

RESEARCH ARTICLE

Fertilization influences overyielding through dominance of species with high specific leaf area in young tree mixtures

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Handling Editor: Sabrina Russo**Abstract**

1. In the context of anthropogenic eutrophication of the biosphere, understanding the impact of nutrient addition on plant diversity–productivity relationships remains a major challenge. In particular, the indirect effect of nutrient addition on productivity in tree mixtures via changes in the functional structure of tree communities has never been experimentally quantified and may play an important role in mediating diversity–productivity relationships.
2. Here, we present results from young experimental tree communities 4 years after planting, including monocultures and two- and four-species mixtures of six European species (*Acer platanoides*, *Betula pendula*, *Larix decidua*, *Picea abies*, *Pinus sylvestris* and *Quercus robur*) with or without 4 years of mineral fertilizer addition. Using a response-effect trait framework that links plant functional traits with ecosystem processes, we specifically examined how functional diversity (FD) and community weighted means (CWM) of tree height (H) and specific leaf area (SLA) were influenced by fertilization and to what extent they mediated the fertilization effect on above-ground productivity in woody tissues.
3. The overall fertilization effect on the degree of community-level overyielding was marginally positive, yet the influence of fertilization varied significantly depending on species composition. Fertilization affected community functional trait structure primarily by increasing CWM of SLA through dominance of species with high SLA, rather than through intraspecific trait variability. Interestingly, the fertilization-induced change in CWM of SLA reduced community-level overyielding. Irrespective of fertilization, CWM of H and SLA influenced community-level overyielding, while FD had no significant effects.

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4. Our results indicate that changes in nutrient availability can influence the magnitude of overyielding indirectly through dominance of species with high SLA in young tree communities. This result improves our understanding of the context dependency of diversity–productivity relationships, which strongly depends on nutrient availability influencing the competitive relationships among tree species. The occurrence of such effects early after tree planting could potentially produce long-term consequences for tree community composition, and even more so in naturally regenerating forests with less control on tree species selection.

KEYWORDS

community weighted mean, fertilization, functional diversity, IDENT, mixed-species plantations, overyielding, plant–plant interactions, TreeDivNet

1 | INTRODUCTION

The effects of biodiversity on ecosystem functioning have been a focal topic of ecological research since the 1990s (Cardinale et al., 2012; Chapin et al., 2000; Hooper et al., 2005). Meta-analyses have demonstrated that increased plant diversity enhances ecosystem functioning, such as biomass production and nutrient cycling, across various ecosystems (Balvanera et al., 2006; Cardinale et al., 2011). This growing evidence raises concerns about the impacts of biodiversity loss on ecosystem services in the context of global change (Isbell et al., 2017).

In forestry, biodiversity–ecosystem functioning research underpins discussions on the transition from conventional monocultures to mixed-species approaches (Bauhus et al., 2017; Messier et al., 2021; Mori et al., 2017). Mixed-species forests often exhibit overyielding, where productivity exceeds expectations based on monocultures (Chen et al., 2025; Feng et al., 2022; Zhang et al., 2012). However, this phenomenon is context-dependent, with studies reporting both positive and negative effects of species mixing (Ammer, 2018; Kawaletz et al., 2013). Understanding the mechanisms underlying overyielding is essential to reconcile these findings (Forrester, 2014).

Overyielding is driven by two primary mechanisms: selection effects and complementarity effects (Loreau & Hector, 2001). Selection effects occur when high-performing species dominate a community, leading to greater productivity. In contrast, complementarity effects arise when species interact positively, such as through resource partitioning, abiotic facilitation or biotic feedback, enhancing overall ecosystem functioning (Barry, Mommer, et al., 2019). These mechanisms, which depend on niche and fitness differences between species (Godoy et al., 2020), are inherently linked to functional traits, providing a framework for understanding biodiversity's influence on productivity.

Functional traits are morphological, physiological or phenological characteristics that influence plant fitness and performance and are measurable at the individual level (Violle et al., 2007). Trait-based approaches link individual species performance to ecosystem functioning by analysing functional trait distributions in communities (Cadotte, 2017; Díaz et al., 2007; Enquist et al., 2015). Within this

framework, two non-exclusive hypotheses explain how community functional trait structure shapes productivity. The mass ratio hypothesis posits that the dominant species' functional traits, quantified as community weighted mean traits (CWM), primarily drive ecosystem functioning (Grime, 1998), aligning conceptually with selection effects. In contrast, the niche complementarity hypothesis suggests that the variability of functional traits among species in a community–functional diversity (FD)—enhances ecosystem functioning (Tilman et al., 1996), corresponding to complementarity effects. Recent meta-analyses suggest that both CWM and FD contribute to overyielding (Chen et al., 2025; Zheng et al., 2021). However, their relative importance remains debated. Some studies suggest that CWM better predicts overyielding in young tree communities (Luo et al., 2020; Tobner et al., 2016), whereas others report stronger effects of FD (Grossman et al., 2017). These discrepancies suggest that environmental conditions play a crucial role in shaping the explanatory power of CWM and FD in determining the magnitude of overyielding in tree species mixtures. To properly disentangle these context-dependent effects, it is essential to design experiments that control for the correlation between CWM and FD (Dias et al., 2013) and explicitly manipulate environmental conditions such as soil nutrient availability (Eisenhauer et al., 2019; Wardle, 2016).

Anthropogenic activities, such as fossil fuel combustion and fertilization, have significantly increased nitrogen (N) and phosphorus (P) levels in terrestrial ecosystems (Falkowski et al., 2000; Galloway et al., 2008). While the impact of nutrient enrichment on diversity–productivity relationships has been widely studied in grasslands, research in forest ecosystems remains scarce, despite the growing demand for mixed-species plantations (Messier et al., 2021) and the common use of fertilization in intensively managed forests (Fox, 2000). Grassland studies suggest that nutrient addition can weaken complementarity effects (Craven et al., 2016) or enhance selection effects (Mason et al., 2020; Roscher et al., 2016), but similar patterns in forests remain largely unexplored. The few existing studies indicate that fertilization influences overyielding depending on species composition and associated functional traits, rather than species richness per se (Dziedek et al., 2016), yet the relative roles of CWM and FD under nutrient enrichment are still unclear.

Moreover, nutrient addition affects productivity not only by alleviating nutrient limitations but also by altering community functional trait structure through shifts in species composition, abundance and intraspecific trait variation (Lavorel & Garnier, 2002; Suding et al., 2008). In grasslands, fertilization often reduces species diversity (Clark & Tilman, 2008; Isbell et al., 2013), and similar trends are observed in forests (Siddique et al., 2010; Thomas et al., 1999). Additionally, N addition influences key plant functional traits related to leaf economics and hydraulics (Zhang et al., 2018), which in turn influence community-level productivity (Zheng et al., 2021). However, how these trait-mediated responses influence species-mixing effects in forests remains unknown. Addressing this knowledge gap may provide new insights into the context dependency of diversity–productivity relationships.

Here, we analysed interactive effects between community functional trait structure (i.e. CWM and FD) and fertilization on community-level accumulation of above-ground woody phytomass—a proxy for productivity—in a young tree diversity experiment. The community response was further explored by examining changes in functional traits and species abundance of individual species. Since fertilization may increase plant biomass and intensify above-ground size-asymmetric competition with a higher light acquisition per unit biomass for larger plants (Hautier et al., 2009; Newman, 1973; Xiao et al., 2021), we used functional traits linked to fast growth and light acquisition strategies—specific leaf area (SLA) and tree height (H)—to capture community responses to fertilization as influenced by CWM and FD. These two traits were selected with reference to the two-dimensional global plant trait spectrum proposed by Díaz et al. (2016), which includes the leaf economics spectrum and plant size axes, although we applied conceptual adjustments tailored to the aims of our study. Specific leaf area (SLA) aligns directly with the leaf economics spectrum and is positively related to relative growth rate and leaf net carbon assimilation rate (Wright et al., 2001), but generally negatively related to shade tolerance (Kitajima, 1994; Walters & Reich, 1999, but see Lusk & Warton, 2007; Poorter, 2009). Moreover, tree species with high SLA tend to have a comparatively smaller negative influence on their neighbours than species with low SLA (Kunstler et al., 2016). For the plant size dimension, however, Díaz et al. (2016) typically use species-level maximum (adult) height, whereas we used individual tree height measured 4 years after planting as a dynamic, realized trait that reflects vertical growth directionality during early stand development. This trait captures species- and context-dependent variation in competitive positioning within the canopy, and in our context, it indicates the potential for competitive advantage through prior access to light (Westoby et al., 2002; see Section 2.5 for further details).

Specifically, we tested the following three hypotheses (H1, H2 and H3):

- H1** Fertilization increases overyielding in mixed communities, with stronger effects in young tree communities with more high-SLA (hypothetically fast-growing) and tall species (hypothetically very competitive for light interception)

- H2** Fertilization increases CWM but decreases FD of both SLA and H due to increasing abundance of fast-growing species that are superior in competition for light
- H3** Fertilization increases overyielding indirectly through increasing abundance of fast-growing tree species superior in competition for light (CWM) rather than by mechanisms linked to higher diversity (FD)

2 | MATERIALS AND METHODS

2.1 | Replication statement

Scale of inference	Scale at which the factor of interest is applied	Number of replicates at the appropriate scale
Communities & Species population	Plots	Monocultures ($n=6$) and mixtures of two ($n=6$) and four species ($n=6$), with each of the 18 species compositions replicated 4 times under each of two fertilization treatments (fertilized, unfertilized), totalling 144 plots
Individuals	Plots	12–100 trees per treatment for H measurement (see Table S3) 6 trees per species-treatment group for SLA measurement (see Table S4)

2.2 | Study site

The study site is located in Freiburg, southwestern Germany (48°01'10" N/7°49'37" E, 240 m a.s.l.). The area is characterized by temperate oceanic climate (Köppen–Geiger classification: Cfb), with a mean annual temperature of 11.8°C and a mean annual precipitation of 832 mm (period from 1990 to 2018). The soil at the field site is a shallow, sandy-loamy Cambisol (40 cm) with high gravel content. Average available field capacity of the soil is 22.8% at 0 to 20 cm soil depth, and 19.4% at 20 to 40 cm soil depth. Prior to establishment of the experiment, the study site was used as a grass airfield between 1888 and 1992, and subsequently, the grassland was used for sheep grazing (Wein et al., 2016). No specific permits or licences were required for this fieldwork, as the experiment was conducted on land owned by the authors' institutions.

