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Research

Mycorrhizal associations modify tree diversity–productivity relationships across experimental tree plantations

Shan Luo[1,2], Bernhard Schmid[3], Andy Hector[4], Michael Scherer-Lorenzen[5], Kris Verheyen[6], Nadia Barsoum[7], Juergen Bauhus[8], Friderike Beyer[8], Helge Bruelheide[1,9], Olga Ferlian[1,2], Douglas Godbold[10,11], Jefferson S. Hall[12], Peter Hajek[5], Yuanyuan Huang[1,2], Dirk Hölscher[13], Holger Kreft[14,15], Xiaojuan Liu[16], Christian Messier[17,18], Charles Nock[19], Alain Paquette[17], John D. Parker[20], William C. Parker[21], Gustavo B. Paterno[14], Peter B. Reich[22,23,24], Boris Rewald[10,11], Hans Sandén[10], Katherine Sinacore[12], Artur Stefanski[22], Laura Williams[23] and Nico Eisenhauer[1,2]

[1]German Centre for Integrative Biodiversity Research (iDiv) Halle-Jena-Leipzig, Leipzig, 04103, Germany; [2]Institute of Biology, Leipzig University, Leipzig, 04103, Germany; [3]Department of Geography, Remote Sensing Laboratories, University of Zürich, Zürich, CH-8006, Switzerland; [4]Department of Biology, University of Oxford, South Parks Road, Oxford, OX1 3RB, UK; [5]Geobotany, Faculty of Biology, University of Freiburg, Freiburg, 79104, Germany; [6]Department of Environment, Forest & Nature Lab, Ghent University, Melle-Gontorde, B-9090, Belgium; [7]Forest Research, Alice Holt Lodge, Farnham, Surrey, GU10 4LH, UK; [8]Chair of Silviculture, Faculty of Environment and Natural Resources, University of Freiburg, Freiburg, 79108, Germany; [9]Institute of Biology/Geobotany and Botanical Garden, Martin Luther University Halle-Wittenberg, Halle, 06108, Germany; [10]Department of Forest and Soil Sciences, Forest Ecology, University of Natural Resources and Life Sciences (BOKU), Vienna, 1190, Austria; [11]Faculty of Forestry and Wood Technology, Mendel University in Brno, Brno, 61300, Czech Republic; [12]Agua Salud Project, Smithsonian Tropical Research Institute, Balboa, 401 Ancón, Panamá, Panama; [13]Tropical Silviculture and Forest Ecology, University of Goettingen, Göttingen, 37077, Germany; [14]Biodiversity, Macroecology and Biogeography, Faculty of Forest Sciences and Forest Ecology, University of Göttingen, Göttingen, 37077, Germany; [15]Centre of Biodiversity and Sustainable Land Use (CBL), University of Göttingen, Göttingen, 37077, Germany; [16]State Key Laboratory of Vegetation and Environmental Change, Institute of Botany, Chinese Academy of Sciences, Beijing, 100093, China; [17]Centre for Forest Research, Université du Québec à Montréal, Montréal, QC, H2X 3Y7, Canada; [18]Institut des Sciences de la Forêt Tempérée, Université du Québec en Outaouais, Ripon, QC, J0V 1V0, Canada; [19]Department of Renewables Resources, University of Alberta, Edmonton, AB, T6G 2R3, Canada; [20]Smithsonian Environmental Research Center, Edgewater, MD 21037, USA; [21]Ontario Ministry of Natural Resources and Forestry, Sault Ste. Marie, ON, P6A 2E5, Canada; [22]Department of Forest Resources, University of Minnesota, St. Paul, MN 55108, USA; [23]Hawkesbury Institute for the Environment, Western Sydney University, Penrith, NSW, 2751, Australia; [24]Institute for Global Change Biology, University of Michigan, Ann Arbor, MI 48109, USA

Author for correspondence:
Shan Luo
Email: luoshan.hi@gmail.com

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Summary

- Decades of studies have demonstrated links between biodiversity and ecosystem functioning, yet the generality of the relationships and the underlying mechanisms remain unclear, especially for forest ecosystems.
- Using 11 tree-diversity experiments, we tested tree species richness–community productivity relationships and the role of arbuscular (AM) or ectomycorrhizal (ECM) fungal-associated tree species in these relationships.
- Tree species richness had a positive effect on community productivity across experiments, modified by the diversity of tree mycorrhizal associations. In communities with both AM and ECM trees, species richness showed positive effects on community productivity, which could have resulted from complementarity between AM and ECM trees. Moreover, both AM and ECM trees were more productive in mixed communities with both AM and ECM trees than in communities assembled by their own mycorrhizal type of trees. In communities containing only ECM trees, species richness had a significant positive effect on productivity, whereas species richness did not show any significant effects on productivity in communities containing only AM trees.
- Our study provides novel explanations for variations in diversity–productivity relationships by suggesting that tree–mycorrhiza interactions can shape productivity in mixed-species forest ecosystems.

Introduction

Global environmental changes affect the diversity, composition, and functioning of ecosystems, invoking research to evaluate the relationship between biodiversity and ecosystem functioning (BEF; Loreau *et al.*, 2001; Hooper *et al.*, 2005; Tilman *et al.*, 2014). Many studies have demonstrated that greater tree species richness can increase forest productivity (Zhang *et al.*, 2012; Huang *et al.*, 2018; Ammer, 2019; Feng *et al.*, 2022). However, evidence is also mounting that the magnitude and shape of BEF relationships vary with environmental context (Luo *et al.*, 2017; Ratcliffe *et al.*, 2017; van der Plas, 2019; Luo *et al.*, 2022). The generality of, and mechanisms behind, BEF relationships remains unclear, especially for forest ecosystems that are highly contingent on tree–mycorrhiza interactions (Eisenhauer *et al.*, 2022; S. Luo *et al.*, 2023). This lack of understanding hampers our ability to predict the response of forest ecosystem functioning to biodiversity loss and the effectiveness of mixed-species tree plantations in restoring ecosystem functioning.

To explain BEF relationships, two classes of biodiversity effects have been proposed, complementarity and selection effects calculated using an additive partitioning method (Loreau & Hector, 2001; Forrester & Bauhus, 2016). The complementarity effect refers to niche complementarity and interspecific facilitation that increase species functioning in mixtures. The selection effect is caused by the dominance of one or few species with high functional contributions (Loreau & Hector, 2001). In addition to plant species interactions, positive biodiversity effects can result from positive trophic interactions (Cook-Patton *et al.*, 2014; Laforest-Lapointe *et al.*, 2017; Li *et al.*, 2023) or reduced density-dependent pathogen effects in diverse communities (Schnitzer *et al.*, 2011; Mommer *et al.*, 2018; Liang *et al.*, 2019). Moreover, there is emerging evidence that mycorrhizal fungi play important roles in regulating the relationship between tree species diversity and community productivity (Luo *et al.*, 2018; Deng *et al.*, 2023; Dietrich *et al.*, 2023; Fahey *et al.*, 2023; S. Luo *et al.*, 2023; Mao *et al.*, 2023). For example, mycorrhizal fungi can promote complementarity effects among tree species through soil nitrogen partitioning (Luo *et al.*, 2018). While biodiversity effects have been shown to be influenced by abiotic environmental conditions (Forrester, 2014; Jucker *et al.*, 2014; Luo *et al.*, 2017; Ratcliffe *et al.*, 2017), much less is known about how biotic interactions between trees and mycorrhizal fungi modify biodiversity effects and tree species richness–community productivity relationships (Luo *et al.*, 2018; Eisenhauer *et al.*, 2022; Dietrich *et al.*, 2023).

Most tree species primarily form symbiotic associations with either arbuscular mycorrhizal (AM) or ectomycorrhizal (ECM) fungi (Tedersoo *et al.*, 2020), which can facilitate nutrient uptake of plants in exchange for carbon (Read, 1991; van der Heijden *et al.*, 2015) and alter biogeochemical responses to other major environmental drivers (Terrer *et al.*, 2021). This suggests that mycorrhizal association might also mediate the impacts of plant biodiversity loss. AM and ECM fungi differ substantially in their access to, and alteration of, nutrient availability (Tedersoo & Bahram, 2019). ECM fungi are capable of using organic forms of nutrients, and AM fungi mainly use mineral nutrients; therefore, AM and ECM tree species may partition resources by utilizing different chemical forms of nutrients (Liu *et al.*, 2018; Luo *et al.*, 2018). AM and ECM tree species can also differentially influence soil nutrient availability. For instance, some AM tree species are N fixers that can promote the growth of ECM tree species (Binkley *et al.*, 2003). Moreover, most AM tree species produce high-quality litter that degrades more rapidly and promotes nutrient mineralization, whereas most ECM trees produce low-quality litter that degrades more slowly and inhibits nutrient mineralization (Phillips *et al.*, 2013). Thus, ECM trees can favor a more conservative nutrient-use strategy than AM trees, especially in the temperate biome (Deng *et al.*, 2018; Zhang *et al.*, 2018). Collectively, the contrasting strategies of AM and ECM fungi may lead to complementary nutrient use between AM and ECM trees in communities containing both types of trees (Eisenhauer *et al.*, 2022; S. Luo *et al.*, 2023). However, environmental changes are shifting the relative abundance of AM and ECM trees (Averill *et al.*, 2018; Jo *et al.*, 2019). It has not been explicitly tested how different mycorrhizal associations influence tree species richness–community productivity relationships across experiments with different environmental conditions. This knowledge gap remains a major obstacle for understanding and predicting the form and generality of BEF relationships in forest ecosystems.

Globally distributed tree-diversity experiments, capturing major variation in species compositions and environmental conditions, hold the potential to improve our mechanistic understanding of BEF relationships (Verheyen *et al.*, 2016; Paquette *et al.*, 2018). By combining 11 tree-diversity experiments, we tested the effects of tree species richness and mycorrhizal associations on tree community productivity. Species-rich communities can have a greater chance of including more productive species and a more complete utilization of resources than species-poor communities (Tilman, 1999). Our first hypothesis was that tree species richness–community productivity relationships would be generally positive. Given the functional differences between AM and ECM fungi and the potential niche complementarity between AM and ECM tree species (Liu *et al.*, 2018; Luo *et al.*, 2018), it is conceivable that the composition of mycorrhizal functional groups (mixed AM–ECM vs only AM or ECM) may modify tree species richness–community productivity relationships. Our second hypothesis was that communities containing both AM and ECM trees (i.e. mixed AM–ECM tree communities) would show stronger species richness–productivity relationships than communities containing only AM or ECM trees. Moreover, AM and ECM trees have dissimilar functional roles in nutrient cycling (Phillips *et al.*, 2013), and differ in resistance against and response to abiotic and biotic stresses and resources (Augé, 2001; Tedersoo & Bahram, 2019; Tedersoo *et al.*, 2020; Terrer *et al.*, 2021; Eisenhauer *et al.*, 2022; Yi *et al.*, 2024). Our third hypothesis was that a stronger BEF relationship in mixed AM–ECM tree communities would be mostly due to complementarity between AM and ECM trees.

