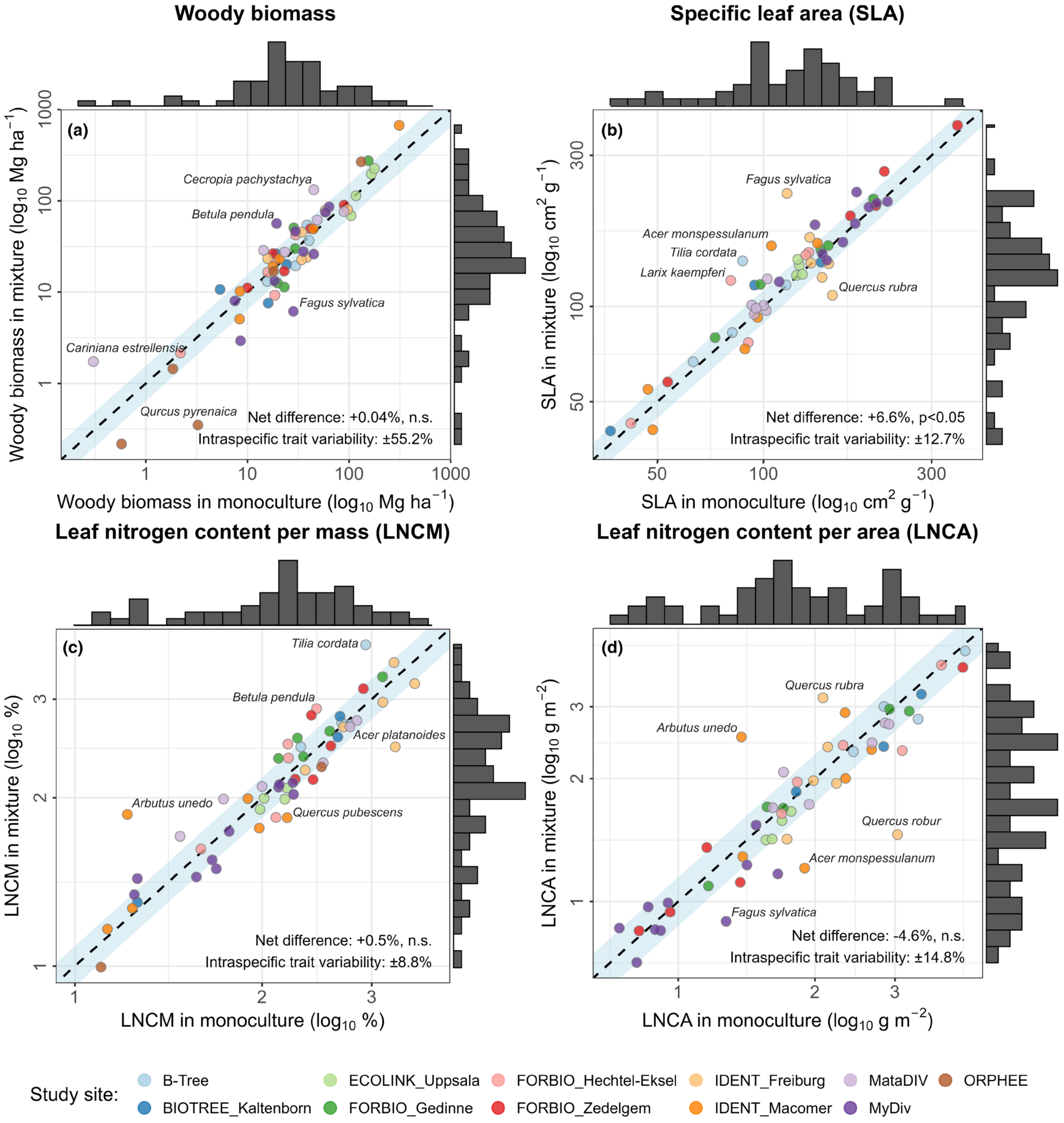

FIGURE 5 Relationships between species-per-plot-level values in monoculture (*x*-axis) and mixture (*y*-axis) across sites for four variables: (a) woody biomass, (b) specific leaf area (SLA), (c) leaf nitrogen content per mass (LNCM) and (d) leaf nitrogen content per area (LNCA). All axes are plotted along a logarithmic scale and tick labels are shown on the original scale. The dashed black 1:1 line indicates no difference between monoculture and mixture values. The shaded blue ribbon shows the average intraspecific variation, calculated as a symmetric deviation from the 1:1 line in $\log_{10}$ space. Because the log scale is multiplicative, this ribbon corresponds to a fixed relative change (reported as a percentage in the bottom right of each panel). Net trait shifts (mean $\log_{10}$ differences between mixture and monoculture values) and their statistical significance are also reported. Histograms along the top and right margins show the distribution of species values in monoculture and mixture, respectively. The five most responsive species (i.e. those with the largest absolute deviations from the 1:1 line) are labelled in each plot. Points are coloured by study site. A version of these figures on the original scale is provided in Figure S8. Additional traits (height increment, wood density and LPCM) are shown in Figure S9.