2.3 | Experimental design

This experiment is part of the International Diversity Experiment Network with Trees (IDENT; Tobner et al., 2014; Wein et al., 2016), which is part of TreeDivNet, the global network of tree biodiversity

experiments (Verheyen et al., 2016). IDENT experiments focus on the early stages of stand development and aim to investigate the role of tree species richness and functional diversity for ecosystem functioning. The experiment is characterized by a replicated design of high-density tree plots of fixed species richness levels varying in functional diversity (FD) (Figure S1). This decoupling between species richness and FD allows us to test the relative importance of community weighted mean trait values (CWM) and FD on ecosystem processes, which otherwise cannot be easily disentangled (Dias et al., 2013).

The general design of IDENT-Freiburg has been described in detail in Wein et al. (2016). In brief, in November 2013, nearly 20,000 tree seedlings were planted in 13 m² square plots of 7 × 7 individuals, with 45 cm spacing within and between rows of trees and 1.8-m corridors between plots. While the overall experiment includes a broader range of species and treatments, our study specifically focuses on six European temperate tree species: *Acer platanoides* L., *Betula pendula* Roth, B., *Quercus robur* L., *Larix decidua* Mill., *Picea abies* (L.) H. Karst. and *Pinus sylvestris* L. The target tree communities, composed of these six species, include monocultures and mixtures of two and four species. The species mixtures were developed to maximize an FD gradient for each species richness level. This design resulted in orthogonal variation between FD and tree species richness (see Table S1 for the detail of functional traits used to construct the functional diversity gradients; Appendix S1 for the detail of the FD calculation and the selection procedure of the species mixtures). Note that FD values were recalculated for our data analyses, using field-measured SLA and H (see Section 2.6).

The IDENT-Freiburg experiment is also designed to test the interaction of tree diversity with soil resources, namely, N and P. Thus, additional tree communities were planted and these plots received 130 g of elemental N and 65 g of elemental P in combination on an annual basis in the form of a granular fertilizer (i.e. 100 kg/ha and 50 kg/ha for N and P, respectively). Nitrogen was added in the form of ammonium nitrate and P in the form of Ca(H₂PO₄)₂. The total amount was applied in three doses per year (25% spring, 50% early summer, 25% late summer to early autumn). Soil mineral nitrogen stocks (i.e. ammonium- and nitrate-N) in the upper 20 cm of the soil profile are on average at 30.0 kg/ha for the non-fertilized plots, and at 40.3 kg/ha in the NP-fertilized plots. Average soil phosphate-P values range from 19.5 kg/ha in the non-fertilized, to 43.1 kg/ha in the NP-fertilized plots. For this study, we focused on all plots containing the six European species with NP co-addition and their corresponding non-fertilized plots, resulting in monocultures ($n=6$) and mixtures of two ($n=6$), and four species ($n=6$), with each of the 18 tree communities replicated four times in each of two fertilization treatments in a randomized block design (in total 144 plots). See Table S2 for more details on plot design and species composition in this study.

2.4 | Above-ground woody phytomass estimation

To estimate cumulative biomass production over the four growing seasons following tree planting in 2013, we used the community-level

(i.e. plot level) above-ground woody phytomass (branch + stem) of living and dead trees in the winter of 2017/18. Given the synchronized planting time and complete tracking of individual trees, standing phytomass after 4 years of growth served as a proxy for community productivity.

To estimate woody phytomass, we developed species-specific biomass equations by semi-destructive measurements (see Appendix S2, Figure S2 and Tables S10–S14 for complete details on biomass equations; Figures S3 and S5 for the estimated woody phytomass). Stem diameter is a standard predictor in biomass equations, but our approach uniquely incorporates the effects of experimental treatments, such as fertilization and species richness, on tree allometry. These treatment effects are often overlooked, yet they play a crucial role in accurately estimating productivity and understanding forest biodiversity–productivity relationships (Chisholm & Dutta Gupta, 2023).

Stem diameters were obtained from annual inventories conducted during the non-growing season. Stem diameter at 10 cm above ground (mm) was measured for all living trees in the central five rows and five columns (25 central trees) of each 7 × 7 tree plot. The outer trees served as buffer rows. Woody biomass of living trees was estimated based on stem diameter data collected at the end of winter 2017/18, while necromass of dead trees was estimated from the last year they were recorded alive. In total, stem diameter data were available for 3338 living trees in 2018 (out of 3600 initially planted) and 208 dead trees that died between 2016 and 2018. Dead trees that died before 2016 ($n=54$) were excluded because dead seedlings had been replanted in fall 2014 (Wein et al., 2016), making it difficult to distinguish early mortality due to establishment failure from treatment effects. Their contribution to total necromass was also negligible compared to the 2018 biomass of surviving trees.

2.5 | Tree height and specific leaf area

To evaluate community responses to fertilization, we focused on two functional traits: tree height (H, cm) and specific leaf area (SLA, mm² mg^{−1}). These traits reflect distinct axes of plant function and broadly correspond to the two-dimensional global plant trait spectrum (Díaz et al., 2016): SLA aligns with the leaf economics spectrum, while tree height relates to the plant size axis. However, whereas the global framework typically uses species-level maximum (adult) height to represent plant size, we used individual tree height measured 4 years after planting as a dynamic, realized trait that captures vertical growth directionality during early stand development, shaped by species identity, biotic interactions and environmental conditions.

We treated tree height as a process trait reflecting cumulative structural growth over time, and SLA as a pattern trait representing species' resource-use strategies at a given moment (sensu Volaire et al., 2020). The ecological function of organ-level traits like SLA is better understood in the context of whole-plant structure and

ontogenetic development (Laurans et al., 2024). For example, high SLA may enhance productivity only when paired with sufficient height to access light in crowded stands. By combining pattern and process traits, we aimed to assess how fertilization and species interactions influence productivity under light competition during early stand development (Eskelinen et al., 2022).

Tree height (H) was measured 4 years after planting, at the end of winter in 2017/18, for all 3338 living trees (Figure S7, Table S3). Height was defined as the shortest distance between the upper boundary of the main photosynthetic tissues on a tree and the ground level (Pérez-Harguindeguy et al., 2013). While H varies across individuals and increases over time, species' maximum height—typically reported in trait handbooks and databases (e.g. Pérez-Harguindeguy et al., 2013)—does not reflect necessarily the nonlinear trajectory of height growth, which is rapid in early development and slows with age (Bowman et al., 2013). To capture the vertical development of dynamically growing young trees over the first 4 years, we used realized H. In this study, growth is defined as community-level accumulation of above-ground woody phytomass, representing mass flow rate, while H reflects vertical flow velocity—how fast this growth is directed upward. Crucially, H was not used in phytomass calculation itself (instead stem diameter was used as a variable in the allometric equations to estimate phytomass), but only as an explanatory trait in CWM and FD metrics for predicting overyielding indices (D). This helped maintain, as much as possible, independence between predictor and response variables (see Sections 2.6–2.8) and justifying our classification of H as a process trait relevant to light competition.

For the determination of SLA and collection of leaf samples, we selected six trees per species and per species composition in each fertilization treatment (see Table S4). These sample trees were representative of the range of tree dimensions. Leaf samples were collected between July and September 2017. To account for within-crown leaf trait variations, crowns of the selected trees were divided into either two (upper and lower layers for species with relatively short crowns: *P. abies*, *P. sylvestris* and *Q. robur* with 1.5, 1.7 and 1.8 m average crown length, respectively) or three vertical layers (upper, middle and lower layers for species with relatively long crowns: *A. platanooides*, *B. pendula* and *L. decidua* with an average crown length of 3.2, 2.8 and 2.6 m, respectively) with equal intervals. One branch with fresh green leaves was harvested from each crown layer (see Appendix S2 for more details of the branch selection procedure, which was adjusted to develop species-specific branch/leaf biomass equations at the same time). To minimize potential phenological variation of leaf functional traits within species (Fajardo & Siefert, 2016), leaf sampling for all species in each block was done in a few weeks, and the time-lags in sampling between blocks (ca. 2.5 months, at maximum) were taken into account on the later analysis by including block effects in statistical models (see Section 2.8.2).

The SLA of each branch sample was calculated as the total projected area of leaves (excluding the petiole) or needles divided by their total dry leaf mass. When branches had many leaves, at least 20 leaves or 50 needles per branch were randomly chosen and

measured. For branches with few leaves, particularly in *A. platanooides* with small branch collar diameter, all leaves or needles were measured, with a minimum of two leaves per branch. To measure the one-sided area of leaves, we used the LI-3000A Portable Leaf Area Meter with the LI-3050A Transparent Belt Conveyor Accessory (Li-COR, Lincoln Ne, USA). Needles were scanned with an Epson Expression 10000XL flat-bed scanner (Tokyo, Japan), and the needle projected area was calculated with the software WinSEEDLE (Regent Instruments, Canada). Subsequently, leaf samples were dried to constant mass at 60°C for at least 48 h and weighed. Finally, mean tree-level SLA values for each of the 501 sampled trees were calculated by averaging SLA between crown layers (Figure S8).

