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Summary

• Multispecies planting is an important approach to deliver ecosystem functions in afforestation projects. However, the importance of species richness vs specific species composition in this context remains unresolved.

• To estimate species or functional group richness and compositional change between two communities, we calculated nestedness, where one community contains a subset of the species of another, and turnover, where two communities differ in species composition but not in species richness. We evaluated the effects of species/functional group nestedness and turnover on stand productivity using 315 mixed plots from a pool of 40 tree species in a large forest biodiversity experiment in subtropical China.

• We found that the greater the differences in species or functional group nestedness and turnover, the greater the differences in stand productivity between plots. Additionally, the strong effects of both nestedness and turnover on stand productivity developed over the 11-yr observation period.

• Our results indicate that selection of specific tree species is as important as planting a large number of species to support the productivity function of forests. Furthermore, the selection of specific tree species should be based on functionality, because beneficial effects of functional group composition were stronger than those of species composition.

Introduction

Forest ecosystems are the most important terrestrial carbon sinks and wildlife habitats (Canadell & Raupach, 2008; Levin, 2013) and are threatened by biodiversity loss (IPBES, 2019; IPCC, 2022). Restoring forest ecosystems is therefore an important tool for protecting biodiversity, maintaining ecosystem functioning (Griscom *et al.*, 2017; Bastin *et al.*, 2019; Buzhdygan *et al.*, 2020; Schnabel *et al.*, 2021), and increasing the resilience of forest ecosystems to climate change (Lewis *et al.*, 2019; Palmer, 2021; Zhang *et al.*, 2021). Recent experimental and observational studies suggest that planting multiple tree species may be beneficial for these goals, as increased tree species richness generally increases forest productivity, a major ecosystem function (Barrufol *et al.*, 2013; Scherer-Lorenzen, 2014; Liang *et al.*, 2016; Huang *et al.*, 2018; Liu *et al.*, 2018; Chen *et al.*, 2020; Feng *et al.*, 2022). However, it is unclear to what extent species richness, that is the number of species in general, or the combination of specific species within a community,

influences forest productivity (Huang *et al.*, 2018; Morin *et al.*, 2018; Jonsson *et al.*, 2019). To answer this question, we introduce two important processes, that is species nestedness and species turnover, which reflect species richness and compositional change between communities, respectively, and ultimately drive species assemblages in natural forests. We believe that it is important to analyze these often confounded effects separately, as this provides direct evidence for the importance of these two processes in influencing forest productivity.

Species nestedness and species turnover are two processes that can cause differences in productivity and other ecosystem functions between two forest communities (Baselga, 2010; Baselga & Orme, 2012). Species nestedness refers to the degree of species loss (Fig. 1a). One community is derived from the other by the extinction of some species (without immigration of new species), and the less species-rich community therefore shares all its species with the more species-rich community. Numerous studies show that plant species richness is generally positively related to forest productivity, both in natural ecosystems and in experimental
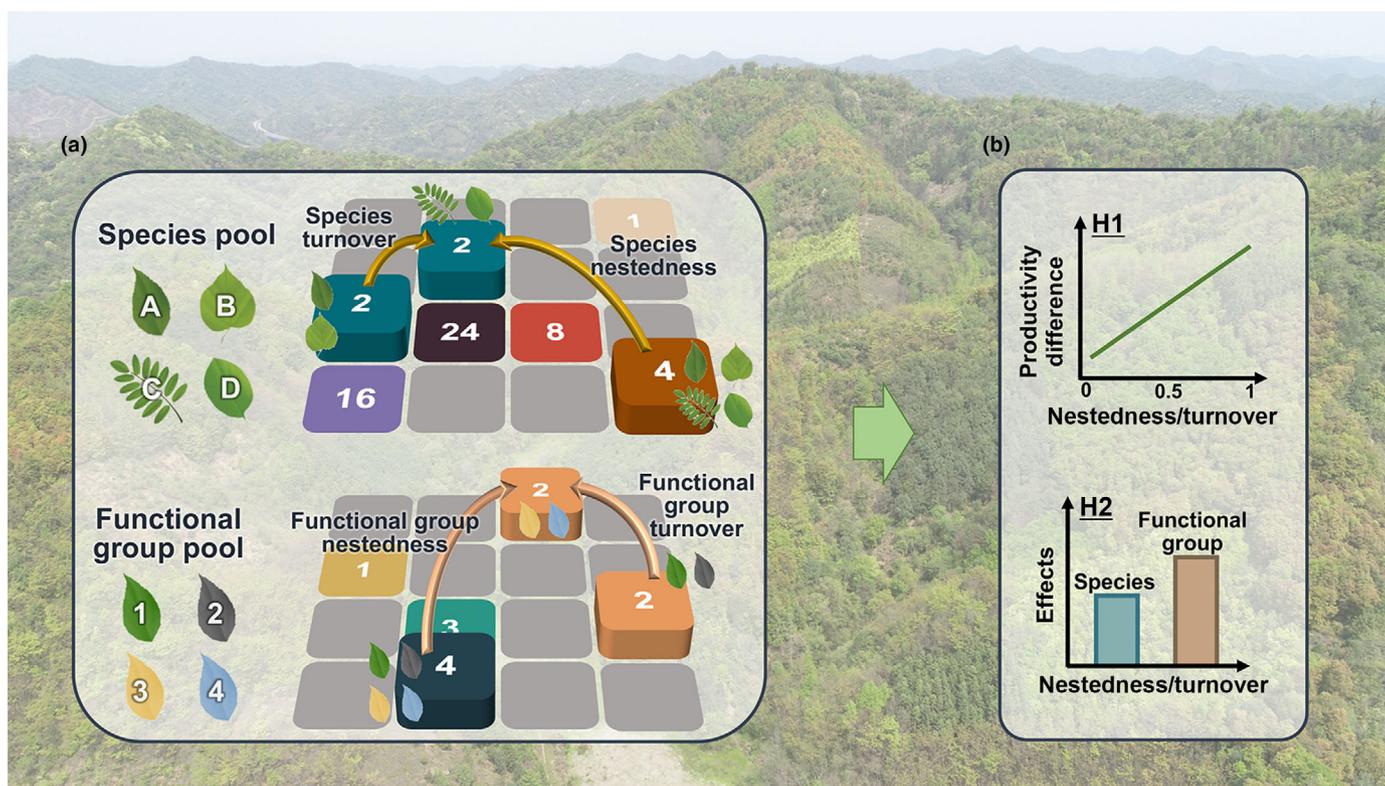
Fig. 1 Conceptual illustration of species/functional group nestedness and turnover, representing richness and compositional change between pairs of plots, and key hypotheses. (a) The upper panel describes species nestedness and turnover between pairs of plots, while the lower panel describes functional group nestedness and turnover between pairs of plots (only one of each situation is shown as an example). Species or functional group nestedness is defined as a reduction in species or functional group richness without replacement of resident species or functional groups at the lower richness level (i.e. extinction without immigration). Species or functional group turnover is defined as the replacement of resident species or functional groups without a change in species or functional group richness. Each square represents one plot, and each number indicates the species or functional group richness in that plot. At the species level, each leaf shape represents one of the four species A–D; at the functional group level, each leaf color represents one of the four functional groups 1–4. (b) We hypothesize that H1: with increasing species/functional group nestedness and turnover, the interspecific interaction patterns and functional trait space will change, leading to greater absolute differences in productivity; H2: because functional groups are important dimensions of species strategies, we predict that the effects of nestedness or turnover at the functional group level will be greater than the effects at the species level.