Materials and Methods

Data acquisition and description of tree-diversity experiments

Long-term tree-diversity experiments were identified through the global network TreeDivNet (Verheyen *et al.*, 2016; http://www.treedivnet.ugent.be/). In these experiments, gradients in tree species richness are created by planting monoculture stands as well as stands of different species richness and composition, allowing us to investigate the relationship between tree diversity and ecosystem functioning (Verheyen *et al.*, 2016; Paquette *et al.*, 2018).

Experiments were included if (1) trees had been planted in the field for at least 5 yr, and (2) basal area data were available at the species level. Our study included nine experiments with basal-area data from two points in time from different years and two experiments with basal-area data from a single time point (see Table 1). Basal area ($\mathrm{m}^2\ \mathrm{ha}^{-1}$) of each species on each plot was calculated using Eqn 1:

$$\text{Basal area} = \pi * \frac{\sum \mathrm{DBH}^2}{4a} \qquad \text{Eqn 1}$$

where DBH is the diameter at breast height (m), and a is the area of the plot (ha). Basal area was calculated using diameter at the stem base instead of DBH for the Agua Salud, B-TREE, BEF-China, FORBIO-Zedelgem, IDENT-Cloquet, IDENT-Freiburg, IDENT-SSM, and MyDiv experiments. While the basal area calculated at breast height will be lower than the one calculated for the stem base due to stem tapering, it should not influence the detection of the effects of tree species richness and mycorrhizal associations within each experiment.

We used the nine experiments with data from two time points to calculate annual increment of basal area at the plot level using Eqn (2):

$$\text{Annual increment of basal area} = \frac{\mathrm{TBA}_2 - \mathrm{TBA}_1}{T_2 - T_1} \qquad \text{Eqn 2}$$

where TBA_2 and TBA_1 are the total basal area of all species within a plot at time 2 (T_2) and time 1 (T_1), respectively. We considered annual increment of basal area as a proxy of community productivity (Guerrero-Ramírez *et al.*, 2017; Schnabel *et al.*, 2019; Bongers *et al.*, 2020) and used community productivity in the following text for consistency. The two experiments without repeated measurements of basal area were only used to test the relationship between tree species richness and accumulated basal area of communities (Supporting Information Table S1; Fig. S1). Accumulated basal area was calculated as the total basal area of all species within a plot at the latest time point of acquired data for the 11 experiments. Since accumulated basal area was strongly correlated with stand age, we focused on community productivity throughout the main text.

Mycorrhizal type (i.e. AM and ECM) for each tree species was assigned based on a recently published database (Steidinger *et al.*, 2019). All species in our dataset are either AM or ECM trees (see Dataset S1 for a list of species). To quantify mycorrhizal composition of tree communities, we calculated relative AM tree abundance of each plot by dividing the number of planted trees belonging to AM tree species by the total number of planted trees. Six out of 109 species in our dataset are nitrogen (N)-fixing species, including four species in the Agua Salud experiment and two species in the EFForTS-BEE experiment.

Statistical analysis

Effects of tree species richness and mycorrhizal associations on community productivity We tested the effects of tree species richness and mycorrhizal associations on tree community productivity. In all models, community productivity was square-root transformed to achieve homoscedasticity and normality of

Table 1 List of tree-diversity experiments included in the analysis.

Experiment	Biome	Country	MAP (mm)	MAT (°C)	Planted year	Tree age	Tree distance (m)	Tree species richness treatments	AM tree abundance
Agua Salud	Tropical	Panama	2712	25.5	2008	5, 11	3	1, 2, 5, 6	1.00
BEF-China	Subtropical	China	1762	17.2	2009	5, 9	1.29	1, 2, 4, 8, 16, 24	0.00–1.00
BIOTREE-Species Kaltenborn	Temperate	Germany	693	7.4	2004	14, 19	2	1, 2, 3, 4	0.00
B-Tree	Temperate	Austria	624	9.7	2013	8, 10	1	1, 2, 4	0.00–1.00
EFForTS-BEE	Tropical	Indonesia	2491	26.8	2013	8, 9	2	1, 2, 3, 6	0.00–1.00
FORBIO-Zedelgem	Temperate	Belgium	713	10.1	2010	3, 9	1.5	1, 2, 3, 4	0.00
IDENT-Cloquet	Temperate	USA	762	3.7	2009	6, 12	0.4	1, 2, 6	0.00–1.00
IDENT-SSM	Temperate	Canada	916	3.7	2013	5, 9	0.4	1, 2, 4, 6	0.00–1.00
MyDiv	Temperate	Germany	493	8.9	2015	1, 6	1	1, 2, 4	0.00–1.00
BiodiversiTREE[a]	Temperate	USA	1068	13.2	2013	8	2.4	1, 4, 12	0.00–1.00
IDENT-Freiburg[a]	Temperate	Germany	841	10.5	2013	7	0.45	1, 2, 4, 6	0.00–1.00

MAP, mean annual precipitation; MAT, mean annual temperature; Tree age, ages of trees in acquired data; Tree distance, the planting distance between trees; AM tree abundance, range of relative abundance of AM trees (based on the number of planted trees). Experiments also differ in their species pools (see Supporting Information Dataset S1).

[a] Tree DBH was only measured once for BiodiversiTREE and IDENT-Freiburg in the data we obtained; we therefore excluded these two experiments when calculating community productivity.

residuals. First, we used linear mixed-effects models to assess how tree species richness influenced community productivity across nine experiments (M1):

$$\text{Community productivity} \sim \text{richness} * \text{experiment} + \text{age} + \textit{block} + \textit{composition} \qquad \text{M1}$$

We included tree species richness, experiment, and their interaction as fixed effects (factorial indicated with operator '*' in M1), and stand age as a covariate. We defined stand age as the age of trees at Time 2. Tree species richness was the planted richness. We included both linear and factorial terms of richness to test for linearity and deviation from linearity (Hector *et al*., 1999). Significance of factorial richness when fitted after linear richness would indicate a nonlinear effect of richness in addition to the linear relationship. We included experiment and its interaction with richness as fixed-effects terms to test whether richness–productivity relationships changed across experiments. Random effects were blocks within experiment and species composition (which could sometimes be identical between experiments). To check the robustness of our results, we ran the same model after excluding communities with more than eight species of the BEF-China experiment, making its richness levels comparable to that of the other eight experiments. Second, we tested whether tree mycorrhizal associations modified the effects of tree species richness on community productivity. We changed the above model (i.e. M1) by adding relative AM tree abundance (linear and quadratic terms to account for a potentially unimodal relationship with community productivity; total abundance of AM and ECM trees based on basal area as defined in Eqn 1) and its interactions with species richness (linear and factorial terms) and experiment (M2, interactions indicated with operator '×'):

$$\text{Community productivity} \sim (\text{linear AM} + \text{quadratic AM}) * \text{richness} + \text{experiment} + (\text{linear AM} + \text{quadratic AM}) \times \text{experiment} + \text{richness} \times \text{experiment} + \text{age} + \textit{block} + \textit{composition} \qquad \text{M2}$$

A unimodal relationship between AM tree abundance and productivity was expected under the assumption that mixtures of AM and ECM trees had higher productivity than communities with low or high relative abundance of AM trees (S. Luo *et al*. 2023). We included the interactions between AM tree abundance and experiment as fixed-effects terms to test whether relationships between AM tree abundance and productivity changed across experiments.

In addition, we tested how tree species richness and mycorrhizal associations influenced community productivity for each of the nine experiments separately. Note that the significance of differences in tree species richness and mycorrhizal effects on productivity across experiments were tested using interaction terms as error s (i.e. richness × experiment, linear AM × experiment, and quadratic AM × experiment) in the above models. First, to assess how species richness influenced community productivity, we used linear mixed-effects models, with linear and factorial richness as fixed-effects terms and block and species composition as random-effects terms (M3):

$$\text{Community productivity} \sim \text{linear richness} + \text{factorial richness} + \textit{block} + \textit{composition} \qquad \text{M3}$$

Second, for six experiments containing both AM and ECM tree species (i.e. BEF-China, B-Tree, EFForTS-BEE, IDENT-Cloquet, IDENT-SSM, and MyDiv), we used linear mixed-effects models to test whether tree mycorrhizal associations modified the effects of species richness on community productivity in each experiment. The fixed-effects terms were relative AM tree abundance (linear and quadratic), species richness (linear and factorial), and their interactions, while the random-effects terms were block and species composition (M4):

$$\text{Community productivity} \sim (\text{linear AM} + \text{quadratic AM}) * (\text{linear richness} + \text{factorial richness}) + \textit{block} + \textit{composition} \qquad \text{M4}$$

We excluded communities with more than eight species of the BEF-China experiment, making its richness levels comparable to that of the other five experiments. Third, for these six experiments we tested how mycorrhizal associations influenced richness–productivity relationships across experiments and in individual experiments. We divided communities into three groups based on the composition of tree mycorrhizal associations, namely communities containing both AM and ECM tree species (i.e. mixed AM–ECM tree communities, $n = 288$), communities containing only ECM tree species (i.e. ECM tree communities, $n = 393$), and communities containing only AM tree species (i.e. AM tree communities, $n = 243$). We fitted linear mixed-effects models for each community group, with linear and factorial species richness as fixed-effects terms. We included experiment, block, and species composition as random-effects terms (M5):

$$\text{Community productivity} \sim \text{linear richness} + \text{factorial richness} + \textit{experiment} + \textit{block} + \textit{composition} \qquad \text{M5}$$

For each experiment, we also divided communities into three groups based on the composition of tree mycorrhizal associations. We fitted linear mixed-effects models for each group of each experiment, with linear and factorial species richness as fixed-effects terms and block and species composition as random-effects terms (M6):

$$\text{Community productivity} \sim \text{linear richness} + \text{factorial richness} + \textit{block} + \textit{composition} \qquad \text{M6}$$

Effects of tree species richness and mycorrhizal associations on community productivity via complementarity and selection effects For four experiments (i.e. BEF-China, IDENT-Cloquet, IDENT-SSM, and MyDiv) showing significant overall species richness–community productivity relationships, we also tested how tree species richness influenced community productivity via complementarity effects and selection effects, respectively. We excluded communities with more than eight species of the BEF-China experiment as above. We partitioned net biodiversity effects (NEs) into complementarity effects (CEs) and selection effects (SEs) using additive partitioning (Loreau & Hector, 2001). Calculations were based on the difference between the observed yield of each species in the mixture and mean monoculture yield of that species for the specific experiment and block. Yield was quantified by annual increment of basal area (i.e. productivity). Absolute values of NEs, CEs, and SEs were square-root transformed, with the transformed values preserving their original signs for analysis (Loreau & Hector, 2001). We used hierarchical ANOVA (i.e. the classical form of mixed-model analysis, see Schmid *et al.*, 2017) by including linear and factorial species richness, stand age, experiment, and the interaction between richness and experiment as fixed-effects explanatory terms for NE, CE, and SE in separate models. We included block, the interactions between richness and block, and species composition as random-effects error terms. We also tested whether the overall means of the NE, CE, and SE were different from zero by listing the significance of the intercept in corresponding ANOVAs (M7):

$$\begin{aligned}\text{NE, CE or SE} \sim\ & \text{intercept} + (\text{linear richness}\\ & + \text{factorial richness}) * \text{experiment} + \text{age} + \textit{block}\\ & + \textit{richness} \times \textit{block} + \textit{composition}\end{aligned} \qquad \text{M7}$$

The *F*-values for species richness and richness-by-experiment interactions were calculated with the mean square of species composition and richness-by-block interaction as error terms, respectively; the *F*-values for the experiment were calculated with the mean square of the block as error term.