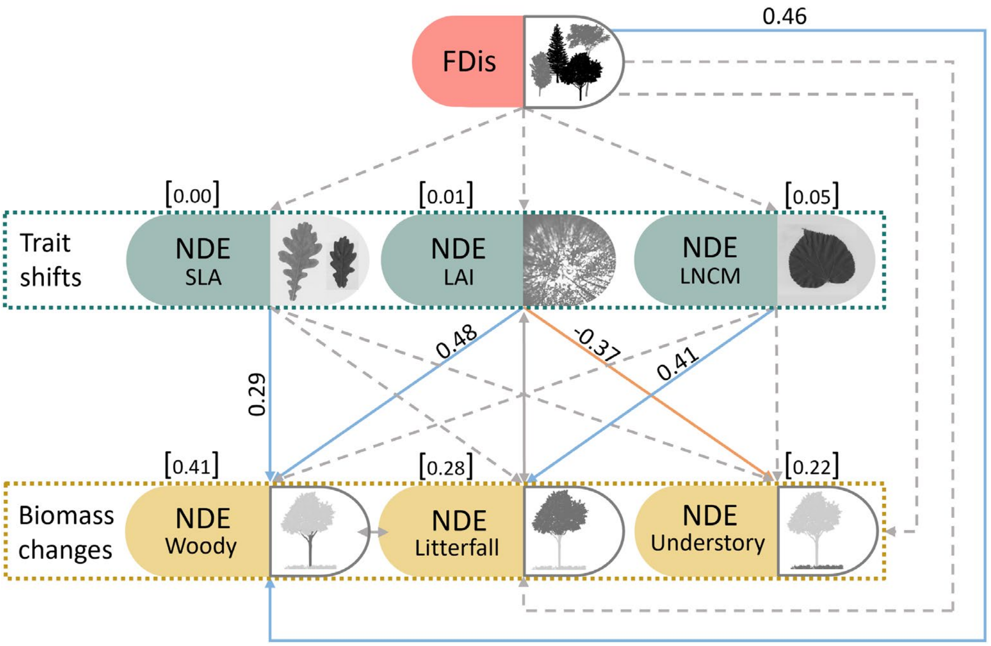

FIGURE 6 Structural equation model (SEM) illustrating the direct and indirect relationships between functional diversity (FDis), and net diversity effects (NDE) on specific leaf area (SLA), leaf area index (LAI), leaf nitrogen content per mass (LNCM), as well as woody biomass, litterfall biomass and understory biomass at the plot level across six experiments. NDE values were weighted by the basal area proportion per tree species per plot for traits derived from species-level means (SLA and LNCM; Equation 3), and unweighted otherwise (LAI and biomass components; Equation 4). The model presents standardised path coefficients for each significant causal pathway, along with marginal R^2 values for all endogenous variables. Solid blue pathways represent positive effects, solid orange pathways represent negative effects, and solid grey pathways represent non-causal relationships. Individual pathways are modelled separately in Figure S10, an alternative model using LNCA instead of LNCM can be found in Figure S11 ($C=6.58$, $p=0.584$) and an a priori model can be found in Figure S12.