plantations at local and global scale. This is due to higher functional diversity, niche differentiation and complementarity in species-rich communities (Liang *et al.*, 2016; Huang *et al.*, 2018; Feng *et al.*, 2022). Consequently, species nestedness in forest ecosystems can influence productivity through changes in species richness. On the other hand, species turnover refers to the degree of species replacement (Fig. 1a). Thus, one community is derived from another by replacing some species with new ones, maintaining species richness but changing composition. Species composition also has been shown to affect forest productivity as the co-occurrence of different species groups represent different interaction patterns, such as resource use or competition between species (Jonsson *et al.*, 2019; García-Valdés *et al.*, 2020; Ma *et al.*, 2021). Therefore, species turnover can influence forest productivity through changes in species composition. In a similar way that species nestedness and turnover can affect forest productivity, even stronger effects can be expected from changes in functional group nestedness and turnover, because different functional groups are expected to contribute to high ecosystem productivity in an even more complementary way than different

species (Hector *et al.*, 1999; Hooper *et al.*, 2005; Liang *et al.*, 2016).

To investigate the effects of species and functional group nestedness and turnover on forest productivity, we tested two hypotheses (H1 and H2, Fig. 1b), using 11 yr of data from 315 mixture plots, that is plots with at least two tree species, from a forest biodiversity experiment. This is a unique dataset in which multiple nested extinction series were simulated, allowing us to separate nestedness and turnover by experimental design (BEF-China experiment; see Bruelheide *et al.*, 2014; Huang *et al.*, 2018; Chen *et al.*, 2020). First, we hypothesized that (H1) with increasing species/functional group nestedness, that is nestedness close to 1 in Fig. 1(b), the larger difference in species/functional group richness would lead to a higher productivity difference, and that (H1) with increasing species/functional group turnover, that is turnover close to 1 in Fig. 1(b), the larger difference in species/functional group composition (with the same species/functional group richness) would also lead to a higher productivity difference, but without specifying the direction of the difference.

Second, as species richness increases, functional redundancy among species may increase, and thus, the effects on productivity and other ecosystem functions may decrease. Therefore, functional group richness is often expected to be a better predictor of ecosystem functioning (Hector *et al.*, 1999; Hooper *et al.*, 2005). Accordingly, it is important to distinguish the importance of species nestedness and functional group nestedness. We hypothesized that (H2) functional group nestedness would have stronger influence on forest productivity than the corresponding measure at species level (Fig. 1b). Because functional groups are an important dimension of species strategies and underpin the essential character of a group of species, a change in species composition is not necessarily associated with a change in functional group composition. As functional group composition is more strongly related to functional diversity, which in turn affects productivity (Liang *et al.*, 2016; Tang *et al.*, 2022), we also expected (H2) functional group turnover to have a stronger effect on forest productivity than the corresponding species-level measure (Fig. 1b). Finally, we aimed to test whether the effects of nestedness and turnover differ in magnitude in order to derive recommendations on the relative importance of considering species richness and species composition in multispecies reforestation and afforestation projects.

The basic data we analyzed are pairs of plots. To ensure that nestedness was not confounded by turnover, we used plots where species from the lower richness plot were always present in the higher richness plot. To ensure that turnover was not confounded by nestedness, we only used plots with equal richness to calculate turnover (Fig. 1a). Plot pairs in which the plots differed in richness, but one was not a subset of the other in terms of species composition, were excluded from the analysis because they would have resulted in mixing of nestedness and turnover as defined here.