In addition, we tested whether AM tree abundance modified the effects of tree species richness on NE, CE, and SE using mixed-effects models (M8):

$$\begin{aligned}\text{NE, CE or SE} \sim\ & (\text{linear AM} + \text{quadratic AM})\\ & * (\text{linear richness} + \text{factorial richness})\\ & + \text{experiment} + (\text{linear AM} + \text{quadratic AM}) \times \text{experiment}\\ & + \text{age} + \textit{block} + \textit{composition}\end{aligned} \qquad \text{M8}$$

We further tested how the effects of species richness on NE, CE, and SE differed among the three groups of communities with different mycorrhizal associations (i.e. mixed AM–ECM tree communities, ECM tree communities, AM tree communities) by fitting linear mixed-effects models for each group. We included linear species richness as a fixed-effects term and dropped factorial species richness from our final models due to small deviation from linearity. We included experiment, block, and species composition as random-effects terms (M9):

$$\begin{aligned}\text{NE, CE or SE} \sim\ & \text{linear richness} + \textit{experiment}\\ & + \textit{block} + \textit{composition}\end{aligned} \qquad \text{M9}$$

Relative yield of AM and ECM tree species in mixed AM–ECM communities vs AM or ECM communities To gain further insights into the performance of AM and ECM trees in mixtures, we tested whether AM or ECM tree species were more productive in mixed AM–ECM communities than in communities containing only AM or ECM trees. We calculated the relative yield for 62 of 79 species occurring in the six experiments with both AM and ECM trees (i.e. BEF-China, B-Tree, EFForTS-BEE, IDENT-Cloquet, IDENT-SSM, and MyDiv). We excluded the remaining 17 species due to missing data in monocultures or mixtures. The relative yield of a species (RY) is the quotient of the yield of a species in mixture and the mean yield of this species in monocultures. The mean monoculture yield of a species was calculated within a specific experiment and block. Again, yield was quantified by annual increment of basal area (i.e. productivity). We then calculated mean RY of each AM (or ECM) tree species within community groups based on the composition of mycorrhizal associations: mixed AM–ECM communities vs AM (or ECM) communities. We used mixed-effects models to test whether species mean RY was influenced by community mycorrhizal composition (mixed mycorrhizal types vs single mycorrhizal type), mycorrhizal type (AM vs ECM tree species), and the interaction between them. The random-effects terms were experiment, block, and species composition (M10):

$$\begin{aligned}\text{RY} \sim\ & \text{mycorrhizal compositon} * \text{mycorrhizal type}\\ & + \textit{experiment} + \textit{block} + \textit{composition}\end{aligned} \qquad \text{M10}$$

We did not include stand age in our final model, because it did not show any significant effects. In this analysis, only the EFForTS-BEE experiment included two AM tree species that had N-fixing ability. Therefore, we did not have enough data to test whether ECM tree species performed differently when mixing with N-fixing or non-N-fixing AM tree species. Nevertheless, we can refer to Feng *et al.* (2022) who did not find any differences in tree-diversity effects on productivity when mixing N-fixing or non-N-fixing species only or when mixing N-fixing with non-N-fixing species.

Where not otherwise stated, we used restricted maximum likelihood estimation for linear mixed-effects models and assessed the significance of the fixed effects using type-I ANOVA and *F*-tests with adjusted error terms and the Satterthwaite approximation of denominator degrees of freedom. 'LME4' and 'GGPLOT2' packages were used and all statistical analyses were conducted in R v.4.2.1.

Results

Effects of tree species richness on community productivity

Tree species richness showed positive, but relatively modest, effects on tree community productivity (Fig. 1; Table 2;

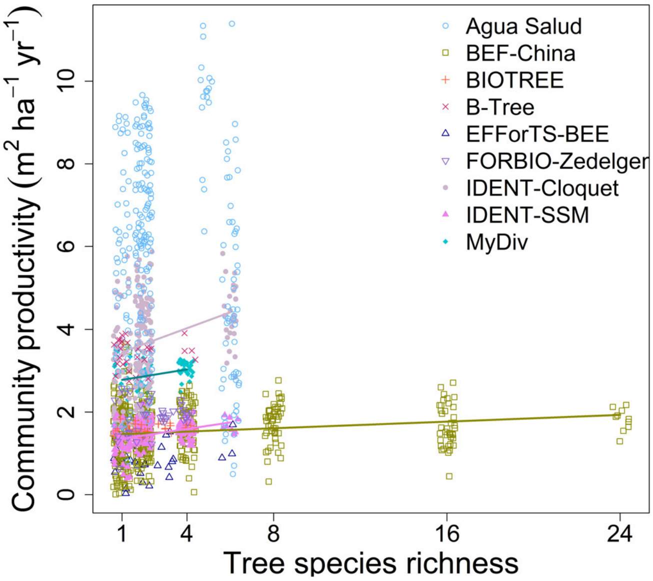

Fig. 1 Relationships between tree species richness and community productivity. Lines indicate significant ($P < 0.05$) relationships between richness and productivity in mixed-effects models, which were fitted separately for each experiment. Productivity (square-root transformed) was quantified by annual increment of basal area. See Supporting Information Table S3 for statistical results.

estimate = 0.022 ± 0.012, $F_{1,289.58} = 8.80$, and $P = 0.003$ for linear richness (LSR); $F_{7,311.30} = 43.70$ and $P < 0.001$ for factorial richness (FSR)). The significance of factorial richness when fitted after linear richness indicated deviation from linearity. That is, the rate at which productivity increased from one richness level to the next was not constant across richness levels. Similarly, species richness had significant positive effects on accumulated basal area (Fig. S1; Table S1; estimate = 0.243 ± 0.087, $F_{1,431.70} = 5.71$, and $P = 0.017$ for LSR; $F_{8,352.58} = 8.80$ and $P < 0.001$ for FSR). Positive species-richness effects remained significant after excluding communities with more than eight tree species (see sensitivity analysis in Table S2). However, the effects of species richness on productivity differed between experiments (Fig. 1; Table 2; $F_{8,460.75} = 3.36$ and $P = 0.001$ for experiment × LSR). Specifically, tree species richness showed significant positive effects on productivity in four out of nine experiments and non-significant effects in the rest of experiments (Fig. 1; Table S3). In experiments with significant positive richness–productivity relationships, net biodiversity effects and complementarity effects were significantly positive (Table S4: $P < 0.001$ for Intercept), whereas selection effects tended to be negative (Table S4: $P = 0.086$ for Intercept). Moreover, net biodiversity effects and complementarity effects were positively related to species richness (Fig. S2; Table S4; $F_{1,203} = 14.29$ and $P < 0.001$; $F_{1,203} = 7.28$ and $P = 0.008$). Consistently, the correlations between species richness and net biodiversity effects differed between experiments (Table S4: $F_{3,12} = 6.72$ and $P = 0.007$ for LSR × experiment).

Effects of mycorrhizal associations on tree species richness–community productivity relationships

The relative abundance of AM trees exhibited an overall concave-negative (i.e. unimodal) relationship with tree community productivity, with its linear and quadratic terms showing overall positive and negative effects, respectively (Table 3: $F_{1,95.80} = 149.27$ and $P < 0.001$ for linear AM; $F_{1,196.64} = 102.87$ and $P < 0.001$ for quadratic AM). Therefore, mixtures of AM and ECM trees had higher productivity than did communities with low or high relative abundance of AM trees. However, the effects of AM tree abundance on productivity differed between experiments (Table 3: $F_{5,471.42} = 3.64$ and $P = 0.003$ for linear AM × experiment), including concave-negative, linear negative, linear positive, and nonsignificant effects (Fig. S3). After accounting for those varying effects of AM tree abundance

Table 2 Summary of mixed-effects ANOVA testing the effects of tree species richness on tree community productivity.

	Tree community productivity			
Fixed terms	numDF	denDF	*F*	*P*
Linear species richness (LSR)	1	289.58	8.80	**0.003**
Factorial species richness (FSR)	7	311.30	43.70	**< 0.001**
Stand age	6	58.53	86.20	**< 0.001**
Experiment	3	78.66	4.27	**0.008**
Experiment × LSR	8	460.75	3.36	**0.001**
Experiment × FSR	10	531.35	1.33	0.212
Random terms				Variance
Block				0.025
Species composition				0.353
Residual				0.614

The explanatory terms include tree species richness (linear richness and factorial richness), stand age, experiment, and the interactions between tree species richness and experiment as fixed-effects terms and block and species composition as random-effects terms. Productivity, which was quantified by annual increment of basal area, was square-root transformed. numDF, degrees of freedom of term; denDF, degrees of freedom of error term (which can be fractional in residual maximum likelihood analysis); *F*, variance ratio; *P*, probability of Type I error. Blocks are labeled continuously across all experiments. The numbers in bold indicate significant effects ($P < 0.05$).

Table 3 Summary of mixed-effects ANOVA testing the effects of arbuscular (AM) tree abundance and tree species richness on tree community productivity.

	Tree community productivity			
Fixed terms	numDF	denDF	*F*	*P*
Linear AM tree abundance (AM)	1	95.80	149.27	<**0.001** +
Quadratic AM tree abundance (AM2)	1	196.64	102.87	<**0.001** –
Linear species richness (LSR)	1	373.61	0.80	0.372
Factorial species richness (FSR)	7	314.41	37.24	< **0.001**
Stand age	6	62.77	83.11	< **0.001**
Experiment	3	81.75	3.01	**0.035**
AM × LSR	1	424.06	9.73	**0.001**
AM × FSR	6	547.10	4.75	< **0.001**
AM2 × LSR	1	682.87	5.08	**0.024**
AM2 × FSR	5	717.46	0.81	0.546
AM × Experiment	5	471.42	3.64	**0.003**
AM2 × Experiment	5	476.96	0.07	0.997
LSR × Experiment	8	428.82	0.86	0.549
FSR × Experiment	9	511.47	0.42	0.923
Random terms				Variance
Block				0.025
Species composition				0.343
Residual				0.616

The explanatory terms include relative AM tree abundance (linear and quadratic), tree species richness (linear and factorial), stand age, experiment, the interactions between AM tree abundance and experiment, and the interactions between tree species richness and experiment as fixed-effects terms and block and species composition as random-effects terms. Productivity (square-root transformed) was quantified by annual increment of basal area. numDF, degrees of freedom of term; denDF, degrees of freedom of error term (which can be fractional in residual maximum likelihood analysis); *F*, variance ratio; *P*, probability of Type I error; + or – besides the *P*-values represents the direction of effects. Blocks are labeled continuously across all experiments. The numbers in bold indicate significant effects ($P < 0.05$).

across experiments, the effects of species richness on productivity did not show significant differences between experiments (Table 3: $F_{8,428.82} = 0.86$ and $P = 0.549$ for LSR × Experiment; $F_{9,511.47} = 0.42$ and $P = 0.923$ for FSR × experiment). Therefore, the variation in richness–productivity relationships across experiments may be attributable to the differential effects of AM tree abundance on productivity. Moreover, AM tree abundance had significant interactive effects with species richness on productivity (Table 3: $F_{1,424.06} = 9.73$ and $P = 0.001$ for linear AM × LSR; $F_{1,682.87} = 5.08$ and $P = 0.024$ for quadratic AM × LSR), indicating that the composition of tree mycorrhizal associations modified species richness–productivity relationships. These results were robust after excluding communities with more than eight species (see sensitivity analysis in Table S5).