2.6 | Calculation of functional diversity and community weighted means

Community functional trait structure was quantified for each mixture by functional diversity (FD) and community weighted means (CWM) of H and SLA. For the purposes of the study, we used FD based on measurements of H and SLA and not the FD that was calculated based on functional traits from the literature to establish the experiment (see Tobner et al., 2014 and Appendix S1).

Functional diversity was calculated as functional dispersion (FDis, Laliberté & Legendre, 2010; Tobner et al., 2014). Although FDis can be quantified on the basis of single and multiple traits, we used univariate FDis but not multivariate FDis, since multivariate trait indices do not allow one to directly identify the contribution of each trait to a specific ecosystem process (Roscher et al., 2012) and can obscure signals when traits included in their calculations have opposing effects (Spasojevic & Suding, 2012). To incorporate intraspecific trait variability, the trait probability density approach was applied (Carmona et al., 2016, 2019). Firstly, the distribution of trait values of each species population was estimated by kernel density functions. For H, the density functions were calculated for individual species at each of the mixture plots. For SLA, due to the small number of samples for each species per plot ($n = 2$), the density functions were calculated for each species-treatment group of five or six trees (see Table S4 for sample size of SLA in each species-treatment group). Secondly, the overlap between the kernel density function of each species pair in each treatment (each plot for H, each species-treatment group for SLA) was computed by the 'dissim' function from the 'TPD' package in R (Carmona et al., 2019). Finally, the overlap-based dissimilarity was used to calculate FDis by the 'fdisp' function from the 'FD' package (Laliberté & Legendre, 2010). The FDis values were weighted by the relative importance of species in mixtures using the species-specific contribution to above-ground biomass (leaf + branch + stem) of living trees in the end of winter in 2017/18 (see Appendix S2 for further details on biomass equations). Hereafter, FDis values of H and SLA are referred to as $FDis_H$ and $FDis_{SLA}$, respectively (see Figures S9 and S10 for mean values of $FDis_H$ and $FDis_{SLA}$ for each species composition).

Community weighted means of trait values (CWM) were defined as the mean trait value of all species present in the community weighted by the relative abundance of species (Garnier et al., 2004; Lavorel et al., 2008). In a similar fashion to FDis, the CWM was calculated with consideration for intraspecific trait variability according to the following equation (Lepš et al., 2011):

$$\text{CWM}_x = \sum_{k=1}^m p_k \times \text{trait}_x \quad (1)$$

where CWM_x is the CWM for trait x (hereafter, CWM values of H and SLA are referred to as CWM_H and CWM_{SLA} , respectively); m is the number of species in the community; p_k is the relative abundance of species k based on above-ground tree biomass in the community; trait_x are specific mean values of trait x for species k in the community. Due to the difference of data availability between H and SLA (Tables S3 and S4), trait_H values were calculated for individual species in each plot, while trait_{SLA} values were calculated for individual species in each of the 12 species compositions with multiple species in each of two fertilization treatments. Mean values of CWM_H and CWM_{SLA} for each species composition were presented in Figures S11 and S12.

2.7 | Biodiversity effects

To quantify overyielding in above-ground woody tree phytomass at the community and species levels for each species mixture and block, we used the proportional deviation approach (Loreau, 1998). The extent of overyielding (D) was assessed by the following equation:

$$D = \frac{O - E}{E} \quad (2)$$

where O is the observed yield in mixtures and E is the expected yield from their corresponding monocultures. For the extent of community-level overyielding (D_T), O is the total observed above-ground woody tree phytomass in a mixture and E is the average yield of the species participating in the mixture when grown in monocultures weighted by their initial relative abundance of species in mixtures (i.e. 0.5 for two species mixtures, 0.25 for four-species mixtures). Although our primary focus is D_T , we also included an assessment of transgressive overyielding as a complementary metric (D_{max}), where E is the maximum monoculture yield of the species found in a given mixture, providing additional insights for conservation applications (Chisholm & Dutta Gupta, 2023). For the extent of species-level overyielding (D_i), O is the observed above-ground woody phytomass of the species i in the mixture plot, and E is its expected value based on woody phytomass of the species i in monoculture, weighted by their initial relative abundance of species i in mixtures. Positive values of the D indices indicate overyielding (transgressive overyielding for D_{max}), while negative values indicate underyielding. The values of the D indices can also be used to compare mixtures that differ in species composition and fertilization

treatments, since these indices are standardized by their expected values.

2.8 | Data analysis

The first and second hypotheses were tested by linear mixed-effects models (Table S6), while the third hypothesis was tested by a piecewise structural equation model (pSEM, Lefcheck, 2016) based on linear mixed-effects models. All analyses were conducted in the statistical platform R 4.0.4 (R Core Team, 2021). Mixed-effects models were fitted using the 'lme' function in the 'nlme' package (Pinheiro et al., 2020); the piecewise structural equation model was fitted using the 'psem' function in the 'piecewiseSEM' package (Lefcheck, 2016). Residual plots of the statistical models are presented in Figures S18–S21.

To meet the normality and homogeneity assumptions for both linear mixed-effects models and pSEM, the proportional deviation of community-level and species-level above-ground woody phytomass (D_T and D_i) were transformed by taking their natural logarithm after adding 1 to all values; SLA and CWM_{SLA} values were natural logarithm and quadratic transformed, respectively. Note that the log-transformed proportional deviation with the shift value '1' is strictly equivalent to the log-transformed response ratio ($\log[RR]$, $\log[\text{observed/expected}]$) (Loreau, 1998). Although the p values of the test depend on how the added constant number is chosen (Feng et al., 2013), the non-arbitrary nature of this transformation can avoid the conclusion subjective to investigator's bias. To facilitate interpretation, we transformed $\log[RR]$ (i.e. $\log[D_T + 1]$ and $\log[D_i + 1]$) and its corresponding confidence intervals (CIs) back to percentage change using $(e^{\log[RR]} - 1) \times 100\%$.

2.8.1 | H1: Fertilization increases overyielding in mixed communities, with stronger effects in communities with more fast-growing (high SLA) and tall species (high H)

To test H1, we fitted a linear mixed-effects model (model M1 in Table S6) to assess the effect of fertilization (a binary variable: 0, unfertilized; 1, fertilized) on the proportional deviation of community-level above-ground woody phytomass ($\log[D_T + 1]$). Blocks (four levels, fixed effect) were included to account for spatial heterogeneity, and species composition (12 combinations, random effect) was included to account for repeated sampling of the same species mixtures. It should be noted that, although blocks can be fitted either as fixed or as random-effect terms, we fitted blocks as a fixed effect for all models throughout this paper (see Appendix S1 for biomass equations as an exception) because the four blocks of our experiment are not random samples from some larger population of blocks and because the number of levels is too low for a reliable estimation of a variance component (Dixon, 2016; Schmid et al., 2017). Furthermore, one plot with a

high standardized residual (-3.87 ; the *B. pendula* – *P. sylvestris* mixture without fertilization, having extremely low woody phytomass of *B. pendula*) was identified and removed from the analysis to capture the general trend of the dataset (see Figure S18, Table S7 for the analysis with the extreme value).

To assess effects of fertilization on the degree of community-level overyielding through species-level processes, we analysed species-level overyielding ($\log[D_i + 1]$), using a mixed-effects model that included fertilization treatments, species identity (six species), and their interaction as fixed effects (model M2 in Table S6). Plot identity nested within species composition was included as a random effect to account for repeated measurements.

2.8.2 | H2: Fertilization increases CWM but decreases FD of both SLA and H due to increasing abundance of fast-growing species that are superior in competition for light

Responses of community functional trait structure (i.e. CWM and FDis) to environmental factors can result not only from species turnover, which is related to the degree of species-level overyielding (D_i) in this study, but also from intraspecific trait variability (de Bello et al., 2011; Lepš et al., 2011). Thus, we first tested single and interactive effects of fertilization and species identity on each tree-level trait (H or log-transformed SLA), using mixed-effects models (model M3-a and M3-b in Table S6). To reduce residual heteroskedasticity, we weighted the model variance by species identity, using the function 'varIdent' in the 'nlme' package (Pinheiro et al., 2020). If the interaction term between fertilization and species identity was not significant, the interaction term was excluded from the model and each single term was tested.

In a next step, we tested fertilization effects on each of four community functional trait structure indices (CWM and FDis of H and SLA) by linear mixed-effects models with fertilization and blocks

as fixed effects and species composition as a random effect (model M4-a, M4-b, M4-c and M4-d in Table S6).

2.8.3 | H3: Fertilization increases overyielding indirectly through increasing abundance of fast-growing species superior in competition for light (CWM) rather than by mechanisms linked to higher diversity (FD)

To test for fertilization effects on the strength of community-level overyielding indirectly through fertilization-induced changes in community functional trait structure (i.e. CWM and FDis), we used a piecewise structural equation model (pSEM). Its pathways were constructed in accordance with the response-effect trait framework proposed by Lavorel and Garnier (2002), which formulates a unidirectional causal path from abiotic conditions to ecosystem functions via community functional trait structure. The pSEM included indirect paths from fertilization (a binary variable: 0, unfertilized; 1, fertilized) to community-level overyielding (D_T) via four indices of community functional trait structure (CWM and FDis of H and SLA). We also included a direct path from fertilization to D_T to test for mechanisms not mediated by community functional trait structure. Each individual pathway was fitted with a mixed-effects model including species composition as a random effect. Considering non-significant blocking effects on community functional trait structure and D_T in the models on the earlier analysis (see Tables 1 and 3), the blocking effect in our experimental design was not considered in the pSEM to reduce model complexity relative to the small sample size ($n = 95$) and avoid unreliable evaluation of the goodness-of-fit (Lefcheck, 2016). For each mixed-effects model, its residuals were graphically plotted to check for normality, homogeneity and outliers, and one outlier, which is the same as the one for the model M1 in Table S6, was identified and removed from the dataset (see Figure S14 for analysis with the extreme

TABLE 1 ANOVA tables of linear mixed-effects models testing the effects of fertilization on D_T (log-transformed) of community-level woody phytomass (type-II ANOVA) and the effects of fertilization and species identity on D_i of species-level woody phytomass (type-III ANOVA).