Although mixtures have generally shown higher productivity than constituent monocultures in experimental studies (referred to as overyielding; Schmid *et al.*, 2008; Feng *et al.*, 2022), it is not yet clear whether overyielding will continue to be realized after years of forest growth at different diversity levels. Therefore, in an additional analysis, we compared the mixtures with their constituent monocultures at the end of the time course to test whether overyielding still occurs after 10 yr of forest growth.

Materials and Methods

### Study site and experimental design

This study was conducted at the BEF-China experimental platform (www.bef-china.com) in Jiangxi Province, China (29°05′–29°08′N, 117°54′–117°56′E, Bruelheide *et al.*, 2014). The region is characterized as subtropical, with a mean annual temperature and precipitation of 16.7°C and 1821 mm, respectively. In 2009 and 2010, two sites, A and B, were established with forest plots of 1 mu (25.8×25.8 m, 0.067 ha). Each plot was planted with 400 tree individuals in a square grid of 20×20 trees (1.675 m^2 per tree individual at planting), and planting abundances of species within plots was always the same for each

species richness level. The species pool consisted of 40 angiosperm tree species, of which eight species used at both sites and 16 at only one site (Supporting Information Table S1; Fig. S1; see also Huang *et al.*, 2018). Random and nonrandom (trait-based) extinction series were generated to examine the effects of species loss on ecosystem functioning. For the random extinction series, three pools of 16 species were created at each site. The species in each 16-species pool were randomly ordered and then halved, quartered, etc., until only one species remained for monoculture plots of the 40 species. For the nonrandom extinction series, four 16-species pools ranked by specific leaf area (SLA) or species rarity were similarly partitioned, but only the partitions with lower SLA or more common species were retained in the design. A total of 478 plots were used in this study, including 163, 135, 80, 52, 38, and 10 plots with one, two, four, eight, 16, and 24 species per plot, respectively (Table S2). Plots with different species richness from the same species pool reflect nested extinction series and thus represent species nestedness, while plots with the same species richness but different species composition represent species turnover (Fig. 1a).

Functional groups

We classified our tree species into four functional groups using principal component analysis (PCA) so that the effects of changes in functional group nestedness and functional group turnover on forest productivity could be estimated in the same way as the effects of species nestedness and turnover. Functional groups were determined based on eight functional traits collected in the BEF-China experiment from 2011 to 2012 (Kröber & Bruelheide, 2014). These traits were related to the ability to transport water and accumulate carbon (Table S3; Fig. 2): specific leaf area (SLA, m^2 kg^{-1}), cavitation resistance (PSI50, MPa), maximum xylem-specific hydraulic conductivity (HYDCOND, kg m^{-1} s^{-1} MPa^{-1}), leaf thickness (LEAFTHICK, μm), carbon : nitrogen ratio (CN), xylem water potential (WPOT, MPa), leaf dry matter content (LDMC, mg g^{-1}), and wood density (WD, g cm^{-3}). PSI50, HYDCOND, and WPOT together reflect the plant's ability to transport water and its resistance to drought. A high HYDCOND value with a more negative WPOT value indicates better water transport capacity, and a more negative PSI50 value reveals greater drought resistance. LDMC and WD reflect the carbon accumulation strategy, as higher LDMC and WD indicate greater amounts of carbon in the leaf and stem. SLA, LEAFTHICK, and CN are comprehensive indicators of both water transport and carbon accumulation strategy (Chen *et al.*, 2016, 2021; Zhang *et al.*, 2020).

The PCA was calculated using these eight traits with the *rda* function in the VEGAN package of R, v.2.5-7 (Oksanen *et al.*, 2019). Varimax rotation was used to achieve good alignment of the first two PCA axes with the two trait groups reflecting water transport (PC1) and carbon accumulation (PC2), respectively (R Core Team, 2021; Fig. 2). Species were then classified into four functional groups based on which quadrant they occupied (Fig. 2; Table S1). Functional group 1 includes species that have a high ability to transport water but a low carbon
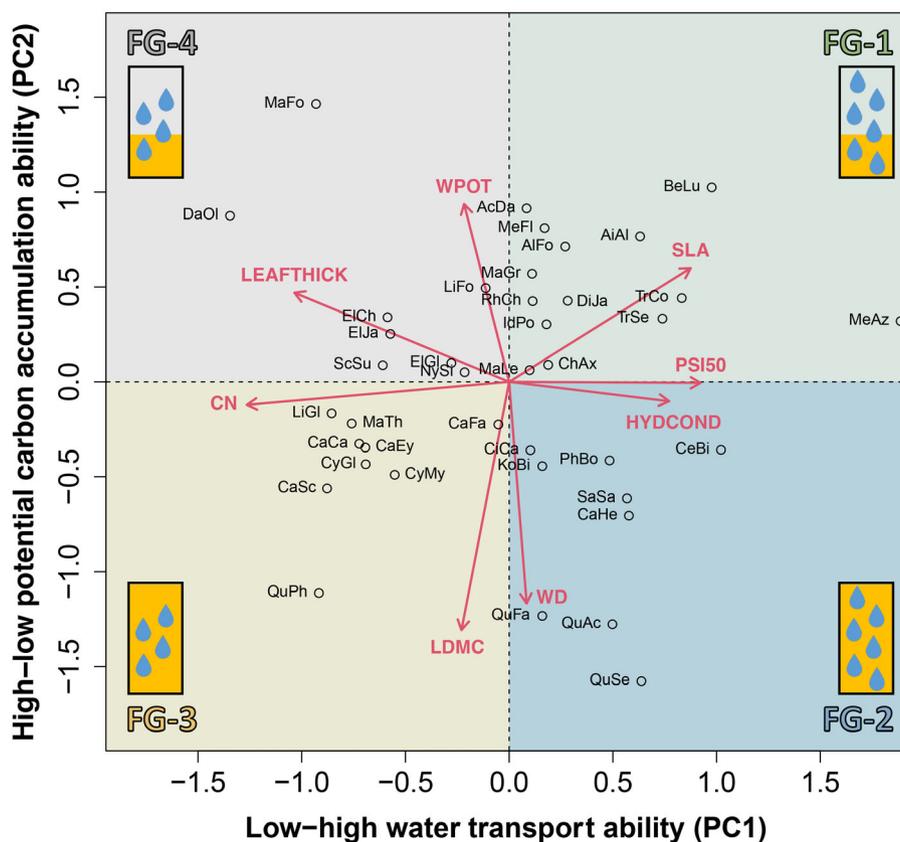
Fig. 2 Principal component analysis biplot for the trait-based water transport and carbon accumulation ability gradients. Red abbreviations indicate eight functional traits and black abbreviations represent 40 species. Abbreviations of traits (red font): water transport: HYDCOND, maximum xylem-specific hydraulic conductivity; PSI50, cavitation resistance; carbon accumulation: LDMC, leaf dry matter content; WD, wood density; others: CN, leaf carbon : nitrogen ratio; LEAFTHICK, leaf thickness; SLA, specific leaf area; WPOT, xylem water potential. For abbreviation of species, see Supporting Information Table S1. Four quadrants indicate four functional groups (FG). The amount of water drops indicates low and high water transport ability. Yellow fill represents low and high carbon accumulation ability. Functional group 1: high water transport-low carbon accumulation, these species keep high water transport ability but build low-density tissue (fast growers); functional group 2: high water transport-high carbon accumulation, these species keep high water transport ability and dense tissue (competitive); functional group 3: low water transport-high carbon accumulation, these species have low water transport ability but dense tissue (slow growers); functional group 4: low water transport-low carbon accumulation, these species have low water transport ability and low tissue density (tolerant).