Across six experiments containing both AM and ECM tree species, there was a significant positive richness–productivity relationship in ECM tree communities (Fig. 2a; Table S6; estimate = 0.115 ± 0.058, $F_{1,103.40} = 4.44$, and $P = 0.038$ for LSR). As predicted, productivity also significantly increased with increasing richness in mixed AM–ECM tree communities (Fig. 2b; Table S6; estimate = 0.099 ± 0.021, $F_{1,107.84} = 25.93$, and $P < 0.001$ for LSR). However, richness–productivity relationship was not significant in AM tree communities (Fig. 2c; Table S6; $F_{1,71.15} = 2.70$ and $P = 0.105$ for LSR). Moreover, in five out of six experiments, productivity consistently increased with increasing richness in mixed AM–ECM communities, but not in AM- or ECM-only communities (Fig. 3; Table S7).

Effects of mycorrhizal associations on community productivity via complementarity and selection effects

Although tree species richness and AM tree abundance did not show any significant interactive effects on net biodiversity effects, they interactively influenced complementarity and selection effects (Fig. 4a–c; Table S8; $F_{1,164.93} = 6.13$ & $P = 0.014$ and $F_{1,170.54} = 6.28$ & $P = 0.013$ for linear AM × LSR on complementarity and selection effects, respectively). This was consistent with that tree species richness and AM tree abundance had significant interactive effects on productivity, suggesting that the composition of tree mycorrhizal associations modified the effects of species richness on productivity by modulating complementarity and selection effects. In mixed AM–ECM tree communities, species richness was positively related to complementarity effects (Fig. 4h; Table S8; $F_{1,100.86} = 6.71$ and $P = 0.011$), leading to a positive correlation between richness and net biodiversity effects (Fig. 4g; Table S8; $F_{1,94.47} = 21.27$ and $P < 0.001$). In mixtures with only ECM trees, biodiversity effects did not further increase with increasing species richness (beyond the increase from monoculture to mixtures; Fig. 4d–f; Table S8; $F_{1,209.75} = 0.76$ and $P = 0.383$ for net biodiversity effect). In mixtures of only AM trees, complementarity effects decreased and selection effects increased with increasing species richness (Fig. 4k,l; Table S8; $F_{1,44.11} = 6.42$ and $P = 0.015$ for complementarity effect; $F_{1,85.67} = 11.97$ and $P < 0.001$ for selection effect),

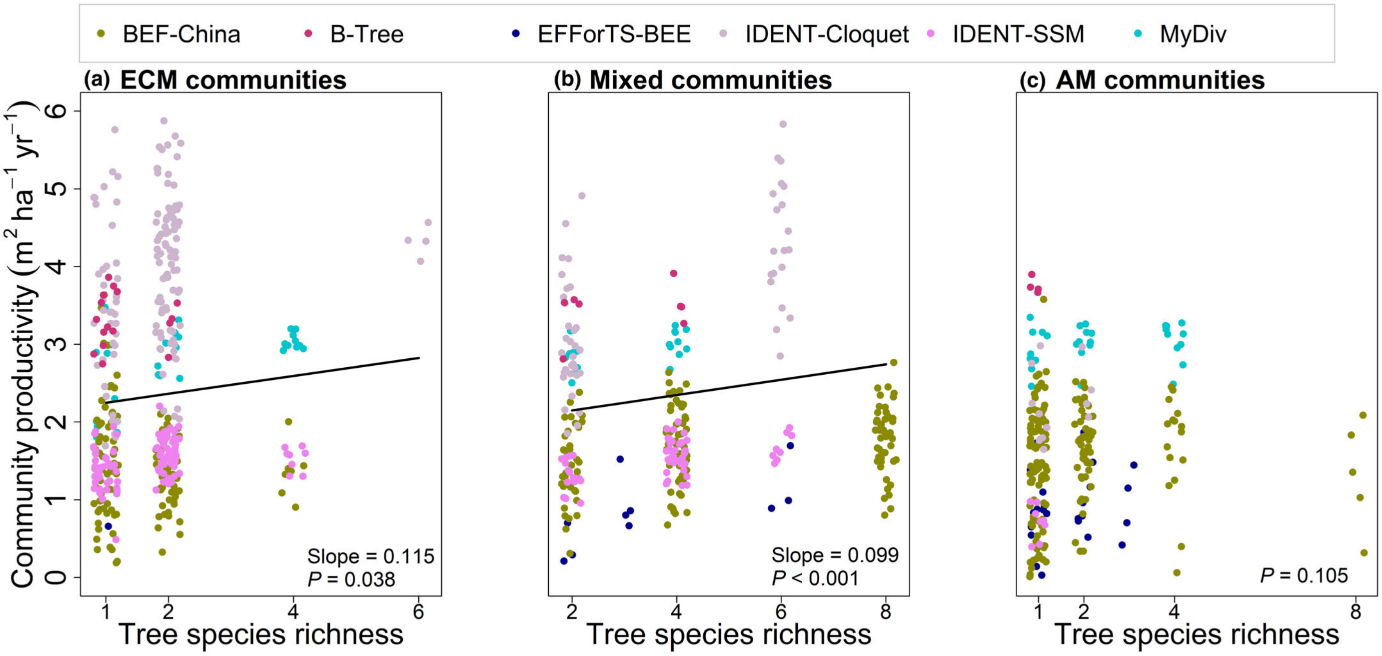

Fig. 2 Tree species richness–community productivity relationships in communities with different compositions of tree mycorrhizal associations: communities containing only ectomycorrhizal (ECM) tree species (a; $n = 393$); communities containing both arbuscular (AM) and ECM tree species (b; $n = 288$); communities containing only AM tree species (c; $n = 243$). Lines are mixed-effects model fits for community groups. Only experiments (i.e. BEF-China, B-Tree, EFForTS-BEE, IDENT-Cloquet, IDENT-SSM, and MyDiv) containing both AM and ECM tree species were included in the analysis. See Supporting Information Table S6 for statistical results. BEF, biodiversity and ecosystem functioning.

resulting in a constantly positive net biodiversity effect across mixtures (Fig. 4j; Table S8; $F_{1,39.63} = 1.06$ and $P = 0.310$).

Relative yield of AM and ECM tree species in mixed AM–ECM communities vs AM or ECM communities

AM tree species had higher relative yield than ECM tree species (Fig. 5; Table S9; $F_{1,847.18} = 32.95$ and $P < 0.001$ for mycorrhizal type), although both of them were on average more productive in mixtures than monocultures (Fig. 5; relative yield > 1). Both AM and ECM tree species had higher relative yield in mixed AM–ECM communities than communities assembled by species of their own mycorrhizal type (Fig. 5; Table S9; $F_{1,220.29} = 5.31$ and $P = 0.022$ for community mycorrhizal composition), suggesting that both of them were on average more productive when mixed with trees of the other mycorrhizal type. However, relative yield of AM tree species increased to a greater extent from AM communities to mixed AM–ECM communities when compared with ECM tree species (Fig. 5; Table S9; $F_{1,474.00} = 4.44$ and $P = 0.036$ for interaction mycorrhizal composition × mycorrhizal type).

Discussion

We found an overall positive tree species richness–community productivity relationship across a range of tree diversity experiments, but the strength of richness–productivity relationships varied between experiments. We also found that tree mycorrhizal associations modified richness–productivity relationships. Specifically, mixed AM–ECM communities showed a significant positive richness–productivity relationship that was driven by complementarity effects. Both AM and ECM tree species were more productive in mixed AM–ECM communities than in communities assembled by species of their own mycorrhizal type. In ECM tree communities, species richness had a significant positive effect on productivity and net biodiversity effects did not further increase from monoculture to mixtures. By contrast, AM tree communities showed a nonsignificant richness–productivity relationship. Our study indicates that tree mycorrhizal associations can modify species-diversity effects on the functioning of forest ecosystems.

Tree species richness–community productivity relationships

Tree species richness had positive, but relatively modest, effects on community productivity across experiments. Increasing species richness was correlated with increased net biodiversity effects and complementarity effects. This supports our first hypothesis that species richness–community productivity relationships would be positive. It also suggests that already during the early establishment phase (*c.* 10 yr on average), tree communities can benefit from increased species richness, potentially via species complementarity in resource use and enhanced by greater functional diversity of fungal symbiont partners. It is conceivable that species differences in aboveground and belowground functional traits can increase resource-use efficiency, which promotes complementarity effects and productivity in diverse communities