Our two leaf stoichiometric values, C:N and N:P, did not shift in either direction, neither weighted nor unweighted, indicating that C-nutrient and nutrient-nutrient balances, and the nature of the growth-limiting factors, were not significantly changed by mixtures in the stands investigated here.

In cases where average trait values did not differ between expected values from monocultures and observed values in mixtures but varied with the functional diversity (FDis) of mixtures, different underlying mechanisms may have been driving trait shifts or traits shifted in different directions for different species so that the average remained the same. This pattern supports our earlier suggestion that dominance dynamics and competition may exert a stronger influence on certain trait changes than functional diversity. For instance, SLA and LAI were higher, while LNCA was lower in observed compared to expected mixture values, yet their diversity effects remained unchanged across functional diversity levels. In contrast, diversity effects on WD and the leaf C:N ratio varied with functional diversity but did not differ between observed and expected mixture values. These findings warrant further exploration to disentangle the relative contributions of competition, dominance and functional diversity to trait variation in mixtures.

Overall, the community traits that differed between mixed and monoculture stands in this study primarily relate to light acquisition and use, highlighting light competition as a key driver of species interactions in mixed forests. However, we note that the studied experiments comprised relatively young trees, and given that the functional expression of a community can be expected to change over time (Koricheva et al., 2025), the relationships established in this study may differ in more mature forests. Future research should explore the role of trait shifts and plasticity in diversity-productivity relationships across both younger and older tree communities.

4.2 | Above-ground biomass and mechanistic links through functional trait shifts

When comparing mixtures to monocultures across all sites, biomass ratios were 1.3:1 for woody biomass, 1.2:1 for litterfall biomass and 1:1 for understory biomass. This suggests that the effects of species mixing on community biomass are more pronounced in components more directly linked to tree growth. It is worth noting that the allometric equations used to estimate woody biomass were developed using trees grown in monoculture, potentially overlooking effects of species mixing. However, Forrester et al. (2017) found tree species diversity to be the least influential factor among those affecting allometric relationships.

The findings support our hypothesis (H1) that woody biomass and litterfall biomass would be significantly higher in mixtures compared to monocultures. Moreover, as the effect of mixing on biomass increased with the interspecific functional diversity of mixed stands, it is likely that functional diversity plays a key role in driving these differences between mixed and monoculture stands. In contrast, understory biomass did not differ significantly between mixtures and monocultures. This suggests that the potential trade-off between above-ground biomass components, as proposed in the introduction, is not necessarily important in the forest systems studied here. However, there are caveats to this conclusion. Firstly, this study did not account for above-ground dead wood biomass or belowground biomass, and potential trade-offs involving root system biomass may also exist. Secondly, understory dynamics are influenced by site-specific factors, experimental design, stand age and the timing of sampling within the growing season, and should be taken into account when interpreting effects of species mixing on understory biomass. Additionally, it is important to note that the woody biomass results exhibited a degree of bimodality, which was driven both by overall differences in site responses and, in some cases, by bimodal patterns within individual sites. This variability suggests that species mixing effects on woody biomass may be more complex than reflected by mean responses alone and represents an avenue for future research to explore the mechanisms underlying site-specific and within-site bimodal responses. While between-site variability in our data was high, given the number of experiments included in this study and their broad geographical distribution, forest managers across Europe can generally expect higher woody biomass and litterfall biomass in mixed stands and that this effect is likely to be amplified when incorporating a greater diversity of functionally distinct species. As these relationships remained consistent across experiments in temperate, boreal, mediterranean and even a tropical (MataDIV) site, the conclusions of our findings may also extend to other continents and ecosystems.