accumulation ability. Functional group 2 includes species that have a high water transport ability and a high carbon accumulation ability. Functional group 3 includes species that have a low water transport ability and a high carbon accumulation ability. Functional group 4 includes species that have a low water transport ability and a low carbon accumulation ability.

Calculation of nestedness and turnover

Species and functional group nestedness and turnover were calculated using Bray–Curtis dissimilarity, while specific subsets of paired plots were used to examine nestedness or turnover, following Baselga (2016) using the BETAPART package in R (Baselga & Orme, 2012) (for details, see Methods S1). Species or functional group nestedness was calculated between pairs of plots that had different levels of species or functional group richness, where the species or functional group composition of the plot with lower richness had to be nested in the composition of the paired plot

with higher richness. In this case, Bray–Curtis dissimilarity was determined by species or functional group nesting. Species or functional group turnover was calculated between pairs of plots that had the same species or functional group richness levels, but different species or functional group composition. In this case, Bray–Curtis dissimilarity was determined by species or functional group turnover. Mixed plots of two to 24 species were used to calculate nestedness and turnover (Fig. S1). Although the same equation was used, we selected different pairs of plots to separate the effects of species nestedness and turnover, as mentioned above (see examples in Methods S1); and analyzed nested and turnover pairs of plots in separate models. When looking at species nestedness, β_{bc} values close to 0 indicate that two plots have low species/functional group nestedness (low richness difference), whereas β_{bc} values close to 1 indicate that two plots have high species/functional group nestedness (high richness difference). For species turnover, β_{bc} values close to 0 indicate that two plots have low species/functional group turnover (similar

composition), whereas β_{bc} values close to 1 indicate that two plots have high species/functional group turnover (dissimilar composition).

Stand productivity

Stand productivity was estimated based on plot-level tree volume, which reflects the ability to store carbon (Huang *et al.*, 2018). First, the cylindrical volume (tree basal area × height) of each individual tree was calculated. The cylindrical volume was then corrected to actual volume using conversion factors (0.5412–-0.1985 × cylindrical volume; equation taken from Huang *et al.*, 2018). The stand volume was the sum of individual tree volumes of each plot. Annual increment in stand volume was calculated as the difference between the stand volume of the current year and that of the previous year. Absolute differences in stand volume and annual increment between plots were calculated for each nestedness or turnover pair of plots over the 11-yr observation period from 2011 to 2021. Wood density was not included in the estimation of annual stand productivity in our study because it was not possible to measure it for each tree.

Mixture overyielding

To estimate overyielding, we first calculated the expected stand volume of each plot per year using the monocultures that comprised the mixed plots (Eqn 1):

$$Y_{ex,j} = \sum_{i=1}^{N} P_i Y_{mono,i,j} \qquad \text{Eqn 1}$$

where $Y_{ex,j}$ is the expected stand volume in year j; N is number of species or functional groups in the mixed plot; P is the proportion of species/functional group i planted in the mixed plot; $Y_{mono,i,j}$ is the mean stand volume of species/functional group i in monoculture in year j.

Overyielding per year was then calculated as the relative difference between the observed and expected productivity at the plot level (Eqn 2) (Feng *et al.*, 2022):

$$ES_j = \frac{Y_{ob,j} - Y_{ex,j}}{Y_{ex,j}} \qquad \text{Eqn 2}$$

where ES_j is the effect size at the plot level in year j; $Y_{ob,j}$ and $Y_{ex,j}$ are the observed and expected stand volume in year j, respectively. $ES_j > 0$ represents higher productivity, that is overyielding, while $ES_j < 0$ represents lower productivity of mixed plots compared with matched monocultures.