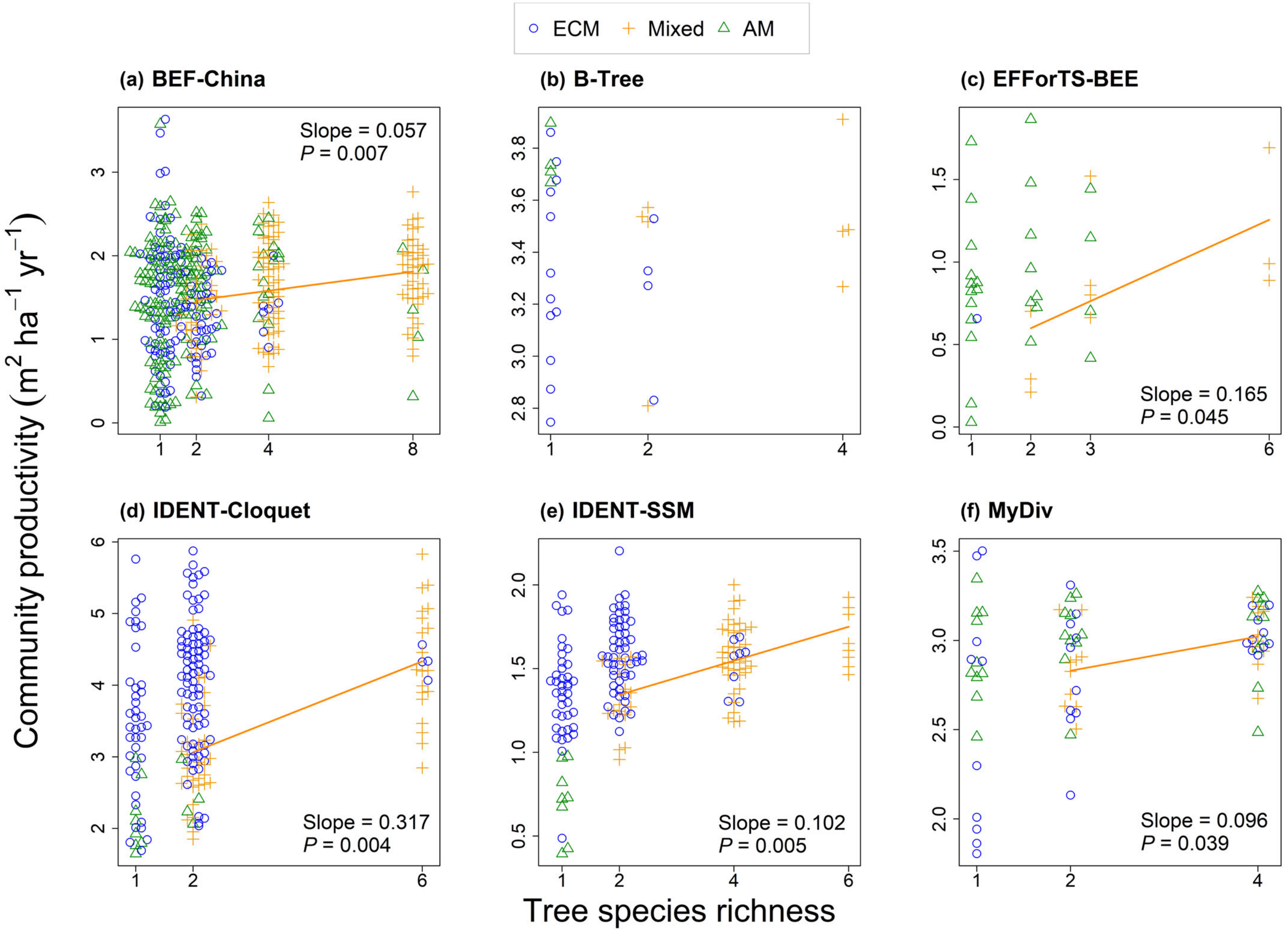

Fig. 3 Tree species richness–community productivity relationships in communities with different compositions of tree mycorrhizal associations: 'ECM', communities containing only ECM tree species; 'Mixed', communities containing both arbuscular (AM) and ectomycorrhizal (ECM) tree species; 'AM', communities containing only AM tree species. Six experiments are included: BEF-China (a), B-Tree (b), EFForTS-BEE (c), IDENT-Cloquet (d), IDENT-SSM (e), and MyDiv (f). Lines are mixed-effects model fits for community groups. Lines indicate significant ($P < 0.05$) relationships between richness and productivity. Productivity (square-root transformed) was quantified by annual increment of basal area. See Supporting Information Table S7 for statistical results. BEF, biodiversity and ecosystem functioning.

(Van de Peer *et al*., 2018; Bongers *et al*., 2021; Jing *et al*., 2021; Urgoiti *et al*., 2022; Deng *et al*., 2023; Ray *et al*., 2023). However, individual experiments were variable in the strength of richness–productivity relationships. Five out of nine experiments did not show significant richness–productivity relationships when tested individually. This could be at least partly attributed to a lack of statistical power of individual experiments when analyzed separately. Environmental or experimental context may also explain the relatively weak richness–productivity relationship (e.g. Luo *et al*., 2017; Ratcliffe *et al*., 2017; van der Plas, 2019). For instance, soil nutrient deficiency may have limited tree growth and complementarity among tree species in one experiment (i.e. Agua Salud; Mayoral *et al*., 2017, 2019). The duration of experiments was still short, and species-diversity effects (especially via complementarity) grow stronger with time during ecosystem development (Reich *et al*., 2012; Huang *et al*., 2018; Urgoiti *et al*., 2022). In cases with greater planting distances between individuals or species (e.g. 2 m in BIOTREE), species-diversity effects may take longer to develop (Table S10: $P < 0.001$ for tree density and tree density × LSR in Model A). Nevertheless, we expect positive BEF relationships to strengthen over time since those experiments are still at the early developing phase (Guerrero-Ramírez *et al*., 2017; Bongers *et al*., 2021; Urgoiti *et al*., 2022).

Effects of mycorrhizal associations on tree species richness–community productivity relationships

There was an overall significant concave-negative relationship between AM tree abundance and community productivity, suggesting that mixing AM and ECM trees had positive effects on productivity (S. Luo *et al*., 2023). When fitted after AM tree abundance in the same model, tree species richness did not show any significant effects on community productivity. However, this

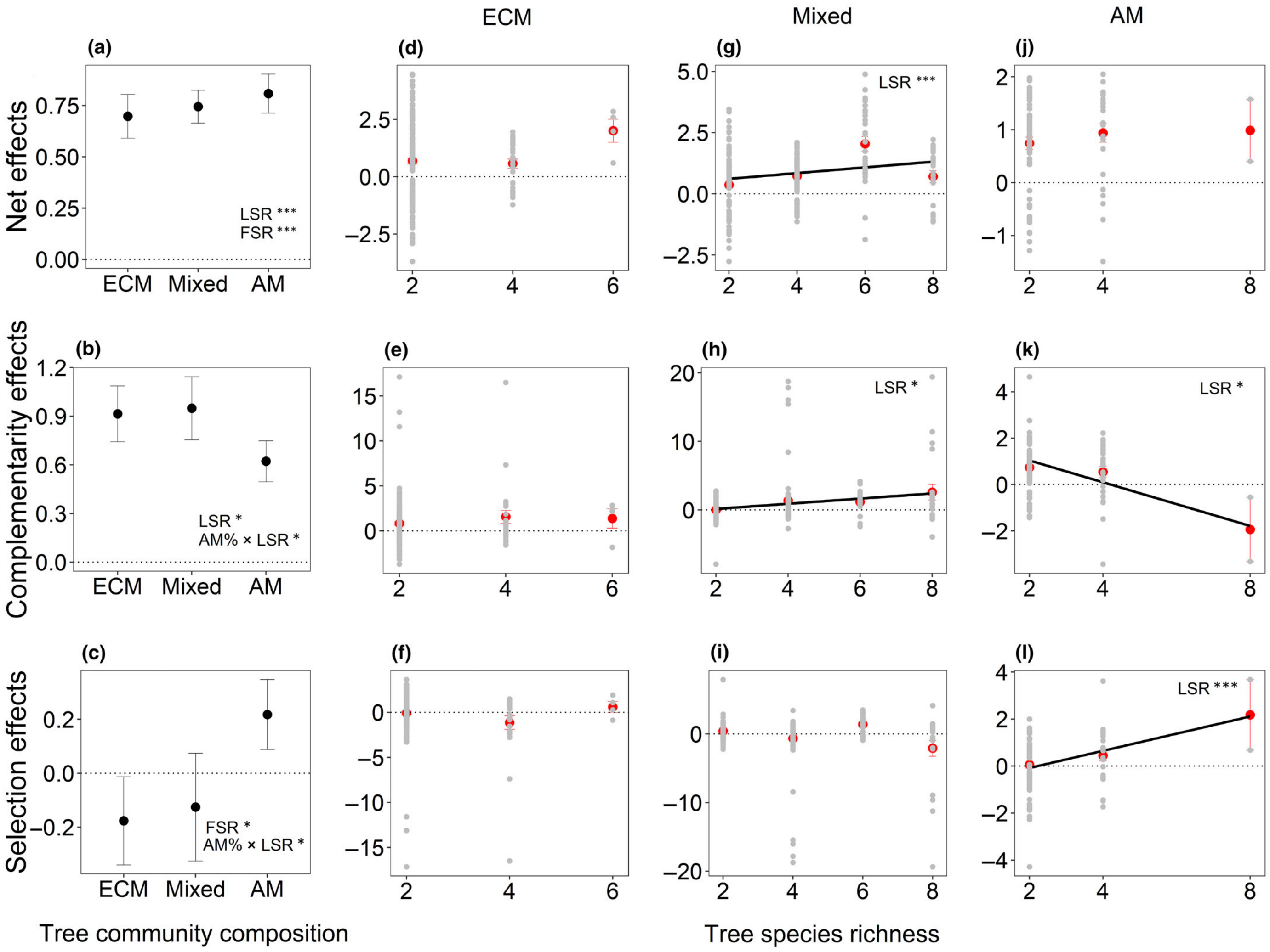

Fig. 4 Biodiversity effects in experiments showing significant richness–productivity relationships. Four experiments were included in the analysis (i.e. BEF-China, IDENT-Cloquet, IDENT-SSM, MyDiv). (a–c) Biodiversity effects split into net, complementarity, and sampling effects per community group: 'ECM' represents communities containing only ECM tree species; 'Mixed' represents communities containing both arbuscular (AM) and ectomycorrhizal (ECM) tree species; 'AM' represents communities containing only AM tree species. Biodiversity effects per species-richness level are shown for communities containing only ECM tree species (d–f), communities containing both ECM and AM tree species (g–i), and communities containing only AM tree species (j–l). Black dots and red dots represent means (± SE) calculated from observed values, whereas gray dots represent observed values. Asterisks indicate the significant effects of tree species richness (linear species richness (LSR); factorial species richness (FSR)) and the interactions between richness and relative AM tree abundance (LSR × AM) on biodiversity effects: *, $P < 0.05$; ***, $P < 0.001$. See Supporting Information Table S8 for statistical results.

does not necessarily mean that species richness had no effects on community productivity, because communities with higher richness were also more likely to contain both mycorrhizal types. In our dataset, AM tree abundance was created by manipulating species richness and can represent some variation in functional traits of the component species (Averill *et al*., 2019). Therefore, the impacts of species richness on productivity may have been partially explained by AM tree abundance represented in the studied communities.

Nevertheless, species richness and AM tree abundance (both linear and quadratic terms) had significant interactive effects on community productivity. This suggests that AM tree abundance can modify species richness–community productivity relationships. Specifically, in mixed AM–ECM tree communities, species richness was positively related to productivity across experiments and in five out of six experiments. In ECM tree communities, species richness showed significant positive effects on productivity when tested across six experiments, but no such significant effects were found in AM tree communities. This supports our second hypothesis that communities containing both AM and ECM trees would have stronger richness–productivity relationships than those communities containing only AM trees. These patterns were unlikely influenced by tree planting density in experiments, as planting density did not show any significant effects on productivity after accounting for the effects of AM tree abundance (Table S10: $P > 0.05$ for tree density and tree density × LSR in Model B). Therefore, our study provides experimental evidence for recent findings in natural forests that mixed stands containing AM and ECM trees achieve higher productivity than stands dominated by a single type of mycorrhizal