To test our third hypothesis (H3), i.e. to assess whether diversity-driven changes in biomass components were mediated by trait shifts, we conducted a SEM using a subset of six study sites with complete data coverage. According to the SEM, trait shifts in LAI and SLA, in that order of importance, mediated the diversity effects on woody biomass. Given that SLA and LAI are both associated with a growth strategic dimension (Díaz et al., 2016; Poorter et al., 2008; Poorter & Bongers, 2006; Wright et al., 2004, 2010), our findings suggest that diversity effects on biomass production were here primarily driven by adjustments in light acquisition. Specifically, the highest woody biomass accumulation occurred in mixtures where community functional identity shifted toward greater canopy cover (high LAI) and thinner leaves (high SLA), adaptations that enhance light interception (Reich, 2012), likely in response to intensified competition for this resource. However, LAI can also reflect differences in overall tree size, meaning that higher LAI in mixtures could result from trees being larger on average due to other mechanisms. This would lead to a more nuanced interpretation of LAI as purely a driver of biomass production.

The observed positive association between increases in woody biomass and SLA in mixtures may reflect a plastic response by less dominant species to shading by taller, more competitive neighbours. Such adjustments could promote both persistence and performance under the reduced light conditions imposed by stronger competitors, potentially both responding to and contributing to increased canopy packing. This interpretation is supported by our finding that SLA values were higher when not weighted by species dominance, suggesting that less dominant species largely drove these trait shifts. Such adjustments may explain the positive diversity effects on growth, whereby competitive species thrived, while less competitive species maintained viability, by modifying their traits to enhance survival under higher competitive pressure. Overall, our results support our third hypothesis (H3), demonstrating that functional trait adjustments in even-aged mixed forests optimise resource acquisition, thereby enhancing productivity. However, while total understory biomass did not differ between mixtures and monocultures, increasing LAI in mixtures negatively affected diversity-driven gains in understory biomass, likely due to reduced light availability under denser canopies (Gilliam, 2007; Neufeld & Young, 2014). This indicates a trade-off between biomass components in mixtures when the mixtures increase canopy cover. We found that while trait shifts influenced biomass components, and functional diversity directly promoted positive diversity effects on woody biomass, functional diversity did not significantly drive changes in trait expression. This suggests that an alternative mechanism, or a set of mechanisms, governs these trait adjustments in response to species diversity.

4.3 | Species-specific trait shifts and intraspecific variation

In our study, large intraspecific variability in response to species mixing was found in some cases, but not in others. In general, plant phenotypic intraspecific trait variability is not a certainty (Palacio-López et al., 2015), it does not necessarily result in shifts in mean values (Valladares et al., 2006) and can also vary substantially across species, traits and environments (Westerband et al., 2021). It is therefore not a foregone conclusion that species trait values would change in response to species mixing. Although in line with our fourth hypothesis (H4), our findings reveal variable intraspecific variation in response to species mixing across all tested traits, even WD. Only in SLA was there a significant shift in the overall trait values, indicating that for the other traits, positive and negative species trait shifts may have cancelled each other out. Prior research by Forey et al. (2016), Davrinche and Haider (2021) and Castro Sánchez-Bermejo et al. (2024) also found higher SLA for some species when grown in mixture.