Statistical analysis

The effects of nestedness and turnover were analyzed in different models, and by comparing the effects of species nestedness and species turnover, we assessed the relative importance of species richness and species composition for forest productivity. We note

that it is not possible to fully isolate the contribution of species composition in this test, as even nested communities differ in species composition, but all effects here are attributed to species richness. Furthermore, since many possible pairs could be formed from the 315 mixed plots, this must be taken into account when statistically analyzing the effects. Therefore, we used a new approach with general mixed models and appropriate random effects as error terms to avoid pseudo-replication issues (see next paragraph).

To test the first hypothesis (H1), we used mixed models (Schmid *et al.*, 2017) with the fixed explanatory terms species/functional group nestedness or turnover, mean species richness of the plot pair, year (continuous) and interactions of all fixed terms with year, and the dependent variables absolute difference in accumulated stand volume or absolute difference in annual increment of stand volume. Random-effect terms were year (as multilevel factor) and the interactions of all fixed terms with year (as multilevel factor). Using these random effects ensures that the fixed effects are tested against error terms that avoid pseudoreplication due to the formation of a larger number of pairs from a smaller number of plots (any single plot could occur in multiple pairs of plots). For example, our mixed-model testing for species nestedness and its interaction with continuous year used the interaction species nestedness × factorial year as an error term (resulting in denominator degrees of freedom < 20 for these two fixed terms, see Table 1). Basically, this is equivalent to using the annual slopes of the absolute differences in stand volumes vs nestedness as replicates when constructing an error variance. This approach is similar to Mantel test approaches (see e.g. Mokany *et al.*, 2022) but is more flexible when complex explanatory formulas, such as those used in Table 1, are required to explain the variation in the dependent variables calculated for plot pairs. Finally, the residuals were checked and found to be normally distributed. Mixed models were fitted with ASREML-R (Butler *et al.*, 2007) in R 4.1.3 (R Core Team, 2021).

To test the second hypothesis (H2), the slopes of the linear relationships between nestedness or turnover and productivity differences were recorded for each of the 11 measurement years. We then used meta-regression (Allan *et al.*, 2013; Bongers *et al.*, 2021) models with the fixed explanatory terms year, species vs functional measures, nestedness vs turnover measures and their interactions, and the slopes as dependent variables. We found that functional turnover appeared to have stronger effects than the other three combinations of species vs functional and nestedness vs turnover. Therefore, we conducted an additional analysis specifically comparing functional turnover to these three other combinations. In this additional analysis, year, functional turnover vs others (species nestedness, species turnover, and functional richness), category within others (species nestedness, species turnover, and functional richness), and their interactions were set as fixed factors with slopes as the dependent variable. In the meta-regression for differences in annual increment of stand volume, we used quadratic annuals in addition to continuous ones to account for the nonlinearity of the annual course of the slopes.

Table 1 Mixed models testing the effects of species or functional nestedness, species or functional turnover, (mean) species or functional group richness, year (continuous) and their interactions on absolute differences in stand volumes between plots.

Fixed terms	df_{num}	df_{den}	F	P	n	Var.	SE
Species nestedness	1	15.5	17.61	< **0.001**[↑]			
Mean species richness	1	97.1	19.42	< **0.001**[↓]			
Year (continuous)	1	8.5	341.00	< **0.001**[↑]			
Species nestedness × year	1	15.6	18.88	< **0.001**			
Mean species richness × year	1	97.1	8.15	**0.0053**			
Random terms							
f. Year (as factor)					11	7.01	7.66
Species nestedness × f. year					1628	17.30	16.33
f. Mean species richness × f. year					99	10.15	1.87
Species turnover	1	10.2	768.20	< **0.001**[↑]			
Species richness	1	71.8	0.00	0.990			
Year (continuous)	1	9.0	297.30	< **0.001**[↑]			
Species turnover × year	1	10.3	260.30	< **0.001**			
Species richness × year	1	71.8	2.16	0.146			
Random terms							
f. Year (as factor)					11	16.38	8.78
Species turnover × f. year					1771	1.14	2.07
f. Species richness × f. year					55	5.52	1.73
Functional nestedness	1	9.3	135.30	< **0.001**[↑]			
Mean functional group richness	1	21.0	0.008	0.929			
Year (continuous)	1	8.9	168.30	< **0.001**[↑]			
Functional nestedness × year	1	9.3	28.92	< **0.001**			
Mean functional group richness × year	1	21.0	1.20	0.286			
Random terms							
f. Year (as factor)					11	27.01	15.02
Functional nestedness × f. year					2189	15.62	10.79
f. Mean functional group richness × f. year					33	9.80	3.25
Functional turnover	1	9.2	372.5	< **0.001**[↑]			
Functional group richness	1	19.8	0.0	0.979			
Year (continuous)	1	8.9	367.1	< **0.001**[↑]			
Functional turnover × year	1	9.2	216.5	< **0.001**			
Functional group richness × year	1	19.8	0.0	0.998			
Random terms							
f. Year (as factor)					11	2.27	5.79
Functional turnover × f. year					1936	10.55	6.74
f. Functional group richness × f. year					33	23.59	7.78

Random-effect terms included year as an 11-level factor and its interactions with species or functional nestedness and turnover, and with (mean) species or functional group richness. ↑ indicates positive relations, while ↓ indicates negative relations. df_{den}, denominator degree of freedom (Satterthwaite's method); df_{num}, numerator degree of freedom; F, variance ratio; f., variable used as a factor; n, number of replicates; P, probability of type-I error (bold indicates probability below 0.05); SE, standard error of variance component; Var., variance component.