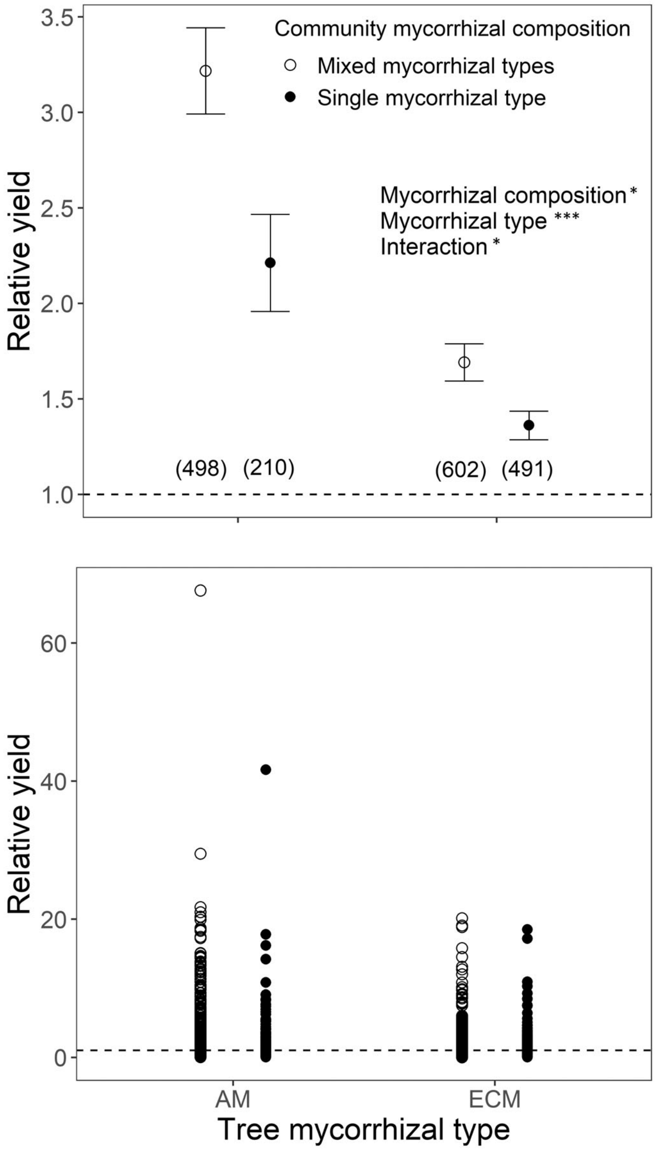

Fig. 5 Mean relative yield of arbuscular (AM) and ectomycorrhizal (ECM) tree species in communities with mixed mycorrhizal types (AM + ECM) or single mycorrhizal type (only AM or ECM). In the upper panel, symbols are means (± SE), calculated from raw data, in the lower panel symbols are observed values. The dashed line marks a relative yield equal to 1, with dots above the line indicating overyielding. *n* per treatment level is shown in parentheses. Statistically significant factors in mixed-effects ANOVA are marked with '*': *, $P < 0.05$; ***, $P < 0.001$ (see Supporting Information Table S9 for statistical results).

association (S. Luo *et al.*, 2023), and that monodominance of AM trees can weaken positive tree species richness–community biomass relationships (Mao *et al.*, 2023).

In mixed AM–ECM tree communities, species richness was positively related to complementarity effects and thus net biodiversity effects. In support of the complementarity effects, both AM and ECM tree species were more productive in mixed AM–ECM communities than in communities assembled by species of their own mycorrhizal type. This is consistent with our third hypothesis that the positive richness–productivity relationship in mixed AM–ECM tree communities was mainly driven by complementarity between AM and ECM tree species. It is also consistent with a previous experiment showing that mixtures of AM and ECM trees can promote complementarity effects and thus community productivity, because AM and ECM trees may preferentially use different chemical forms of nitrogen and phosphorus (Liu *et al.*, 2018; Luo *et al.*, 2018). Therefore, AM and ECM tree species may have complementary resource niches that can enhance the nutrient uptake efficiency of mixed AM–ECM tree communities. Although we did not directly test whether N-fixing or non-N-fixing AM trees differentially influenced ECM trees, the presence of N-fixing AM trees and AM tree abundance did not show any significant interactive effects on community productivity (Table S11: $P = 0.804$ and $P = 0.192$ for linear AM × presence of N fixers and quadratic AM × presence of N fixers, respectively). This suggests that the effects of AM tree abundance on productivity were independent of the N-fixing ability of AM trees in our dataset. In other words, the positive richness–productivity relationship in mixed AM–ECM tree communities was unlikely a result of the 'fertilization effect' of N-fixing AM trees. Similarly, in a large-scale global study, Feng *et al.* (2022) did not find any difference in tree-diversity effects when mixing N-fixing or non-N-fixing species only or when mixing N-fixing with non-N-fixing species. In addition to resource partitioning, other processes could contribute to complementarity between AM and ECM trees, such as biotic feedbacks mediated by mycorrhizal fungi (Barry *et al.*, 2019; Yang *et al.*, 2022; Yi *et al.*, 2024). For instance, different types of mycorrhizal fungal partners can complement each other in protecting their host plants against pathogens and herbivores (Tedersoo *et al.*, 2020), which should benefit mixed AM–ECM tree communities (Tedersoo & Bahram, 2019), and they may provide better protection against abiotic stresses like drought (Augé, 2001; Eisenhauer *et al.*, 2022). We also suspect that mixed AM–ECM tree communities are likely to elevate nutrient levels in circulation (Bönisch *et al.*, 2024). These processes may have collectively led to complementarity between AM and ECM trees and driven the positive richness–productivity relationship in mixed AM–ECM tree communities.

In AM tree communities, community productivity did not increase with increasing species richness, whereas selection effects did. Consistently, one study in a subtropical ecosystem reported increased selection effects in diverse AM tree communities (Deng *et al.*, 2023). This may be attributable to the dominance of generally fast-growing AM tree species with acquisitive nutrient strategies (Phillips *et al.*, 2013; Averill *et al.*, 2018; Deng *et al.*, 2023). Beside mycorrhizal associations, soil fertility can mediate the strength of richness–productivity relationships directly and indirectly by interacting with mycorrhizal associations (Luo *et al.*, 2017; Ma *et al.*, 2023; Mao *et al.*, 2023). For instance, it has been shown that the positive association between species richness and biomass of AM trees weakened with increasing soil fertility in a subtropical forest (Ma *et al.*, 2023). Therefore, we suggest that testing the generality of our findings requires long-term studies across a broad range of environmental conditions (Guerrero-Ramírez *et al.*, 2017). In ECM tree communities, species richness showed a significant positive effect on productivity, but nonsignificant effects on complementarity and selection effects. Because the latter can only be assessed for mixtures, we conclude that the diversity effects of ECM trees on productivity were mainly due to a difference between monocultures and mixtures. This is consistent with the findings that species richness of ECM trees was positively related to aboveground biomass of ECM trees in subtropical forest ecosystems (Y. Luo *et al.*, 2023; Ma *et al.*, 2023). We suspect that positive species-diversity effects of ECM trees are likely to strengthen over time (Guerrero-Ramírez *et al.*, 2017; Bongers *et al.*, 2021; Ma *et al.*, 2023), as there is evidence that complementarity effects can emerge and increase over time in communities assembled from ECM tree species (Jucker *et al.*, 2020). By contrast, a previous study found that species richness of ECM trees had a negative association with the biomass of ECM trees at large (50-m), but not small (10-m), spatial scale in a subtropical forest (Ma *et al.*, 2023). Therefore, the form of tree species richness–productivity in ECM-dominated communities remains inconclusive between experimental and observational studies, which is not unusual (Schmid, 2002). In observational studies, the causality of an association between species richness of ECM trees and productivity is unknown and likely to vary with spatial scales and environmental conditions, such as soil fertility (Guerrero-Ramírez *et al.*, 2017; Ma *et al.*, 2023). Overall, our study suggests that the magnitude of, and mechanisms behind, tree species diversity–productivity relationships depended on mycorrhizal associations (Deng *et al.*, 2023; Dietrich *et al.*, 2023; Mao *et al.*, 2023), with mixed AM–ECM tree communities showing a stronger relationship with complementarity effects and community productivity than communities with only AM or ECM trees.

Implications for biodiversity−ecosystem functioning research

Although BEF relationships in natural forests are strongly positive overall (Liang *et al.*, 2016), they are highly variable among forests (Scherer-Lorenzen, 2014; van der Plas, 2019), ranging from positive (Ammer, 2019) to nonsignificant (Wu *et al.*, 2015) or even negative (Szwagrzyk & Gazda, 2007). While previous studies have shown how abiotic factors can explain some of the variation in the strength of BEF relationships across different forest ecosystems (Forrester, 2014; Jucker *et al.*, 2014, 2016; Ratcliffe *et al.*, 2017; Feng *et al.*, 2022), our study provides novel insights into such variation by suggesting that tree species richness−community productivity relationships can be modified by the composition of tree mycorrhizal associations. To better understand the mechanisms underlying BEF relationships, the next step would be disentangling the effects of differences in mycorrhizal traits and differences in other traits between AM- and ECM-associating tree species on complementarity effects.

Potential biases of the dataset

We acknowledge that the dataset used here has potential biases. First, our dataset does not represent all regions of the globe equally, with nine experiments located in the temperate biome and only two experiments in the (sub-) tropical biome. In addition, it does not cover experiments in the boreal biome. The limited number of experiments in the (sub-) tropical biome has restricted our ability to test the generality of species richness−community productivity relationships, especially for AM tree-dominated communities. While our study has provided novel explanations for variation in BEF relationships, we suggest that efforts are needed to acquire data from long-term tree-diversity experiments in underrepresented regions to further test the generality of these relationships (Paquette *et al.*, 2018). Second, some experiments have unequal number of AM and ECM tree species in their design, which could have limited the statistical power when comparing the effects of different tree mycorrhizal associations on species richness−community productivity relationships. Third, there are not many high-richness plots for the AM- or ECM-only communities, in other words, tree species richness and mycorrhizal-type richness are confounded (cor = 0.075 and $P = 0.007$ for the correlation between richness and AM tree abundance). In this case, the effects of AM tree abundance on productivity may partly represent species-richness effects, and this applies the same to the effects of richness on productivity. However, the gradient of AM tree abundance, which was created by manipulating species richness in our dataset, may represent some variation in traits of communities that can influence plant resource use and productivity. Therefore, we cannot fully distinguish tree-diversity effects derived from the gradient of AM tree abundance from that driven by the designed gradient of species richness. More standardized tree diversity experiments (e.g. the MyDiv experiment) that directly manipulate tree mycorrhizal compositions within species-richness levels will help address this point (Tobner *et al.*, 2014; Ferlian *et al.*, 2018), once they are sufficiently well established. Finally, our study focused on aboveground community productivity due to the lack of data on belowground productivity. Martin-Guay *et al.* (2020) showed contrasting above- and belowground biomass responses to tree species diversity at one of the experimental sites used in this synthesis. AM tree species can allocate more biomass to root tissues than ECM tree species (Jevon & Lang, 2022); we therefore suggest that exploring the response of belowground productivity to tree species diversity and mycorrhizal associations may further improve our understanding of forest ecosystem functioning.

Conclusions

In conclusion, we show that tree species richness can promote community productivity via complementarity effects, but the strength of this relationship is contingent upon the diversity of tree mycorrhizal associations. Communities with a mixture of AM and ECM tree species showed positive species richness−community productivity relationships across experiments, which were driven by complementarity effects. Consistently, both AM and ECM tree species were more productive in mixed AM–ECM communities than in communities assembled by species of their own mycorrhizal type. This indicates that complementarity between AM and ECM tree species is likely to enhance community productivity under varying environmental conditions. Therefore, our study provides novel insights into mechanisms underlying the context dependency in BEF relationships by suggesting that tree–mycorrhiza interactions can modify BEF relationships.

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Competing interests

None declared.