Increased woody biomass at the community but not the species level in tree species mixtures indicates that the community-level response may be due to a few species performing well in mixtures, rather than an equal increase for all species. This pattern aligns with the concept of selection effects, whereby productivity is disproportionately influenced by a few dominant species. In contrast, complementarity effects reflect average increases in growth across all species within a mixed stand (Loreau & Hector, 2001). Our findings further support the interpretation of a few productive species driving positive diversity effects on growth as we found many of the most productive species in terms of woody biomass to respond positively to species mixing. We also found that intraspecific variation in LNCA was roughly 70% more variable than in LNCM. While a higher intraspecific variation in LNCA may partially result from its dependence on SLA, the lack of a significant shift in mean values suggests that its response to mixing is not solely driven by changes in SLA. Hallik et al. (2009) showed that across 212 temperate woody species, LNCA, but not LNCM, is linked to lower shade tolerance, suggesting that light limitation may serve as a selective pressure in many mixed stands. Overall, intraspecific trait variation indicates a change in realised niche space occupancy, possibly as a mechanism to minimise niche space overlap (Macarthur & Levins, 1967; Tilman, 1988), thus reducing competition.

While we did not observe an overall difference in community WD between mixtures and monocultures, we found that increases in WD within mixtures relative to monocultures were significantly correlated with mixture functional diversity. This suggests that community WD tends to increase with greater neighbourhood diversity. Yang et al. (2024) reported greater variability in wood densities in response to competitive conditions, which may also be a contributing factor in our study. Variation in species-specific wood densities makes general interpretations of community-level changes difficult. Factors that can influence wood densities include growth, competition, environment or differences between conifers and deciduous tree species (Genet et al., 2013; Oliveira et al., 2022; Pretzsch & Rais, 2016), making it difficult to pinpoint the primary drivers of change. On average, species in our study exhibited a ±3% difference in WD when grown in mixtures compared to monocultures, with the most responsive species showing a −16% difference (*Prunus avium*; Figure S9). While the average intraspecific variation in WD is low, WD in mixtures cannot be assumed to remain constant. Such diversity-driven variability in wood densities may affect planning and decision-making for forest managers and industry.

5 | CONCLUSIONS

Our study demonstrates that species mixing can enhance aboveground biomass accumulation and is associated with shifts in functional traits, reinforcing the role of tree species interactions in forest productivity. Diversity-driven increases in woody and litterfall biomass in mixtures were largely mediated by functional diversity and community shifts in SLA and LAI. However, we found no evidence for functional diversity directly driving these trait shifts, indicating additional underlying mechanisms. While species showed high intraspecific variation for some traits, their trait means remained largely stable, suggesting that species-level responses are tempered by broader community dynamics. These findings suggest that mixing fast-growing species with those exhibiting high plasticity in crown architecture and SLA may effectively enhance above-ground woody biomass accumulation. Our study accentuates the potential of mixed-species forests for increasing biomass production and C sequestration, supporting their viability for sustainable forest management, but also highlights the need for future research exploring a wider set of functional traits and drivers of between-site variability at the community scale.

AUTHOR CONTRIBUTIONS

Joel Jensen, Haben Blondeel, Chloe MacLaren, Petra Fransson, Carolyn Glynn, Adam Felton and Martin Weih conceived the ideas and designed methodology; Joel Jensen, Haben Blondeel, Iftekhar U. Ahmed, Laurent Augusto, Lander Baeten, Mark R. Bakker, Jürgen Bauhus, Christel Baum, Friderike Beyer, Pedro Brancalion, Nico Eisenhauer, Nicolas Fanin, Olga Ferlian, Emmely Fritsch, Douglas L. Godbold, Joannès Guillemot, Peter Hajek, Hervé Jactel, Simone Mereu, Celine Meredieu, Bart Muys, Nils-Erik Nordh, Quentin Ponette, Boris Rewald, Agnès Robin, Dai Saito, Hans Sandén, Michael Scherer-Lorenzen, Hernán Serrano-León, Kris Verheyen, Ramona Werner, Huimin Yi, Elisabeth Bönisch, Martin Weih, Pablo Castro Sánchez-Bermejo, Peter Dietrich, Sylvia Haider and Matthias Steinparzer collected the data; Joel Jensen analysed the data and led the writing of the manuscript. All authors contributed critically to the drafts and gave final approval for publication.

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CONFLICT OF INTEREST STATEMENT

The authors declare no conflict of interest.