To understand whether mixtures show higher productivity than constituent monocultures after years of forest growth, in an additional analysis, we compared the mixtures with their constituent monocultures at the end of the time course to test whether overyielding still occurs after 10 yr of forest growth. To understand how the percentage of overyielding plots at each richness level changed over the years, a two-way ANOVA was used with continuous year, species or functional group richness, and their interaction as fixed explanatory terms and the percentage of overyielding plots at each richness level in each year as the dependent variable.

Results

Effects of nestedness on productivity

We found significant positive effects of species and functional nestedness on stand volume differences between plots (Table 1;

Fig. 3). These effects increased over years (significant interactions of species nestedness × year and functional nestedness × year in Table 1) and were larger when the compared plots had, on average, lower species richness but not lower functional group richness (effects of mean species richness and mean functional group richness in Table 1). Differences in stand volume were greater between plots with different functional group richness than between plots with different species richness. Functional nestedness, but not species nestedness, also had significant positive effects on differences in annual increments of stand volume between plots (Table S4; Fig. S2).

Effects of turnover on productivity

Both the differences in stand volume and its increment increased significantly with increasing species and functional turnover (Tables 1, S4; Figs 3, S2). Similar to nestedness, the effects of
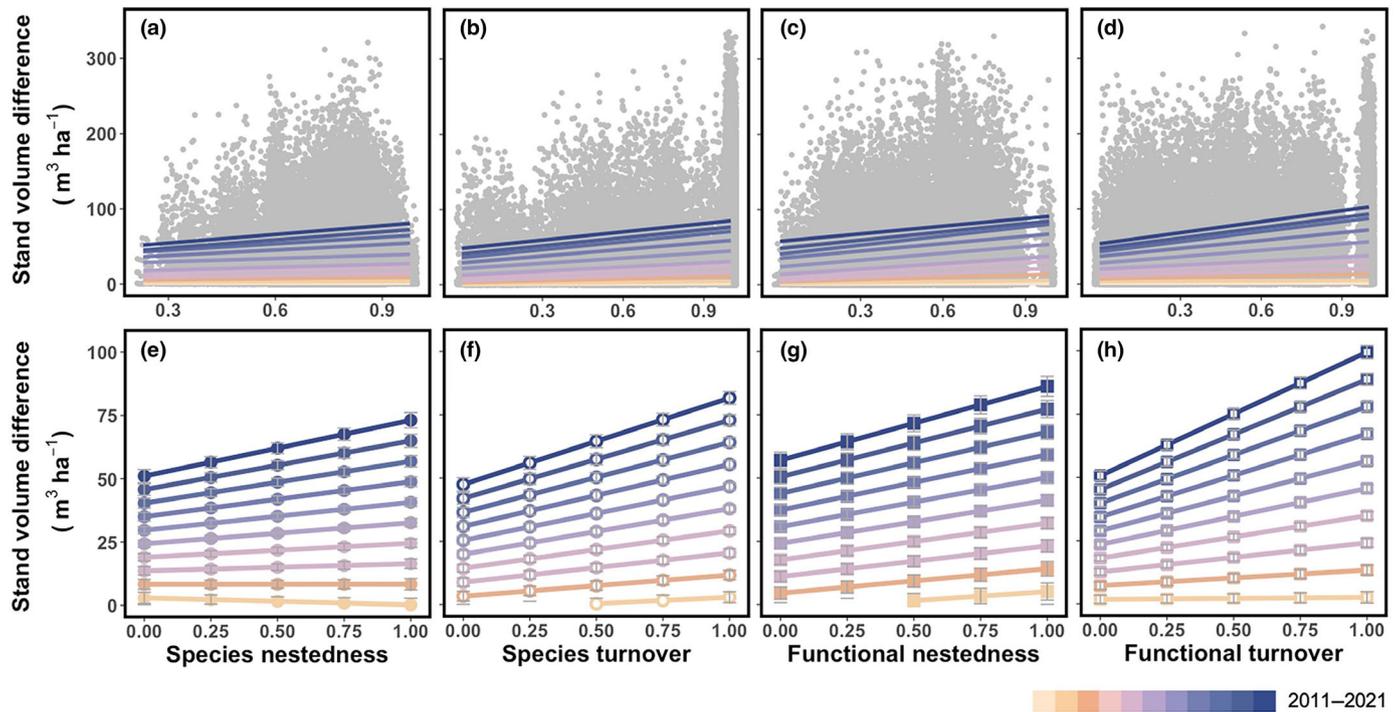
Fig. 3 Differences in stand volume between plots differing in either species or functional group richness (nestedness) or species or functional group composition (turnover) for the period 2011–2021. (a–d) Raw data points of stand volume differences between plots and regression lines for each year. Gray points represent 11-yr data from 2011 to 2021. (e–h) Predicted means of stand volume differences between plots and SE (error bars) based on mixed models (Table 1). Species and functional group nestedness values close to 0 indicate small differences in species/functional group richness, while nestedness values close to 1 indicate large differences in species/functional group richness. Species and functional group turnover values close to 0 indicate small differences in species/functional group composition, while turnover values close to 1 indicate large differences in species/functional group composition.

turnover increased with years (significant interactions species turnover × year and functional turnover × year in Table 1) but were independent of the average level of species or functional group richness of the compared plots. Stand volume differences were greater between plots that differed in functional group composition than between plots that differed in species composition.

