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Diversity and identity of economics traits determine the extent of tree mixture effects on ecosystem productivity

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Abstract

1. Although both observational and experimental studies have shown that positive tree species diversity–productivity relationships are predominant in global forests, weak or the lack of tree species diversity and productivity relationships also exist. Growing evidence has revealed that ecosystem productivity depends more on the functional characteristics of species than on their number. However, exactly to what extent tree diversity effects on ecosystem productivity are influenced by the variability and composition of functional traits have rarely been tested both across and at given species richness (SR) levels.
2. Here, we employed a meta-analysis of global-scale data from 59 tree diversity experiments to examine how the diversity and community-weighted means (CWMs) of economics traits determine the outcomes of tree mixture effects on productivity across and within SR levels.
3. We found that the positive effects of tree mixtures on productivity were strengthened by the increasing multidimensional functional dispersion (FDis) and the CWM of leaf nitrogen content both across and within two- and four-species mixtures. Moreover, the multidimensional FDis and the CWM of leaf nitrogen content increased the complementarity effect rather than the selection effect.
4. *Synthesis*. Our findings suggest that both diversity in the leaf economics spectrum and trait concentration on the 'fast' end of the spectrum strengthen biodiversity–ecosystem functioning relationships. This study provides mechanistic insights into the potent roles of plant economics traits, especially leaf nitrogen content, in determining the magnitude (and even directionality) of the biodiversity–ecosystem functioning relationships in forest ecosystems.

KEYWORDS

across and within species richness levels, community-weighted-mean, diversity–productivity relationships, functional diversity, functional identity, leaf and wood economics spectrum, tree diversity experiment

1 | INTRODUCTION

Positive biodiversity–productivity relationships are predominant in global forests based on both observational and experimental studies (Liang et al., 2016; Zhang et al., 2012). As a surrogate of biodiversity, species richness (SR) has been demonstrated to increase ecosystem productivity (Díaz & Cabido, 2001; Hooper et al., 2012). However, there have been controversies concerning the relationship between

SR and productivity, being either positive, negative, hump-shaped or even neutral in forest ecosystems (Fei et al., 2018; Grossman et al., 2017; Huang et al., 2018; Vila et al., 2003). Traditionally, numerous biodiversity–ecosystem functioning experiments have been implemented through the manipulation of SR to understand the mechanisms that drive this relationship (Grossman et al., 2017; Tobner et al., 2016; Williams et al., 2017). Still, a deeper mechanistic elucidation of which ecological processes drive variant species richness–productivity relationships remains incomplete.

Experimental plant communities involve artificially assembled species mixtures from a species pool (Grossman et al., 2017; Huang et al., 2018; Tilman et al., 1996), which typically have distinct sets of functional traits (Leps, 2004). The functional traits of individual species and their interactions can lead to different species mixtures productivity outcomes (Díaz & Cabido, 2001; Loreau et al., 2001; Tobner et al., 2016). The functional traits of plants explain their fitness and resource-based niches (Kraft et al., 2015; Violle et al., 2007) and are therefore employed to identify the mechanisms that underlie the effects of biodiversity on productivity (Cadotte, 2017; Finegan et al., 2015). Plant communities comprised of species with divergent functional traits, compared to those with similar functional traits, enhance niche partitioning and resource use both spatially and/or temporally (Cardinale et al., 2007; Petchey, 2003), which lead to improved community-level biomass production, that is, the so-called complementarity effects (Cardinale et al., 2011; Tilman et al., 1997). Meanwhile, higher productivity in species mixtures can result from a selection effect, that is, species mixtures may be more productive in contrast to monocultures, due to the increased probability of productive species to dominate in mixtures (Grime, 1997; Loreau & Hector, 2001). Across SR levels, higher SR correlates with higher functional dissimilarity or a higher probability of the presence of species with exceptionally critical traits, which can dominate ecosystem functioning (Cadotte, 2017; Díaz & Cabido, 2001; Finegan et al., 2015). With a given richness level, the outcomes of productivity may still be influenced through the extent of trait variation (Grossman et al., 2017; Tobner et al., 2016; Williams et al., 2017). Thus far, specifically how the functional significance of tree diversity influences ecosystem productivity both across and within SR levels via the contributions of complementarity and selection effect has not been well-understood.

Recent studies have confirmed that the effects of biodiversity on ecosystem functioning may be predicted by the degree of functional differences between the constituent species in mixtures (Chen et al., 2019; Heemsbergen et al., 2004). Functional differences might result in variable interactions between species (Heemsbergen et al., 2004; Laughlin, 2014). Complementarity occurs when species in communities exhibit significant interspecific functional dissimilarities that enable them to increase niche partitioning or interspecific facilitation; thus, enhancing the capture and usage of resources (Brooker et al., 2008; Cardinale et al., 2007), thereby, increasing ecosystem productivity (Loreau et al., 2001; Wright et al., 2017). Functional trait dispersion (FDis) is theoretically associated with niche differentiation (Laliberté & Legendre, 2010). Accordingly, we hypothesize that species mixtures with higher FDis may increase the positive diversity effects on forest productivity both across and within SR levels, arising from strengthened complementarity effects (Figure 1).