Response variables	Explanatory variables	Fixed effects			Random effects (standard deviation)				
		χ^2	df	Pr ($>\chi^2$)	SpComp	Plot (SpComp)	Rsd.	Marg. R^2	Cond. R^2
Community-level $\log(D_T + 1)$ $n = 95$	Block	2.83	3	0.418	0.15		0.19	0.04	0.40
	Fertilization	3.12	1	0.077					
Species-level $\log(D_i + 1)$ $n = 288$	Block	2.98	3	0.395	0.33	0.00	0.47	0.60	0.74
	Fertilization	14.03	1	0.000					
	Species ID	296.44	5	0.000					
	Fertilization $\times$ Species ID	21.66	5	0.001					

Abbreviations: Cond. R^2 , conditional coefficients of determination for both fixed and random effects; Marg. R^2 , marginal coefficients of determination for only fixed effects; Plot (SpComp), plots nested within species composition; Rsd., residual variance; SpComp, species composition. Shading is used to distinguish different models and improve readability.

value). Variance inflation factors (VIF) were calculated to address potential collinearity in the component model for D_T with multiple predictors. All VIF values were lower than three, indicating no severe multicollinearity (Dormann et al., 2013). The goodness-of-fit of pSEM was assessed by Fisher's C statistic, its associated p -value ($p > 0.05$ indicates adequate model fit) and the Akaike information criterion (AIC). We then checked the conditional independence claims of the pSEM with Shipley's test of directed separation (Shipley, 2000) to see whether there are no missing paths between community functional trait structure indices ($p < 0.05$ indicates missing paths). The identified missing relationships were included and specified as partial correlations in the pSEM to improve the model fit. Standardized regression coefficients for causal paths (beta) were reported, and those of indirect effects were obtained by multiplying the corresponding path coefficients.

To understand the community-level results of the pSEM through species-level processes, we fitted a mixed-effects model separately for each community functional trait structure index to test single, two-way, and three-way interactive effects of fertilization, species identity, and community functional trait structure on the strength of species-level overyielding ($\log[D_i + 1]$) (model M5-a, M5-b, M5-c, and M5-d in Table S6). Insignificant interaction terms were removed to develop the final models based on the comparison of nested models using the likelihood ratio test and maximum likelihood estimation.

3 | RESULTS

3.1 | Fertilization effects on community- and species-level above-ground woody phytomass

The magnitude of mean overyielding of community-level woody phytomass ($\log[D_T + 1]$) increased marginally with fertilization ($p < 0.1$, Figure 1, Table 1). On average, tree species mixing increased community-level woody phytomass by 21.4% (95% CI, 6.4–38.6%) over those expected from monocultures in fertilized plots, while there was no significant species mixing effect in unfertilized plots (13.3%, 95% CI = [−0.8]–29.3%). Further, nine out of 12 mixtures showed neutral effects of tree species mixing, while the other three mixtures showed significant overyielding in both unfertilized and fertilized plots or in either of them (Figure 2). No mixtures, however, showed significant transgressive overyielding (Figure S4).

The mean degree of species-level overyielding ($\log[D_i + 1]$) varied with species identity and fertilization treatments (Figure 3, S6, Table 1). Fertilization shifted the tree species mixing effects on species-level woody phytomass from negative to neutral for *A. platanoides* ($p < 0.05$, from underyielding of 43.7% [CI: 7.6%–65.7%] to 6.9% [CI: −52.8% to 43.3%]) and *Q. robur* ($p < 0.1$, from underyielding of 50.3% [CI: 18.4%–69.8%] to 29.2% [CI: −16.4% to 56.9%]). In contrast, *B. pendula* consistently showed overyielding regardless of fertilization (151.6% [CI: 56.5%–304.6%] unfertilized; 160.8% [CI: 62.3%–319.5%] fertilized), *L. decidua* remained neutral (overyielding of 43.7% [CI: −14.8% to 142.4%] unfertilized; 28.0% [CI: −24.1% to

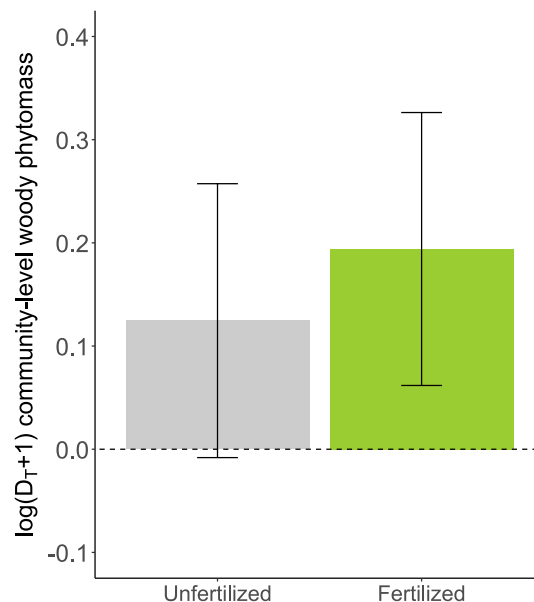


FIGURE 1 Marginal mean proportional deviation of community-level woody phytomass ($\log[D_T + 1]$) in unfertilized and fertilized mixed-species plots in relation to monospecific plots. The zero line separates positive from negative species-mixing effects. Positive values indicate that a community produced more woody phytomass in mixture than expected from monoculture, and negative values indicate the opposite. Vertical bars indicate the marginal means and their 95% confidence intervals, estimated from the model in Table 1 and adjusted by the Šidák method (Šidák, 1967) for two estimates. Results are averaged over the levels of blocks.

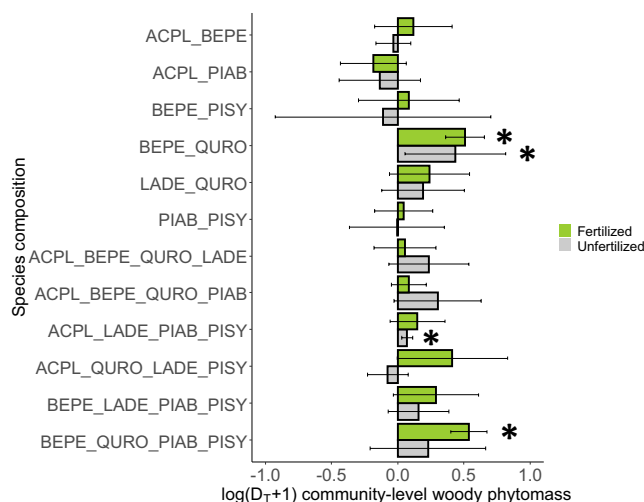


FIGURE 2 Mean proportional deviation of community-level woody phytomass ($\log[D_T + 1]$) for each species composition. The zero line separates positive from negative species-mixing effects. Positive values indicate that a community produced more woody phytomass in mixture than expected from monoculture, and negative values indicate the opposite. Horizontal bars indicate 95% confidence intervals. * denotes significant differences from zero. Species codes are ACPL—*Acer platanoides*, BEPE—*Betula pendula*, LADE—*Larix decidua*, PIAB—*Picea abies*, PISY—*Pinus sylvestris*, QURO—*Quercus robur*.

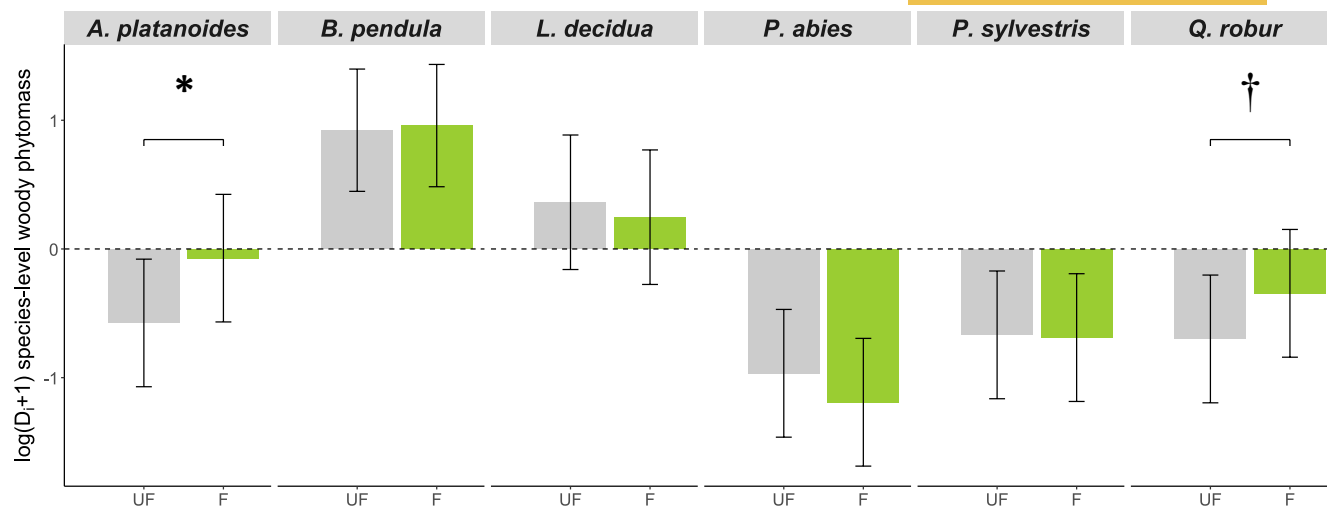


FIGURE 3 Marginal mean proportional deviation of species-level woody phytomass ($\log(D_i + 1)$) in unfertilized (UF, grey colour) and fertilized (F, green colour) mixed-species plots in relation to monospecific plots. The zero line separates positive from negative species-mixing effects. Positive values indicate that a species produced more woody phytomass in mixture than expected from monoculture, and negative values indicate the opposite. Vertical bars indicate the marginal means and their 95% confidence intervals, estimated from the model in Table 1 and adjusted by the Šidák method (Šidák, 1967) for 12 estimates. * and † denote significant ($p < 0.05$) and marginal ($p < 0.1$) differences between fertilization treatments, respectively, with the p values adjusted by the Šidák method for six tests. Results are averaged over the levels of blocks.