Comparison of the effects of nestedness and turnover on productivity

The effects (regression slopes used as meta-data, Tables S5, S6) of species and functional nestedness and turnover on differences in stand volume increased with year, but to varying degrees among the four measures (Table S7; Fig. 4). By the end of the times series in 2021, functional turnover had the strongest effect on differences (Table S8). In addition, the effects on differences in annual increment of stand volume were greatest in the intermediate years, resulting in unimodal time series (Tables S6, S9; Fig. S3).

Overyielding of mixtures compared with constituent monocultures

An increasing percentage of plots, especially in species-rich plots, showed overyielding after 10 yr of forest growth (Table S10; Fig. S4). For example, in 2021, 50% of the 2-species mixed plots were more productive than the corresponding monocultures, while 75% of the 16-species mixed plots had a higher yield than expected from their corresponding monocultures.

Discussion

Multispecies planting is considered a win-win strategy, restoring biodiversity and increasing forest productivity to meet the requirements of the post-2020 biodiversity framework (Huang *et al.*, 2018; Kunming Declaration, 2021; Feng *et al.*, 2022; Gurevitch, 2022). As our results show, a higher proportion of plots, especially species-rich plots, overyielded after 10 yr of forest growth (Table S10; Fig. S4); and a previous study from the same forest biodiversity experiment found a positive relationship between herbivore species richness and tree species richness (Li *et al.*, 2023). However, in such multispecies planting practice, it is still debated whether the focus should be on planting a large number of species in general, or on planting specific species combinations. Both may be important considerations in multispecies planting (Troup, 1921; Kumari *et al.*, 2021; Hua *et al.*, 2022), but the relative importance of these two aspects has not been thoroughly investigated. Here, we used the BEF-China forest biodiversity experiment with a unique nested design (Bruelheide *et al.*, 2014) to address this question, using species nestedness and
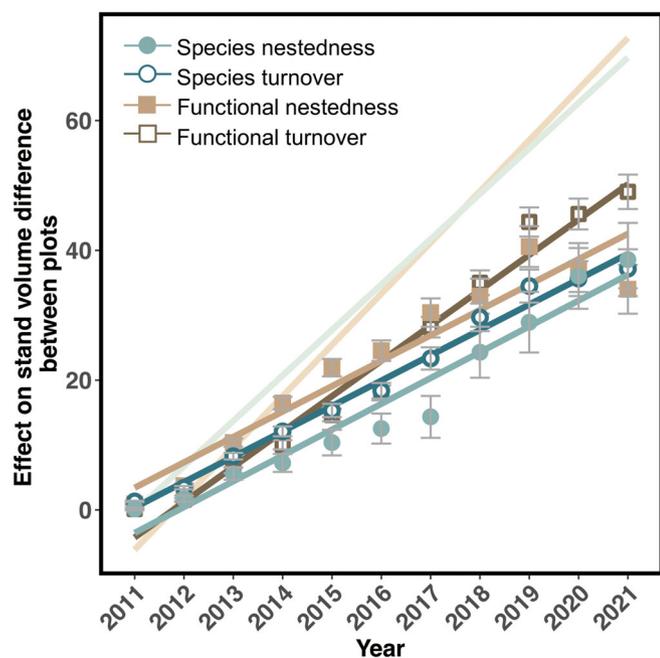
Fig. 4 Species and functional nestedness and turnover effects on differences in stand volume between plots. Regression slopes and SE (error bars) of stand volume differences between plots plotted as meta-data against year with fitted meta-regression lines (Supporting Information Table S5). Overall effects of nestedness and turnover at species vs functional group levels are also shown as a reference in the graph (light green and light brown lines, for species and functional level, respectively) but not included in statistical analyses.

turnover as indicators of species richness and composition, respectively. Additionally, we also examined the effects of functional nestedness and turnover as indicators of functional group richness and composition, respectively. In support of our two hypotheses (Fig. 1b), we found (1) strong positive effects of nestedness and turnover on forest productivity, and (2) even stronger positive effects of functional nestedness and turnover than of species nestedness or turnover.

As we hypothesized, high species or functional nestedness, that is greater changes in species or functional richness, led to greater differences in stand volume over time (Fig. 3a,c,e,g; Table 1), supporting other studies at the species level (Potvin & Gotelli, 2008; Verheyen *et al.*, 2016; Huang *et al.*, 2018) and extending the knowledge to the functional group level (also see positive relationship between functional group richness and forest productivity in Table S11; Fig. S5). This is important because other studies focusing on species richness have made comparisons between non-nested communities, where the less diverse community may contain species not found in the more diverse community. In our study, we deliberately excluded this possibility by using only pairs of nested communities to test the effects of species richness. In addition, we did not account for intraspecific trait variation in this study because we only had a small subset of plots where we manipulated genetic diversity within species. Furthermore, intraspecific trait variation has only recently been measured in the BEF-China experiment. Initial analyses by

Bongers *et al.* (2020) and Tang *et al.* (2022) showed that intraspecific variation generally has a smaller effect on productivity than interspecific variation. We believe that nestedness and turnover based on intraspecific (e.g. genotypic) richness and composition may also have weaker effects than nestedness and turnover at the species and functional group level.