DATA AVAILABILITY STATEMENT

Data supporting the figures and analyses presented in this study are publicly available on Figshare: DOI: https://doi.org/10.6084/m9.figshare.31026004 (Jensen, 2026).

STATEMENT ON INCLUSION

Our study involved collaboration among authors from multiple countries, including researchers based in the countries where the study was conducted. Each author contributed to the study design and research based on their expertise and knowledge of their respective locations, ensuring that diverse and contextually relevant perspectives were integrated from the outset. Where relevant, we cited literature published by scientists from the region.

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SUPPORTING INFORMATION

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

Figure S1. Allometric equations for above-ground woody biomass for all species across all study sites.

Figure S2. Relationship between measured diameter and estimated height per stool in ECOLINK Uppsala in 2022.

Figure S3. Net diversity effect (NDE) for each site across multiple functional traits: specific leaf area (SLA), leaf nitrogen content per mass (LNCM), leaf nitrogen content per area (LNCA), wood density (WD), leaf nitrogen-to-phosphorus ratio (N:P), leaf carbon-to-nitrogen ratio (C:N) and leaf phosphorus content per mass (LPCM).

Figure S4. Principal component analysis (PCA) of functional traits: height increment (HI), leaf area index (LAI), leaf nitrogen content per mass (LNCM), specific leaf area (SLA) and wood density (WD) for each species in each site ($n=60$).

Figure S5. Comparison of functional diversity (FDis) weighted by number of stems per species and unweighted (equal proportions).

Figure S6. Functional diversity (FDis) in mixture plots at each site, unweighted by proportional number of stems per species. Colour indicates species richness.

Figure S7. Relationships between expected (predicted from observations in pure stands; light green) and observed (measured in mixed stands; dark green) mixture values for three functional traits: (A) leaf phosphorus content per mass (LPCM), (B) leaf C:N ratio and (C) leaf N:P ratio.

Figure S8. Original-scale version of Figure 5, showing relationships between species-level values in monoculture (*x*-axis) and mixture (*y*-axis) across sites for four variables: (A) woody biomass, (B) specific leaf area (SLA), (C) leaf nitrogen content per mass (LNCM) and (D) leaf nitrogen content per area (LNCA).

Figure S9. Relationships between species-level values in monoculture (*x*-axis) and mixture (*y*-axis) across sites for three variables: (A) wood density, (B) height increment and (C) leaf phosphorus content per mass (LPCM).

Figure S10. Individual bivariate relationships included in the structural equation model in Figure 6.

Figure S12. A priori structural equation model (SEM) illustrating the hypothetical direct and indirect relationships between functional diversity (FDis) and net diversity effects (NDE) on specific leaf area (SLA), leaf area index (LAI), leaf nitrogen content per area (LNCA), as well as woody biomass, litterfall biomass and understory biomass.

Methods S1. Experimental manipulation of diversity treatments across sites.

Methods S2. Allometric estimation of tree size and biomass.

Methods S3. Leaf sampling protocols and nutrient quantification.

Table S5. ANOVA results for above-ground biomass components (woody, litterfall and understory biomass) comparing expected and observed mixture values.

Table S6. ANOVA results for functional traits comparing expected and observed mixture values: specific leaf area (SLA), leaf area index (LAI), leaf nitrogen content per unit mass (LNCM), leaf nitrogen content per unit area (LNCA), leaf phosphorus content per unit mass (LPCM), leaf carbon-to-nitrogen ratio (C:N), leaf nitrogen-to-phosphorus ratio (N:P), wood density (WD) and height increment.

Table S1. Summary of stand-level characteristics for the 11 experimental sites used in the study.

Table S2. Species-specific trait values for trees used across study sites.

Table S3. Allometric equations used to estimate above-ground woody biomass for tree species in each study site.

Table S4. Overview of key methodolgical considerations at each experimental site for leaf area index (LAI; Table S4.1) and litterfall (Table S4.2).

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