115.9%] fertilized) and negative for *P. abies* and *P. sylvestris* showed consistent underyielding (*P. abies*: 62.0% [CI: 37.5%–76.8%] unfertilized, 69.6% [CI: 50.1%–81.5%] fertilized; *P. sylvestris*: 48.7% [CI: 15.7%–68.8%] unfertilized, 49.8% [CI: 17.5%–69.4%] fertilized).

3.2 | Responses of H and SLA to fertilization

Tree height (H) and specific leaf area (SLA) varied substantially among species (Figure 4, Figures S7 and S8). Fertilization increased H of *A. platanoides* (Šidák post hoc test for six contrasts, $t = -3.06$, $df = 122$, $p < 0.05$) but did not have statistically detectable effects on H of the other five species (Figure 4, Table 2). Fertilization had no significant effect on SLA in any individual species, after controlling for the significant effect of the time-lags in leaf sampling between blocks (i.e. the significant Block effect, $p = 0.001$, Table 2). At the community level, CWM_{SLA} (quadratic-transformed) significantly increased under fertilization ($p < 0.001$), while other indices of community functional trait structure did not vary significantly among fertilization treatments (Figure 5, Table 3).

3.3 | Linkages between fertilization, community functional trait structure and above-ground woody phytomass in mixtures relative to monocultures

Overall, our piecewise structural equation model assessing the direct and indirect effects of fertilization on the degree of community-level overyielding ($\log(D_T + 1)$) showed a good fit (Fishers' $C = 1.33$, $df = 2$, $p = 0.52$) and accounted for 42% of the marginal variation in $\log(D_T + 1)$ (Figure 6, Figure S13). Fertilization had a significant

indirect negative effect on $\log(D_T + 1)$ through quadratic-transformed CWM_{SLA} ($\beta = -0.05$), while indirect fertilization effects through other community functional trait structure indices were not significant. Fertilization also had a significant direct positive effect ($\beta = 0.14$, $p < 0.05$) on $\log(D_T + 1)$.

To complement the pSEM analysis, four separate linear mixed-effect models were fitted to test individual effects of each community functional trait structure index (CWM and FDis) on the performance of each species in mixtures (i.e. $\log(D_i + 1)$), using H and SLA (Figures S16 and S17, Table 4). All of the four selected models included significant interactions between CWM or FDis and species identity on $\log(D_i + 1)$, indicating that the effects of CWM and FDis on species performance in mixtures hinged on species identity. There were significant positive effects of $FDis_H$ and $FDis_{SLA}$ on the $\log(D_i + 1)$ of *P. abies*, but not in other species. The CWM_H had a significant positive effect on the $\log(D_i + 1)$ of *B. pendula* and a significant negative effect on the $\log(D_i + 1)$ of *P. sylvestris*. The quadratic-transformed CWM_{SLA} had a significant negative effect on the $\log(D_i + 1)$ of *L. decidua* and *P. sylvestris*. Moreover, across all species, an interaction between quadratic-transformed CWM_{SLA} and fertilization had significant effects on $\log(D_i + 1)$ (Figure S17, Table 4): the quadratic-transformed CWM_{SLA} had no significant effect on $\log(D_i + 1)$ in unfertilized plots (95% CI for the slope estimate, $[-0.002] - 0.001$) but had a significant negative effect in fertilized plots (95% CI for the slope estimate, $[-0.004] - [-0.000]$), which is consistent with the indirect negative fertilization effect on community-level performance in mixtures (i.e. D_T) through CWM_{SLA} , tested by the piecewise structural equation model (Figure 6).

To test whether the effects of CWM and FD were independent of species richness, we conducted supplementary analyses by

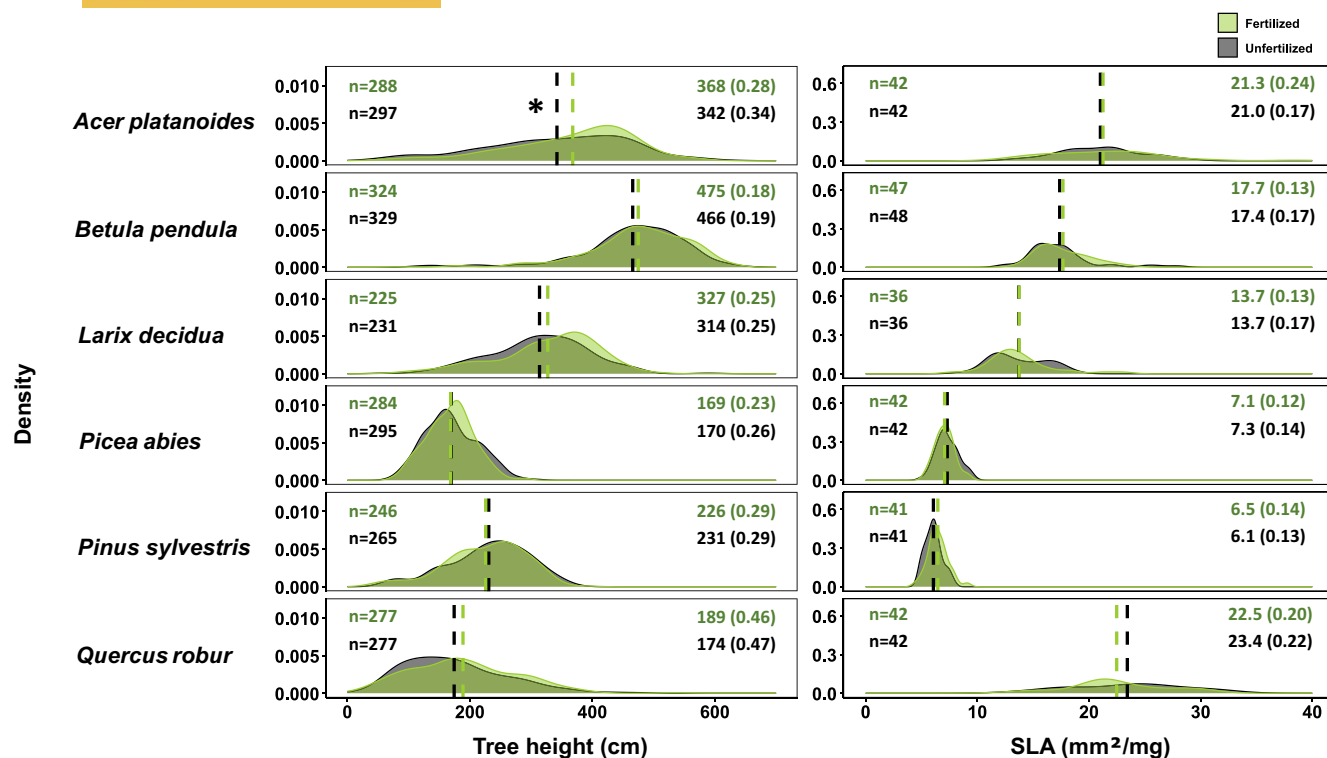


FIGURE 4 Distributions of tree height (left) and specific leaf area (SLA, right) in unfertilized (black colour) and fertilized plots (green colour), illustrated by Kernel density curves. Vertical dotted lines and numbers at the right side of each panel indicate the mean values (with coefficient of variation in parenthesis) of the distributions. * denotes significant differences between fertilization treatments (Šidák post hoc test for six contrasts, $p < 0.05$).

adding species richness as an additional random effect to the pSEM (testing effects on $\log[D_T + 1]$) and the linear mixed-effects models (testing effects on $\log[D_i + 1]$) described above. In these supplementary models, the hierarchical structure of the experimental design was fully considered, with plots nested within species compositions, which were in turn nested within species richness levels. The results, presented in Figure S15 and Table S8, confirmed that the observed effects of CWM and FD on overyielding were robust and not attributable to species richness differences.

4 | DISCUSSION

Although community functional trait structure is often a useful predictor of tree mixture effects on productivity (Zheng et al., 2021), experimental evidence on how the relative importance of CWM and FD varies across environmental conditions remains scarce. In our young tree diversity experiment, fertilization effects on overyielding depended strongly on species composition. Nonetheless, overyielding was associated with two key CWM traits: higher CWM_H (dominance of species with fast height growth) increased community-level overyielding, whereas higher CWM_{SLA} (dominance of acquisitive, high-SLA species) reduced it. In contrast, FDIs had no significant effect, highlighting the predominance of selection effects over complementarity. Moreover, CWM_{SLA} mediated the impact of fertilization: fertilization increased the abundance

of high-SLA species, thereby decreasing overyielding. This reveals a specific mechanism—beyond patterns alone—by which environmental conditions shape community functional trait structure and drive context-dependent diversity–productivity relationships.