Our results on the effects of species and functional turnover show that the greater the differences in species or functional group composition, the greater the differences in productivity (Fig. 3b,d,f,h; Table 1). These results suggest that in addition to planting a large number of species, planting specific species combinations may be an equally important tool for increasing productivity in multispecies afforestation and reforestation projects. A likely reason for the positive effects of species turnover is differences in complementary resource use or enemy niches among species between communities, as the effects are greater for functional than for species turnover between them (our second hypothesis; see Fig. 4; Table S8; Bongers *et al.*, 2021; Ma *et al.*, 2021). For example, a combination of *Castanopsis sclerophylla*, *Cinnamomum camphora*, *Liquidambar formosana*, and *Melia azedarach* showed the highest stand productivity of all 4-species mixtures (Ma *et al.*, 2021). This was probably due to reduced competition between species and improved niche differentiation and complementarity, as these four species belong to four different functional groups in our study (Table S1). At the stand level, the selection of specific species combinations should aim to maximize resource use and minimize competition and enemy damage to promote productivity. This idea has been proposed before (Forrester & Bauhus, 2016; Huang *et al.*, 2018; Ammer, 2019; Feng *et al.*, 2022), but our findings provide perhaps the strongest empirical support for it so far.

The observed effects of species and functional nestedness and turnover on stand volume differences between plots increased over the duration of the experiment, and nestedness and turnover remained similarly important (Tables S7, S9; Figs 4, S3). The effects of nestedness are also likely to be supported by species complementarity, except that in this case this complementarity is due to random addition rather than intentional replacement of species with different functions in a less diverse community. This is plausible because communities with more species or functional groups are likely to have a wider range of functions and therefore better fill the niche space (Cardinale *et al.*, 2011; Bongers *et al.*, 2021) through complementary effects (Cardinale *et al.*, 2011; Chen *et al.*, 2019a, 2019b; Bongers *et al.*, 2021). However, because the expansion of functional range depends on the individual species present in the community (Brun *et al.*, 2019; Jonsson *et al.*, 2019; Chillo *et al.*, 2020; Staude *et al.*, 2020; Zellweger *et al.*, 2020; Feng *et al.*, 2022), there may still be large differences in productivity in the case of a high turnover, where deliberate exchange of species with specific functions between communities of equal species richness may increase productivity. For instance, if the incoming species/functional groups are more productive or better adapted to the local environment, the turnover may increase forest productivity. Thus, higher species or functional group richness would always be helpful to promote forest productivity, but good species selection may also be useful

to ensure higher forest productivity, as certain species or functional groups may complement each other.

For example, species in functional group 1 (high water transport and low carbon accumulation) and functional group 2 (high water transport and high carbon accumulation) may be appropriate if the site is wet, that is if there is no water shortage. However, these two groups of species should not be planted together because they may compete for water resources. Species in functional group 3 (low water transport and high carbon accumulation) may form a good combination with species in functional group 1, because these two groups of species have different water requirements and growth rates (low wood density is generally associated with a fast growth rate, while high wood density is generally associated with a slow growth rate). Together, they are likely to maximize resource use and minimize competition. Species in functional groups 3 and 4 (low water transport and low carbon accumulation) may be planted together in relatively dry areas because they require less water, but differ in their carbon accumulation strategy, which may minimize resource competition.

In conclusion, the selection of appropriate species combinations is likely to be of similar importance to the use of high species richness in forest planting and restoration projects. Although species richness currently receives the most attention in restoration (Holl & Brancalion, 2020), we suggest that more effort should be devoted to the selection of species combinations that can be maintained in practice to maximize ecosystem functioning.

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Competing interests

None declared.

Author contributions

XL and LZ conceived the study. XL, KM, SL and GO were responsible for data collection. LZ and XL performed statistical analyses with contributions from BS. The initial paper was prepared by LZ and XL with contributions from BS, FJB, GO and KM. All co-authors contributed in helping improve the paper.

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Data availability

All data in the analyses are available at Figshare (doi: 10.6084/m9.figshare.27173751).

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Supporting Information

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

Fig. S1 Illustration of BEF-China plot design and pairs of plots used in our study.

Fig. S2 Differences in annual increment of stand volume between plots differing either in species or functional group richness (nestedness) or in species or functional group composition (turnover) from 2011 to 2020.

Fig. S3 Species and functional nestedness and turnover effects on differences in annual increment of stand volume between plots.

Fig. S4 Percentage of mixture plots with overyielding from 2011 to 2021.

Fig. S5 Stand volume and their increments as a function of tree functional group richness from 2011 to 2021.

Methods S1 Calculation of nestedness and turnover.

Table S1 List of 40 native broad-leaved tree species planted in the BEF-China experiment.

Table S2 Number of plots at each species richness level at site A and site B.

Table S3 Eight leaf and stem traits used in this study to separate species into four functional groups.

Table S4 Mixed models testing the effects of species or functional nestedness, species or functional turnover, (mean) species or functional group richness, year (continuous) and their

interactions on between-plot absolute differences in annual increment of stand volume.

Table S5 Linear models testing the effects of species or functional nestedness, species or functional turnover, respectively, on between-plot absolute differences in stand volumes within each year.

Table S6 Linear models testing the effects of species or functional nestedness, species or functional turnover, respectively, on between-plot absolute differences in annual increment of stand volume within each year.

Table S7 Three-way ANOVA testing the effects of year, species vs functional group, nestedness vs turnover and their interactions on the slopes that reflect the effects of nestedness and turnover on stand volume differences between plots.

Table S8 Two-way ANOVA testing the effects of year, the contrast functional turnover vs others, category (within 'others') and their interactions on the slopes that reflect the effects of nestedness and turnover on stand volume differences between plots.

Table S9 Three-way ANOVA testing the effects of continuous and quadratic year, species vs functional group, nestedness vs turnover and their interactions on the slopes that reflect the effects of beta diversity on differences in annual increment of stand volume between plots.

Table S10 Two-way ANOVA testing the effects of year, tree species richness or functional group richness and their interaction on percentage of positive effect sizes.

Table S11 Mixed models testing the effects of functional group richness, year (continuous) and their interaction on stand volume and their annual increments.

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