Author contributions

SL and NE conceived the ideas. SL planned and designed the research. SL and BS analyzed the data. SL wrote the manuscript with inputs from NE, BS, AH, MS-L, KV, and all other authors. BS, MS-L, KV, NB, JB, FB, HB, OF, DG, JSH, PH, YH, DH, HK, XL, CM, CN, AP, JDP, WCP, GBP, PBR, BR, HS, KS, AS, LW and NE provided the data. All authors contributed to the final revisions.

ORCID

Juergen Bauhus https://orcid.org/0000-0002-9673-4986
Friderike Beyer https://orcid.org/0000-0002-3597-5022
Helge Bruelheide https://orcid.org/0000-0003-3135-0356
Nico Eisenhauer https://orcid.org/0000-0002-0371-6720
Olga Ferlian https://orcid.org/0000-0002-2536-7592
Dirk Hölscher https://orcid.org/0000-0002-7097-3102
Peter Hajek https://orcid.org/0000-0001-5268-8917
Yuanyuan Huang https://orcid.org/0000-0002-6990-8864
Xiaojuan Liu https://orcid.org/0000-0002-9292-4432
Shan Luo https://orcid.org/0000-0002-5408-847X
Alain Paquette https://orcid.org/0000-0003-1048-9674
Gustavo B. Paterno https://orcid.org/0000-0001-9719-3037
Peter B. Reich https://orcid.org/0000-0003-4424-662X
Boris Rewald https://orcid.org/0000-0001-8098-0616
Hans Sandén https://orcid.org/0000-0002-2496-6307
Michael Scherer-Lorenzen https://orcid.org/0000-0001-9566-590X
Bernhard Schmid https://orcid.org/0000-0002-8430-3214
Katherine Sinacore https://orcid.org/0000-0002-8719-9248
Artur Stefanski https://orcid.org/0000-0002-5412-1014
Kris Verheyen https://orcid.org/0000-0002-2067-9108
Laura Williams https://orcid.org/0000-0003-3555-4778

Data availability

Data that support the main findings of this study are available at doi: 10.6084/m9.figshare.25813747. Data of the MyDiv experiment are publicly available at doi: 10.25829/20WZ-DC69 and 10.25829/R7N9-MH52.

References

Ammer C. 2019. Diversity and forest productivity in a changing climate. *New Phytologist* 221: 50–66.

Augé RM. 2001. Water relations, drought and vesicular-arbuscular mycorrhizal symbiosis. *Mycorrhiza* 11: 3–42.

Averill C, Bhatnagar JM, Dietze MC, Pearse WD, Kivlin SN. 2019. Global imprint of mycorrhizal fungi on whole-plant nutrient economics. *Proceedings of the National Academy of Sciences, USA* 116: 23163–23168.

Averill C, Dietze MC, Bhatnagar JM. 2018. Continental-scale nitrogen pollution is shifting forest mycorrhizal associations and soil carbon stocks. *Global Change Biology* 24: 4544–4553.

Barry KE, Mommer L, van Ruijven J, Wirth C, Wright AJ, Bai Y, Connolly J, De Deyn GB, de Kroon H, Isbell F *et al.* 2019. The future of complementarity: disentangling causes from consequences. *Trends in Ecology & Evolution* 34: 167–180.

Binkley D, Senock R, Bird S, Cole TG. 2003. Twenty years of stand development in pure and mixed stands of *Eucalyptus saligna* and nitrogen-fixing *Facaltaria moluccana*. *Forest Ecology and Management* 182: 93–102.

Bongers FJ, Schmid B, Bruelheide H, Bongers F, Li S, von Oheimb G, Li Y, Cheng A, Ma K, Liu X. 2021. Functional diversity effects on productivity increase with age in a forest biodiversity experiment. *Nature Ecology & Evolution* 5: 1594–1603.

Bongers FJ, Schmid B, Sun Z, Li Y, Härdtle W, von Oheimb G, Li Y, Li S, Staab M, Ma K *et al.* 2020. Growth–trait relationships in subtropical forest are stronger at higher diversity. *Journal of Ecology* 108: 256–266.

Bönisch E, Blagodatskaya E, Dirzo R, Ferlian O, Fichtner A, Huang Y, Leonard SJ, Maestre FT, Oheimb G v, Ray T *et al.* 2024. Mycorrhizal type and tree diversity affect foliar elemental pools and stoichiometry. *New Phytologist* 242: 1614–1629.

Cook-Patton SC, LaForgia M, Parker JD. 2014. Positive interactions between herbivores and plant diversity shape forest regeneration. *Proceedings of the Royal Society B: Biological Sciences* 281: 20140261.

Deng M, Hu S, Guo L, Jiang L, Huang Y, Schmid B, Liu C, Chang P, Li S, Liu X *et al.* 2023. Tree mycorrhizal association types control biodiversity-productivity relationship in a subtropical forest. *Science Advances* 9: 4468.

Deng M, Liu L, Jiang L, Liu W, Wang X, Li S, Yang S, Wang B. 2018. Ecosystem scale trade-off in nitrogen acquisition pathways. *Nature Ecology & Evolution* 2: 1724–1734.

Dietrich P, Ferlian O, Huang Y, Luo S, Quosh J, Eisenhauer N. 2023. Tree diversity effects on productivity depend on mycorrhizae and life strategies in a temperate forest experiment. *Ecology* 104: 1–16.

Eisenhauer N, Bonfante P, Buscot F, Cesarz S, Guerra C, Heintz-Buschart A, Hines J, Patoine G, Rillig M, Schmid B *et al.* 2022. Biotic interactions as mediators of context-dependent biodiversity-ecosystem functioning relationships. *Research Ideas & Outcomes* 8: e85873.

Fahey C, Parker WC, Paquette A, Messier C, Antunes PM. 2023. Soil fungal communities contribute to the positive diversity–productivity relationship of tree communities under contrasting water availability. *Journal of Ecology* 20: 1–15.

Feng Y, Schmid B, Loreau M, Forrester DI, Fei S, Zhu J, Tang Z, Zhu J, Hong P, Ji C *et al.* 2022. Multispecies forest plantations outyield monocultures across a broad range of conditions. *Science* 376: 865–868.

Ferlian O, Cesarz S, Craven D, Hines J, Barry KE, Bruelheide H, Buscot F, Haider S, Heklau H, Herrmann S *et al.* 2018. Mycorrhiza in tree diversity–ecosystem function relationships: conceptual framework and experimental implementation. *Ecosphere* **9**: e02226.

Forrester DI. 2014. The spatial and temporal dynamics of species interactions in mixed-species forests: from pattern to process. *Forest Ecology and Management* **312**: 282–292.

Forrester DI, Bauhus J. 2016. A review of processes behind diversity—productivity relationships in forests. *Current Forestry Reports* **2**: 45–61.

Guerrero-Ramírez NR, Craven D, Reich PB, Ewel JJ, Isbell F, Koricheva J, Parrotta JA, Auge H, Erickson HE, Forrester DI *et al.* 2017. Diversity-dependent temporal divergence of ecosystem functioning in experimental ecosystems. *Nature Ecology & Evolution* **1**: 1639–1642.

Hector A, Schmid B, Beierkuhnlein C, Caldeira MC, Diemer M, Dimitrakopoulos PG, Finn JA, Freitas H, Giller PS, Good J *et al.* 1999. Plant diversity and productivity experiments in European grasslands. *Science* **286**: 1123–1127.

van der Heijden MGA, Martin FM, Selosse MA, Sanders IR. 2015. Mycorrhizal ecology and evolution: the past, the present, and the future. *New Phytologist* **205**: 1406–1423.

Hooper DU, Chapin FS, Ewel JJ, Hector A, Inchausti P, Lavorel S, Lawton JH, Lodge DM, Loreau M, Naeem S *et al.* 2005. Effects of biodiversity on ecosystem functioning: a consensus of current knowledge. *Ecological Monographs* **75**: 3–35.

Huang Y, Chen Y, Castro-Izaguirre N, Baruffol M, Brezzi M, Lang A, Li Y, Härdtle W, von Oheimb G, Yang X *et al.* 2018. Impacts of species richness on productivity in a large-scale subtropical forest experiment. *Science* **362**: 80–83.

Jevon FV, Lang AK. 2022. Tree biomass allocation differs by mycorrhizal association. *Ecology* **103**: 1–9.

Jing X, Muys B, Bruelheide H, Desie E, Hättenschwiler S, Jactel H, Jaroszewicz B, Kardol P, Ratcliffe S, Scherer-Lorenzen M *et al.* 2021. Above- and below-ground complementarity rather than selection drive tree diversity–productivity relationships in European forests. *Functional Ecology* **35**: 1756–1767.

Jo I, Fei S, Oswalt CM, Domke GM, Phillips RP. 2019. Shifts in dominant tree mycorrhizal associations in response to anthropogenic impacts. *Science Advances* **5**: eaav6358.

Jucker T, Avăcăritei D, Bărnoaiea I, Duduman G, Bouriaud O, Coomes DA. 2016. Climate modulates the effects of tree diversity on forest productivity. *Journal of Ecology* **104**: 388–398.

Jucker T, Bouriaud O, Avacaritei D, D nil I, Duduman G, Valladares F, Coomes DA. 2014. Competition for light and water play contrasting roles in driving diversity-productivity relationships in Iberian forests. *Journal of Ecology* **102**: 1202–1213.

Jucker T, Koricheva J, Finér L, Bouriaud O, Iacopetti G, Coomes DA. 2020. Good things take time—diversity effects on tree growth shift from negative to positive during stand development in boreal forests. *Journal of Ecology* **108**: 2198–2211.

Laforest-Lapointe I, Paquette A, Messier C, Kembel SW. 2017. Leaf bacterial diversity mediates plant diversity and ecosystem function relationships. *Nature* **546**: 145–147.

Li Y, Schmid B, Schuldt A, Li S, Wang MQ, Fornoff F, Staab M, Guo PF, Anttonen P, Chesters D *et al.* 2023. Multitrophic arthropod diversity mediates tree diversity effects on primary productivity. *Nature Ecology & Evolution* **7**: 832–840.

Liang J, Crowther TW, Picard N, Wiser S, Zhou M, Alberti G, Schulze ED, McGuire AD, Bozzato F, Pretzsch H *et al.* 2016. Positive biodiversity-productivity relationship predominant in global forests. *Science* **354**: 8579.

Liang M, Liu X, Parker IM, Johnson D, Zheng Y, Luo S, Gilbert GS, Yu S. 2019. Soil microbes drive phylogenetic diversity-productivity relationships in a subtropical forest. *Science Advances* **5**: 1–9.

Liu X, Burslem DFRP, Taylor JD, Taylor AFS, Khoo E, Majalap-Lee N, Helgason T, Johnson D. 2018. Partitioning of soil phosphorus among arbuscular and ectomycorrhizal trees in tropical and subtropical forests. *Ecology Letters* **21**: 713–723.

Loreau M, Hector A. 2001. Partitioning selection and complementarity in biodiversity experiments. *Nature* **412**: 72–76.

Loreau M, Naeem S, Inchausti P, Bengtsson J, Grime JP, Hector A, Hooper DU, Huston MA, Raffaelli D, Schmid B *et al.* 2001. Biodiversity and ecosystem functioning: current knowledge and future challenges. *Science* **294**: 804–808.