4.1 | The influence of fertilization on overyielding depends on species composition and identity

Partially confirming our first hypothesis, we found that fertilization marginally increased the degree of community-level overyielding (i.e. $\log[D_T + 1]$) averaged over all species assemblages, while the positive fertilization effects at the community level were not necessarily linked to growth responses of faster growing (high SLA) and competitive species (high H). Only three out of 12 mixtures showed significant overyielding (but not transgressive overyielding) in both unfertilized and fertilized plots (i.e. the *B. pendula* – *Q. robur* mixtures) or in either of them (i.e. the *A. platanoides* – *L. decidua* – *P. abies* – *P. sylvestris* mixtures without fertilization; the *B. pendula* – *Q. robur* – *P. abies* – *P. sylvestris* mixtures with fertilization) (Figure 2); in all the cases, the absolute values of overyielding were higher in the fertilized plots. These different community-level responses may result from different species-level responses to fertilization. Fertilization had positive effects on species-level overyielding only in *Q. robur* and *A. platanoides* (i.e. species with the highest and second highest SLA values, respectively; Figures 3 and 4), which reflects that

significant community-level overyielding in fertilized plots occurred only if one of these species was included in the mixture. Yet not every mixture with one of these two species performed significantly better with fertilization.

The marginal positive fertilization effects on the strength of community-level overyielding averaged over all species compositions could result from accelerated tree growth by fertilization, which translates into faster stand development. It has been shown that tree diversity effects on tree growth and forest productivity tend to strengthen with stand development and age (Guerrero-Ramírez et al., 2017; Huang et al., 2018; Jucker et al., 2020; Tatsumi, 2020; Zheng et al., 2024). For example, tree diversity effects on tree growth tended to shift from negative to positive during stand development in boreal forests and the turning point coincided with the period of canopy closure (Jucker et al., 2020). Considering that the time needed to reach a given stage of stand development can be reduced by fertilization (Snowdon, 2002), fertilized stands could reach the stage of canopy closure earlier than unfertilized stands. The high initial planting density in our experiment, which led to rapid canopy closure regardless of fertilization, may explain the marginally positive fertilization effect on the extent of overyielding. It is also worth noting that fertilization not only may advance stand development but also may increase the site carrying capacity for biomass (Snowdon, 2002). Thus, future studies may address if fertilization may have influenced the absolute level of overyielding.

4.2 | Fertilization modifies community functional trait structure via increasing abundance of species with high SLA

Although we expected that fertilization increases CWM but decreases FD of both SLA and H (H2), this was only the case for CWM_{SLA} (Figure 5, Table 3). Responses of CWM trait values to

changes in environmental variables can be due to changes in either or both of the relative abundance of species with different trait values and intraspecific trait variability (Lepš et al., 2011). Considering that fertilization did not affect species-level SLA in our study, in accordance with a previous meta-analysis focusing on N addition (Zhang et al., 2018), the significant positive

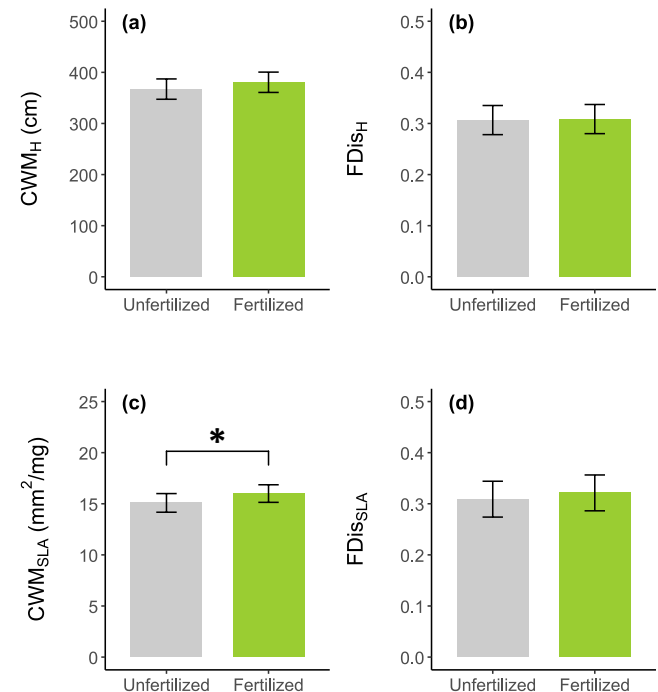


FIGURE 5 Responses of community functional trait structure (a: community weighted means [CWM] of tree height [H], b: functional dispersion [FDis] of H, c: CWM of specific leaf area [SLA, back-transformed after quadratic transformations for analysis], d: FDis of SLA) to fertilization. Vertical bars indicate marginal mean values $\pm$ standard error obtained from the models in Table 3. * denotes significant differences between fertilization treatments, $p < 0.05$. Results are averaged over the levels of blocks.

TABLE 2 ANOVA tables of linear mixed-effects models testing the effects of fertilization and species identity on tree height and SLA (type-III ANOVA for the height model; type-II ANOVA for the SLA model).

Response variables	Explanatory variables	Fixed effects			Random effects (standard deviation)				
		χ^2	df	Pr ($>\chi^2$)	SpComp	Plot (SpComp)	Rsd.	Marg. R^2	Cond. R^2
Tree height <i>n</i> = 3338	Block	3.00	3	0.392	30.98	13.39	108.39	0.56	0.60
	Fertilization	9.37	1	0.002					
	Species ID	3594.08	5	0.000					
	Fertilization $\times$ Species ID	16.89	5	0.005					
log(SLA) <i>n</i> = 501	Block	13.18	2	0.001	0.05	0.02	0.20	0.85	0.86
	Fertilization	0.46	1	0.496					
	Species ID	3713.58	5	0.000					

Abbreviations: Cond. R^2 , conditional coefficients of determination for both fixed and random effects; Marg. R^2 , marginal coefficients of determination for only fixed effects; Plot (SpComp), plots nested within species composition; Rsd., residual variance; SpComp, species composition. Shading is used to distinguish different models and improve readability.

TABLE 3 ANOVA tables (type-II ANOVA) of linear mixed-effects models testing the effects of fertilization on community weighted means (CWM) and functional dispersion (FDis) of tree height (H) and specific leaf area (SLA).

Response variables	Explanatory variables	Fixed effects			Random effects (standard deviation)			
		χ^2	df	Pr(> χ^2)	SpComp	Rsd.	Marg. R^2	Cond. R^2
CWM_H	Block	6.96	3	0.073	65.72	41.43	0.03	0.72
n=96	Fertilization	2.49	1	0.114				
(CWM_SLA) ²	Block	3.42	3	0.332	94.53	24.66	0.02	0.94
n=96	Fertilization	31.82	1	0.000				
FDis_H	Block	3.21	3	0.360	0.10	0.05	0.01	0.76
n=96	Fertilization	0.03	1	0.856				
FDis_SLA	Block	6.30	3	0.098	0.12	0.07	0.02	0.73
n=96	Fertilization	0.70	1	0.403				

Abbreviations: Cond. R^2 , conditional coefficients of determination for both fixed and random effects; R^2 , marginal coefficients of determination for only fixed effects; Rsd., residual variance; Marg. SpComp, species composition. Shading is used to distinguish different models and improve readability.

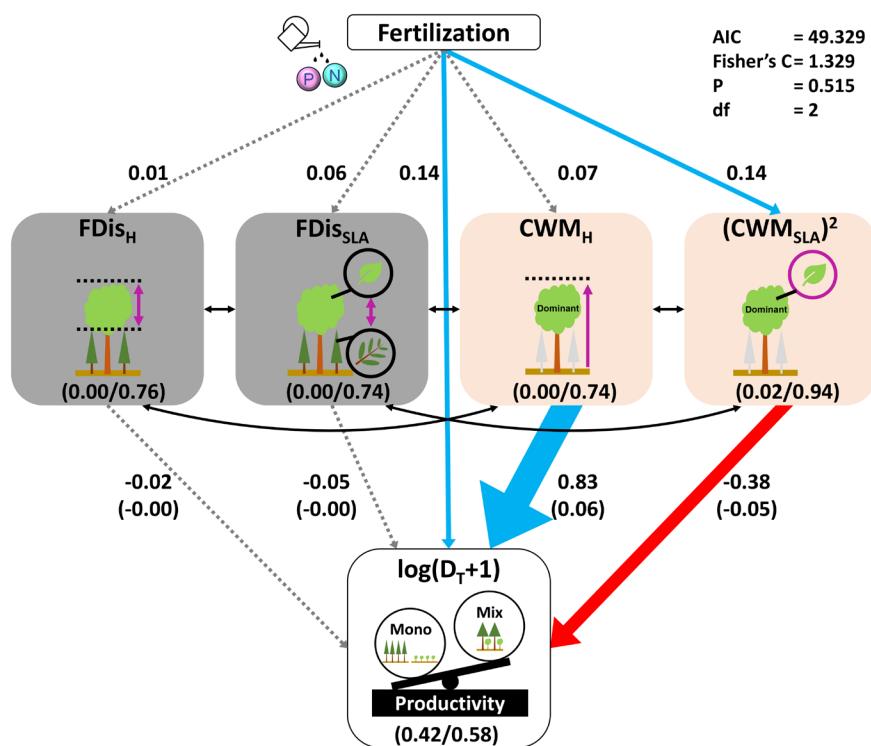


FIGURE 6 The piecewise structural equation model for testing the effects of fertilization (a binary variable: 0, unfertilized; 1, fertilized) on the proportional deviation ($\log[D_T + 1]$) of community-level woody phytomass in mixed-species plots in relation to monospecific plots via community weighted means (CWM) and functional dispersion indices (FDis) of tree height (H) and specific leaf area (SLA). The random effect was species composition. Numbers of single-headed arrows indicate standardized effect sizes (β), and the strength of the indirect effect of fertilization on D_T is listed in parentheses. Black double-headed arrows between endogenous variables (i.e. CWM and FDis) indicate significant partial correlations that remove the effect of fertilization. Solid lines show significant paths ($p < 0.05$) and grey dotted lines show non-significant paths ($p > 0.05$). The colours of single-headed solid arrows represent the direction of effect (red colour for negative and blue colour for positive effects), and path width is proportional to standardized effect sizes. For each endogenous variable, the marginal coefficient of determination for only fixed effects (left in parentheses) and the conditional coefficient of determination for both fixed and random effects (right in parentheses) are listed. Model-fit statistics (Fisher's C, p-value, degree of freedom and AIC) for the piecewise structural equation model are given.

TABLE 4 ANOVA tables of linear mixed-effects models testing the effects of fertilization and community functional trait structure on D_i (log-transformed) of species-level woody phytomass (type-III ANOVA).

Response variables	Explanatory variables	Fixed effects			Random effects (standard deviation)				
		χ^2	df	Pr (> χ^2)	SpComp	Plot (SpComp)	Rsd.	Marg. R^2	Cond. R^2
Model with CWM of tree height									
Species-level	Block	3.43	3	0.330	0.25	0.00	0.44	0.66	0.74
$\log(D_i + 1)$	Fertilization	15.36	1	0.000					
	Species ID	29.18	5	0.000					
$n = 288$	CWM_H	0.00	1	0.977					
	Fertilization $\times$ Species ID	21.20	5	0.001					
	Species ID $\times$ CWM_H	37.56	5	0.000					
Model with (CWM of SLA) ²									
Species-level	Block	2.17	3	0.537	0.23	0.00	0.43	0.67	0.75
$\log(D_i + 1)$	Fertilization	14.57	1	0.000					
	Species ID	101.15	5	0.000					
$n = 288$	(CWM_SLA) ²	0.65	1	0.418					
	Fertilization $\times$ Species ID	22.04	5	0.001					
	Fertilization $\times$ (CWM_SLA) ²	3.85	1	0.050					
	Species ID $\times$ (CWM_SLA) ²	52.13	5	0.000					
Model with FDis of tree height									
Species-level	Block	2.51	3	0.473	0.36	0.00	0.45	0.61	0.76
$\log(D_i + 1)$	Fertilization	15.02	1	0.000					
	Species ID	85.56	5	0.000					
$n = 288$	FDis_H	0.25	1	0.616					
	Fertilization $\times$ Species ID	21.37	5	0.001					
	Species ID $\times$ FDis_H	17.05	5	0.004					
Model with FDis of SLA									
Species-level	Block	2.52	3	0.472	0.38	0.45	0.42	0.61	0.77
$\log(D_i + 1)$	Fertilization	13.36	1	0.000					
	Species ID	137.29	5	0.000					
$n = 288$	FDis_SLA	0.73	1	0.393					
	Fertilization $\times$ Species ID	18.20	5	0.003					
	Species ID $\times$ FDis_SLA	18.49	5	0.002					

Abbreviations: Cond. R^2 , conditional coefficients of determination for both fixed and random effects; CWM, community weighted means; FDis, functional dispersion; H, tree height; Marg. R^2 , marginal coefficients of determination for only fixed effects; Marg. Rsd., residual variance; Plot (SpComp), plots nested within species composition; Rsd., residual variance; SLA, specific leaf area; SpComp, species composition. Shading is used to distinguish different models and improve readability.

fertilization effect on CWM_{SLA} must have resulted mostly from changes in species abundances (in terms of above-ground woody phytomass). In fact, fertilization tended to improve the strength of species-level overyielding (D_i) of species with high SLA, *A. platensis* and *Q. robur*. In line with our results, some grassland studies also reported that nutrient enrichment increased community-level SLA (Dwyer et al., 2014; Li et al., 2017). Specifically, Dwyer

et al. (2014) concluded that the community-level SLA increased by P enrichment resulted from competitive exclusion and species turnover caused by high-SLA species in diverse annual plant communities in southwestern Australia. However, this trend appears to depend on the environmental context. For instance, the effects of N fertilization on CWM_{SLA} were inconsistent (i.e. positive or no effects) over four consecutive years in an alpine meadow (Zhou

et al., 2018). Furthermore, leaf mass per area (LMA, inverse of SLA) of 7-year-old saplings in three temperate tree species responded differently to N addition, depending on drought stress and species identity (Zhang et al., 2020). Moreover, SLA increased with decreasing light access (to the leaf in question) due to increasing community diversity (i.e. species richness and functional difference in shade tolerance between the focal and other species in a community) (Williams et al., 2020). Thus, better understanding of fertilization effects on CWM trait values and the underlying mechanisms (i.e. changes in species turnover, composition, abundance or intraspecific trait variation) requires to further take into account temporal variation and multiple environmental factors (e.g. drought stress and light availability).

In contrast to CWM, FD_{is_H} and $FD_{is_{SLA}}$ did not respond to fertilization (Figure 5, Table 3). This might relate to the short experimental period and/or to environmental factors other than nutrient enrichment. The divergence of FD is theoretically predicted to be maximal at intermediate levels of competition or community biomass accumulation, when the negative effect of competition on the fitness of plant species with non-optimal trait values is balanced by other environmental factors (e.g. drought stress; Navas & Violle, 2009). Under the assumption of the hump-shaped response of FD, the young tree communities in our experiment could be placed at the early stage of biomass accumulation (4 years after planting), that is, in the process of maximizing FD. Nevertheless, fertilization would accelerate biomass accumulation, stand development (Snowdon, 2002) and thus the time of emergence of trait divergence in communities. Indeed, although overyielding was exhibited mainly by mixtures containing *B. pendula*, fertilization tended to increase the magnitude of species-level overyielding of *A. platanooides* and *Q. robur* (Figure 3). This result indicates that different species, either superior in competition (*B. pendula*) or in adapting to other environmental factors (*A. platanooides* and *Q. robur*), may coexist. More specifically, *A. platanooides* and *Q. robur* experienced lower mortality than *B. pendula* after the extreme drought in our experiment in the summer of 2018, just 1 year after the data collection of our study (Hajek et al., 2022). Taken together, both fertilization and drought are likely to increase the fitness of *A. platanooides* and *Q. robur* over that of *B. pendula*, which might lead to higher FD in later stages of stand development. Note that fertilization generally reduces plant diversity through light competition (Eskelinen et al., 2022), likely leading to trait convergence within communities. We expect this trait convergence to occur under a more favourable environment, that is, where the impact of competition on plant fitness largely prevails over that of other environmental factors (e.g. drought).

4.3 | Fertilization reduces the magnitude of community-level overyielding indirectly via increasing abundance of species with high SLA

In contrast to our third hypothesis, fertilization reduced the extent of community-level overyielding indirectly through changes

in CWM_{SLA} . This negative indirect effect may have resulted from a reduced overyielding of lower-SLA species suppressed by high-SLA species. Fertilization tended to improve the extent of species-level overyielding in species with high SLA (*A. platanooides* and *Q. robur*, see Figure 3), while the strength of species-level overyielding in *L. decidua* and *P. sylvestris*, which had lower mean SLA values than *A. platanooides* and *Q. robur*, decreased with increasing CWM_{SLA} (Figure S17b). Irrespective of fertilization treatments, we showed that at this stage of stand development CWM was a better predictor of community-level overyielding than FDis. The effects of CWM_H and CWM_{SLA} on the strength of community-level overyielding were significant, while the effects of FDis were insignificant (Figure 6). These results indicate that the traits (i.e. H and SLA) of the most abundant species in plant communities could drive community-level overyielding, supporting the mass ratio hypothesis (Grime, 1998). Regarding CWM and FD as metrics representing selection and complementarity effects, respectively (Cadotte, 2017; Roscher et al., 2012; Tobner et al., 2016), selection effects seem to be prevailing over complementarity effects in our young tree experiment. In fact, the strong positive relationship of community-level overyielding with CWM_H in our experiment indicates that overyielding was exhibited mainly by mixtures containing *B. pendula*, which is the tallest of the six examined species (Figure 4) and the only species showing significant species-level overyielding (Figure 3). Note that neither H nor abundance (in terms of D_i) of *B. pendula* responded to fertilization (Figures 3 and 4, Table 2), which could explain the insignificant response of CWM_H to fertilization. In line with our results, previous studies reported that CWM can be a better predictor than FD in explaining productivity of young tree communities in a glasshouse experiment (Luo et al., 2020) and a field experiment (Tobner et al., 2016). Given that the importance of complementarity effects on overyielding increase with time (Belluau et al., 2021; Huang et al., 2018; Tatsumi, 2020), our four-year-old experimental stand might be too young to observe a possible predictive power of FD on community-level overyielding. This would be in accordance with recent research in a young forest biodiversity experiment in subtropical China where the effects of CWM values on stand productivity were greater than the effects of FD values during the first 6–7 years of forest growth, but FD effects exceeded CWM effects afterwards (Bongers et al., 2021). Similarly, Urgoiti et al. (2022) also showed that FD of resource-acquisition traits progressively increased the magnitude of overyielding from year 6 in another young IDENT tree diversity experiment spanning 11 years of stand development.