Luo S, Bardgett RD, Schmid B, Johnson D, Png K, Schaffner U, Zhou H, Yao B, Hou X, Ostle NJ. 2022. Historical context modifies plant diversity–community productivity relationships in alpine grassland. *Journal of Ecology* **110**: 2205–2218.

Luo S, De Deyn GB, Jiang B, Yu S. 2017. Soil biota suppress positive plant diversity effects on productivity at high but not low soil fertility. *Journal of Ecology* **105**: 1766–1774.

Luo S, Phillips RP, Jo I, Fei S, Liang J, Schmid B, Eisenhauer N. 2023a. Higher productivity in forests with mixed mycorrhizal strategies. *Nature Communications* **14**: 1377.

Luo S, Schmid B, De Deyn GB, Yu S. 2018. Soil microbes promote complementarity effects among co-existing trees through soil nitrogen partitioning. *Functional Ecology* **32**: 1879–1889.

Luo Y, Ma L, Seibold S, Cadotte MW, Burgess KS, Tan S, Ye L, Zheng W, Zou J, Chen Z *et al.* 2023b. The diversity of mycorrhiza-associated fungi and trees shapes subtropical mountain forest ecosystem functioning. *Journal of Biogeography* **50**: 715–729.

Ma J, Chen L, Mi X, Ren H, Liu X, Wang Y, Wang F, Yao Y, Zhang Y, Ma K. 2023. The interactive effects of soil fertility and tree mycorrhizal association explain spatial variation of diversity–biomass relationships in a subtropical forest. *Journal of Ecology* **111**: 1037–1049.

Mao Z, van der Plas F, Corrales A, Anderson-Teixeira KJ, Bourg NA, Chu C, Hao Z, Jin G, Lian J, Lin F *et al.* 2023. Scale-dependent diversity–biomass relationships can be driven by tree mycorrhizal association and soil fertility. *Ecological Monographs* **93**: e1568.

Martin-Guay M, Paquette A, Reich PB, Messier C. 2020. Implications of contrasted above- and below-ground biomass responses in a diversity experiment with trees. *Journal of Ecology* **108**: 405–414.

Mayoral C, van Breugel M, Cerezo A, Hall JS. 2017. Survival and growth of five *Neotropical timber* species in monocultures and mixtures. *Forest Ecology and Management* **403**: 1–11.

Mayoral C, van Breugel M, Turner BL, Asner GP, Vaughn NR, Hall JS. 2019. Effect of microsite quality and species composition on tree growth: a semi-empirical modeling approach. *Forest Ecology and Management* **432**: 534–545.

Mommer L, Cotton TEA, Raaijmakers JM, Termorshuizen AJ, van Ruijven J, Hendriks M, van Rijssel SQ, van de Mortel JE, van der Paauw JW, Schijlen EGWM *et al.* 2018. Lost in diversity: the interactions between soil-borne fungi, biodiversity and plant productivity. *New Phytologist* **218**: 542–553.

Paquette A, Hector A, Castagneyrol B, Vanhellemont M, Koricheva J, Scherer-Lorenzen M, Verheyen K, Abdala-Roberts L, Auge H, Barsoum N *et al.* 2018. A million and more trees for science. *Nature Ecology & Evolution* **2**: 763–766.

Phillips RP, Brzostek E, Midgley MG. 2013. The mycorrhizal-associated nutrient economy: a new framework for predicting carbon-nutrient couplings in temperate forests. *New Phytologist* **199**: 41–51.

van der Plas F. 2019. Biodiversity and ecosystem functioning in naturally assembled communities. *Biological Reviews* **94**: 1220–1245.

Ratcliffe S, Wirth C, Jucker T, van der Plas F, Scherer-Lorenzen M, Verheyen K, Allan E, Benavides R, Bruelheide H, Ohse B *et al.* 2017. Biodiversity and ecosystem functioning relations in European forests depend on environmental context. *Ecology Letters* **20**: 1414–1426.

Ray T, Delory BM, Beugnon R, Bruelheide H, Cesarz S, Eisenhauer N, Ferlian O, Quosh J, von Oheimb G, Fichtner A. 2023. Tree diversity increases productivity through enhancing structural complexity across mycorrhizal types. *Science Advances* **9**: 1–11.

Read DJ. 1991. Mycorrhizas in ecosystems. *Experientia* **47**: 376–391.

Reich PB, Tilman D, Isbell F, Mueller K, Hobbie SE, Flynn DFB, Eisenhauer N. 2012. Impacts of biodiversity loss escalate through time as redundancy fades. *Science* **336**: 589–592.

Scherer-Lorenzen M. 2014. The functional role of biodiversity in the context of global change. *Forests and Global Change* **1**: 195–238.

Schmid B. 2002. The species richness–productivity controversy. *Trends in Ecology & Evolution* **17**: 113–114.

Schmid B, Baruffol M, Wang Z, Niklaus PA. 2017. A guide to analyzing biodiversity experiments. *Journal of Plant Ecology* **10**: 91–110.

Schnabel F, Schwarz JA, Dănescu A, Fichtner A, Nock CA, Bauhus J, Potvin C. 2019. Drivers of productivity and its temporal stability in a tropical tree diversity experiment. *Global Change Biology* **25**: 4257–4272.

Schnitzer SA, Klironomos JN, HilleRisLambers J, Kinkel LL, Reich PB, Xiao K, Rillig MC, Sikes BA, Callaway RM, Mangan SA *et al.* 2011. Soil microbes drive the classic plant diveristy-productivity pattern. *Ecology* **92**: 296–303.

Steidinger BS, Crowther TW, Liang J, Van Nuland ME, Werner GDA, Reich PB, Nabuurs G, de-Miguel S, Zhou M, Picard N *et al.* 2019. Climatic controls of decomposition drive the global biogeography of forest-tree symbioses. *Nature* **569**: 404–408.

Szwagrzyk J, Gazda A. 2007. Above-ground standing biomass and tree species diversity in natural stands of Central Europe. *Journal of Vegetation Science* **18**: 555–562.

Tedersoo L, Bahram M. 2019. Mycorrhizal types differ in ecophysiology and alter plant nutrition and soil processes. *Biological Reviews* **94**: 1857–1880.

Tedersoo L, Bahram M, Zobel M. 2020. How mycorrhizal associations drive plant population and community biology. *Science* **367**: eaba1223.

Terrer C, Phillips RP, Hungate BA, Rosende J, Pett-Ridge J, Craig ME, van Groenigen KJ, Keenan TF, Sulman BN, Stocker BD *et al.* 2021. A trade-off between plant and soil carbon storage under elevated CO_2. *Nature* **591**: 599–603.

Tilman D. 1999. The ecological consequences of changes in biodiversity: a search for general principles. *Ecology* **80**: 1455–1474.

Tilman D, Isbell F, Cowles JM. 2014. Biodiversity and ecosystem functioning. *Annual Review of Ecology, Evolution, and Systematics* **45**: 471–493.

Tobner CM, Paquette A, Reich PB, Gravel D, Messier C. 2014. Advancing biodiversity–ecosystem functioning science using high-density tree-based experiments over functional diversity gradients. *Oecologia* **174**: 609–621.

Urgoiti J, Messier C, Keeton WS, Reich PB, Gravel D, Paquette A. 2022. No complementarity no gain—Net diversity effects on tree productivity occur once complementarity emerges during early stand development. *Ecology Letters* **25**: 851–862.

Van de Peer T, Verheyen K, Ponette Q, Setiawan NN, Muys B. 2018. Overyielding in young tree plantations is driven by local complementarity and selection effects related to shade tolerance. *Journal of Ecology* **106**: 1096–1105.

Verheyen K, Vanhellemont M, Auge H, Baeten L, Baraloto C, Barsoum N, Bilodeau-Gauthier S, Bruelheide H, Castagneyrol B, Godbold D *et al.* 2016. Contributions of a global network of tree diversity experiments to sustainable forest plantations. *Ambio* **45**: 29–41.

Wu X, Wang X, Tang Z, Shen Z, Zheng C, Xia X, Fang J. 2015. The relationship between species richness and biomass changes from boreal to subtropical forests in China. *Ecography* **38**: 602–613.

Yang B, Liang Y, Schmid B, Baruffol M, Li Y, He L, Salmon Y, Tian Q, Niklaus PA, Ma K. 2022. Soil fungi promote biodiversity–productivity relationships in experimental communities of young trees. *Ecosystems* **25**: 858–871.

Yi H, Eisenhauer N, Austen JC, Rebollo R, Ray T, Bönisch E, von Oheimb G, Fichtner A, Schuldt A, Patoine G *et al.* 2024. Tree diversity and mycorrhizal type co-determine multitrophic ecosystem functions. *Journal of Ecology* **112**: 528–546.

Zhang HY, Xiao-Tao L, Hartmann H, Keller A, Han XG, Trumbore S, Phillips RP. 2018. Foliar nutrient resorption differs between arbuscular mycorrhizal and ectomycorrhizal trees at local and global scales. *Global Ecology and Biogeography* **27**: 875–885.

Zhang Y, Chen HYH, Reich PB. 2012. Forest productivity increases with evenness, species richness and trait variation: a global meta-analysis. *Journal of Ecology* **100**: 742–749.

Supporting Information

Additional Supporting Information may be found online in the Supporting Information section at the end of the article.

Dataset S1 A list of species included in the 11 experiments.

Fig. S1 Relationships between tree species richness and accumulated basal area.

Fig. S2 Biodiversity effects in four experiments showing significant positive effects of tree species richness on community productivity.

Fig. S3 Relationships between AM tree abundance and community productivity.

Table S1 Summary of mixed-effects ANOVA testing the effects of tree species richness on accumulated basal area across all 11 experiments.

Table S2 Summary of mixed-effects ANOVA testing the effects of tree species richness on tree community productivity and accumulated basal area.

Table S3 Summary of mixed-effects ANOVA results for tree community productivity in each of the nine experiments.

Table S4 Summary of ANOVA results for biodiversity effects.

Table S5 Summary of mixed-effects ANOVA testing the effects of arbuscular mycorrhizal tree abundance and tree species richness on tree community productivity.

Table S6 Summary of mixed-effects ANOVA results for tree community productivity in experiments containing both arbuscular mycorrhizal and ectomycorrhizal tree species.

Table S7 Summary of mixed-effects ANOVA results for tree community productivity in each experiment containing both arbuscular mycorrhizal and ectomycorrhizal tree species.

Table S8 Summary of mixed-effects ANOVA results for biodiversity effects in four experiments showing significant positive effects of tree species richness on community productivity.

Table S9 Summary of mixed-effects ANOVA testing whether the mean relative yield of species was influenced by community mycorrhizal composition and tree mycorrhizal type.

Table S10 Summary of mixed-effects ANOVA testing tree species richness–community productivity relationships (Model A) and the effects of AM tree abundance on richness–productivity relationships (Model B), which accounted for the effects of planting density of trees on productivity.

Table S11 Summary of mixed-effects ANOVA testing how AM tree abundance influences richness–productivity relationships, which included the potential effects of nitrogen-fixing tree species.