While our analysis revealed a strong association between community-level overyielding and CWM_H , this relationship may raise concerns about statistical circularity. Although H itself was not used as a variable to estimate phytomass, it is usually closely correlated with stem diameter—the variable used in phytomass estimation. Using CWM_H to explain overyielding indices derived from diameter-based phytomass could therefore introduce statistical dependence. Nevertheless, the observed effects of CWM_H likely

reflect ecological mechanisms beyond size correlation, since height and stem diameter capture distinct ecological functions: H reflects a tree's competitive status for light, while stem diameter relates more to mechanical stability and resource transport. Even within species, individuals differing in competitive status can have very different height–diameter relationships—dominant trees with low, and suppressed trees with high height-to-diameter ratios (Sumida et al., 2013). In our study, species composition also influenced height–diameter ratios (see Figure S22, Table S9), reinforcing the functional distinctiveness of these traits. To further reduce circularity in future work, researchers could separate trait and biomass measurements across matched plots under identical treatments (e.g. the approach by Fichtner et al., 2018), or directly measure above-ground biomass using methods such as terrestrial laser scanning.

One of the remaining questions our experiment could address is how fertilization can modify the emergence of FD effects on the strength of overyielding. This question may be better tackled by understanding fertilization effects on species coexistence and its consequences on productivity. Given that the mechanisms determining stable species coexistence could correlate with those promoting high productivity (Barry, de Kroon, et al., 2019; Godoy et al., 2020), divergence of FD (i.e. one of the consequences of species coexistence) may lead to the emergence of FD effects on overyielding. The divergence of FD is theoretically expected to be maximal at intermediate levels of community biomass accumulation (Navas & Violle, 2009) and could be accelerated by fertilization in our young tree communities (see discussion in Section 4.2. for the rationale). Thus, we assume that significant FD effects on the strength of overyielding might appear in fertilized plots earlier than in unfertilized plots. However, in an environment more favourable for growth than our experiment (e.g. more humid sites), fertilization may largely intensify competition for light among species (Eskelinen et al., 2022), leading to the dominance of species with competitive trait values (e.g. tall/fast-growing species) and thus to the cancellation of the emergence of FD effects on productivity. Note that the species richness gradients and species composition in our experiment are not modelled after naturally occurring tree communities, which may not reflect species interactions under natural conditions and may thus over-/underestimate the real-world impacts of tree diversity on productivity (Chen et al., 2020). Accordingly, realistic trait convergence/divergence processes in response to fertilization and the consequences on productivity could be better addressed by experimental evaluations based not only on random but also on nonrandom/trait-oriented community assembly scenarios (e.g. species richness gradients derived from species pools with decreasing SLA, Bruelheide et al., 2014).

Another important question for future studies is how multiple environmental factors simultaneously influence the relationship between community functional trait structure and overyielding. For example, the FD effect on above-ground biomass overyielding was more strongly pronounced under high-water availability in a young tree experiment within the IDENT framework (Belluau et al., 2021). Furthermore, an interactive effect of nutrient addition and drought on overyielding in a young mixed tree stand also depended on tree

species composition (i.e. trait combination; Dzedek et al., 2016). However, the combined effects of N addition and drought on community functional trait structure and their indirect effects on overyielding were not addressed explicitly. Therefore, future studies should take into account simultaneous limiting factors to further understand the relationship between community functional trait structure and overyielding.

Lastly, the observed direct fertilization effects on the extent of community-level overyielding, along with the higher conditional R^2 values compared to marginal ones in the submodels of the pSEM—indicating substantial effects of species composition as random effects—suggest that the examined traits (i.e. H and SLA) and their distribution in communities (i.e. CWM and FDis) capture only part of community- and species-level responses to fertilization and their effects on overyielding. Assuming that fertilization fosters asymmetric competition for light between species, we used H and SLA, two traits strongly related to tree growth rate and light acquisition strategies. However, there are other dimensions that define plant strategies to grow and acquire resources, particularly below-ground, such as the collaboration gradient (Bergmann et al., 2020) and the plant size gradient for rooting depth (Weigelt et al., 2021). Furthermore, although most studies, including ours, focused on the mean (CWM) and the dispersion (FD) of the trait distribution in a community, which are linked to the two well-studied hypotheses of the biodiversity–ecosystem functioning relationship (i.e. the mass ratio hypothesis and the niche complementarity hypothesis), the shape of complex trait distributions deviating from normal distributions (i.e. skewness and kurtosis) is increasingly used to improve our understanding of community assemblage rules (e.g. Gross et al., 2021; Le Bagousse-Pinguet et al., 2017; Wiczyński et al., 2018) and plant community effects on ecosystem processes (e.g. Brun et al., 2022; Enquist et al., 2015, 2017; Gross et al., 2017; Zhang et al., 2019). Ultimately, to accurately quantify the full distribution of traits in a community, measuring the traits of all individuals, which was not done for SLA in our study, would be ideal (but see Enquist et al., 2015 for methods to approximate community trait distributions without measuring the traits of all individuals). Collectively, for more robust evidence as to tree community responses to nutrient additions and their impacts on the extent of tree overyielding, future work should consider additional traits and the shape of trait distributions which were not investigated in our study.

5 | CONCLUSIONS

Our young tree diversity experiment highlights that the relationship between tree diversity and productivity varies with nutrient enrichment, shedding light on one important aspect of the context dependence of biodiversity–functioning relationships. Fertilization tended to increase productivity of species with high SLA in mixtures relative to monoculture. This fertilization-induced dominance of high-SLA species led to community-level overyielding in some, but not all mixtures including these species. We could further demonstrate

that fertilization reduced the degree of community-level overyielding indirectly through dominance of species with high SLA, which could not compensate the concurrent decreases in yield of low SLA species.

These early stage shifts in interspecific interactions driven by nutrient enrichment may accumulate over time, potentially shaping forest stand structures and future species interactions. Such cumulative changes may become more pronounced in naturally regenerating forests with fewer silvicultural interventions to shape tree species composition. Future research should investigate these processes over longer time-scales and under various forest conditions to better predict the successful establishment and biomass production of mixed-species forests at later successional stages.

AUTHOR CONTRIBUTIONS

Peter B. Reich is one of the initiators of the IDENT experiment network and co-designed the diversity treatments of the IDENT-Freiburg experiment. Jürgen Bauhus and Michael Scherer-Lorenzen developed the design of the IDENT-Freiburg diversity $\times$ fertilization trial and maintained it together with Charles A. Nock; Jürgen Bauhus, Dai F. Saito and Michael Scherer-Lorenzen acquired funding for the presented study; Jürgen Bauhus, Grégoire T. Freschet, Charles A. Nock, Dai F. Saito and Michael Scherer-Lorenzen designed the presented study; Charles A. Nock was responsible for yearly inventory data; Anja Klingler and Dai F. Saito conducted field sampling and the laboratory work under guidance from Jürgen Bauhus, Grégoire T. Freschet, Charles A. Nock and Michael Scherer-Lorenzen; Dai F. Saito analysed the data with contributions from the other authors; Dai F. Saito wrote the first draft of the manuscript with support from Friderike Beyer and Jürgen Bauhus. All authors contributed to the writing.

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CONFLICT OF INTEREST STATEMENT

The authors declare they have no conflict of interest.

DATA AVAILABILITY STATEMENT

Data files and R scripts deposited in the Dryad Digital Repository: <https://doi.org/10.5061/dryad.n5tb2rc94> (Saito et al., 2026).

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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. Relationships between species richness, functional dispersion, and community-weighted mean traits.

Figure S2. Tree sampling procedure for biomass equations.

Figure S3. Mean community-level woody phytomass for each species composition.

Figure S4. Degree of transgressive overyielding for each species composition.

Figure S5. Mean species-level woody phytomass for each species composition.

Figure S6. Degree of species-level overyielding for each species composition.

Figure S7. Mean tree height of each species for each species composition.

Figure S8. Mean specific leaf area of each species for each species composition.

Figure S9. Mean values of functional dispersion of tree height for each species composition.

Figure S10. Mean values of functional dispersion of specific leaf area for each species composition.

Figure S11. Mean values of community weighted means of tree height for each species composition.

Figure S12. Mean values of community weighted means of specific leaf area for each species composition.

Figure S13. Effects of community functional trait structure on community-level overyielding.

Figure S14. Piecewise structural equation model with an outlier.

Figure S15. Piecewise structural equation model with species richness as a random effect.

Figure S16. Effects of functional dispersion on species-level overyielding.

Figure S17. Effects of community weighted means on species-level overyielding.

Figure S18. Residual plots of statistical models to test for fertilization effects on the magnitude of mean overyielding of community-level woody phytomass.

Figure S19. Residual plots of statistical models for the magnitude of mean overyielding of species-level woody phytomass.

Figure S20. Residual plots of statistical models to test for single and interactive effects of fertilization and species identity on tree height and specific leaf area.

Figure S21. Residual plots of statistical models to test for fertilization effects on community functional trait structure.

Figure S22. Relationships between stem diameter and tree height for each species.

Table S1. Functional traits used to construct functional diversity gradient of original experimental design.

Table S2. Plot design and species composition in this study.

Table S3. Number of living trees for each species-treatment group in the end of winter in 2017/18.

Table S4. Number of selected trees to generate species-specific biomass equations and to measure specific leaf area.

Table S5. Beyond optimal models for species-specific biomass estimation.

Table S6. Structure of linear mixed-effects models used to test the three hypotheses in this study.

Table S7. Linear mixed-effects model testing the effects of fertilization on community-level overyielding, with an outlier.

Table S8. Linear mixed-effects models testing the effects of community functional trait structure on species-level overyielding.

Table S9. Linear mixed-effects model testing the interactive effects between stem diameter and species composition on tree height.

Table S10. Species-specific stem biomass equations.

Table S11. Species-specific branch biomass equations at an individual branch level.

Table S12. Species-specific leaf biomass equations at an individual branch level.

Table S13. Species-specific branch biomass equations at a whole-tree level.

Table S14. Species-specific leaf biomass equations at a whole-tree level.

Appendix S1. Design of IDENT-Freiburg to decouple species richness and functional diversity.

Appendix S2. Biomass equations.

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