The effects of plant mixtures on productivity are also driven by the functional identities of species mixtures, which represent community-level functional strategies for resource acquisition (Mokany et al., 2008). For instance, acquisitive species with significant production investments in their stems and leaves exhibit faster acquisition and utilization of resources, compared to conservative species (Díaz et al., 2016; Reich, 2014). Accordingly, the community-weighted means (CWMs) of economics traits do not only explain the high overall productivity in mixtures, but also reflect the intensity of competitive interactions between constituent species in plant communities (Butterfield et al., 2013; Kunstler et al., 2016; Maestre et al., 2009). The varying interactive intensities of species, therefore,

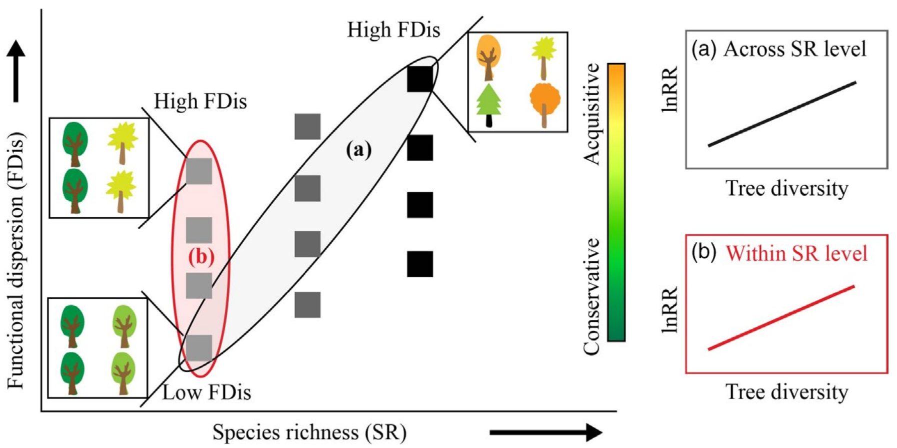


FIGURE 1 Conceptual diagram of how functional trait dispersion and identity influence the tree mixture effects on productivity both across and within species richness levels. Mixtures (represented by squares) consisting of different species are distributed along the gradient of species richness in mixtures (SR), functional dispersion (FDis) and functional identity (from conservative to acquisitive). (a) The increasing FDis or acquisitive strategies with increased SR cause a positive relationship between tree species diversity and the effects of tree mixtures on productivity (lnRR). (b) The lnRR is expected to increase with increasing FDis or acquisitive strategies at a given SR level

can lead to different outcomes of community-level productivity (Fichtner et al., 2017; Lusk et al., 2008). For instance, the intensity of competition between trees can increase complementarity effects, resulting in improved tree growth (Searle & Chen, 2020). Therefore, we hypothesize that the CWM of acquisitive traits strengthens the positive effects of species mixtures on productivity through enhanced complementarity effects.

Here, we aimed to investigate how the diversity and identity of economics traits determine the various outcomes of tree mixture effects on ecosystem productivity, both across and within SR levels. We conducted a global meta-analysis based on 210 paired observations of tree mixtures and corresponding monocultures from 59 tree diversity experiment studies. We collected three leaf and wood economics traits (i.e. specific leaf area: SLA, leaf nitrogen content: LNC and wood density: WD), which are strongly related to forest ecosystem productivity to determine whether FDis and the CWM of traits values of species mixtures were positively correlated with positive diversity effects on forest productivity, both across and within SR levels. We also tested how FDis and the CWM of traits values of species mixtures influenced the two components of diversity effects on productivity, namely complementarity and selection effects.

2 | MATERIALS AND METHODS

2.1 | Data collection

We conducted a survey of suitable studies using the ISI Web of Science and Google Scholar, and cited references in relevant publications up to 1 June 2020. We identified relevant studies using the research terms: '(tree OR forest) AND (tree diversity OR tree richness OR stand mixture OR mixed stand OR mixed plantation OR tree mixture OR mixed forest plantations OR mix tree) AND (experiment) AND (productivity OR biomass OR growth OR volume OR stem OR overyielding) NOT (permanent forest) NOT (grass OR grassland)'. We included studies for the meta-analyses when they met the following criteria: (a) studies contained at least one mixture treatment with corresponding monocultures, (b) all productivity and names of the species in each mixture and corresponding monocultures could be directly extracted from the text, tables and/or figures, (c) the proportion of constituent species in each mixture could be extracted or calculated and (d) studies were specifically implemented to isolate the effects of tree diversity from other factors, such as soil conditions and topographic features.

When the productivity of stand mixtures and corresponding monocultures were measured across multiple years, we extracted data from the latest year. We used the GetData Graph Digitizer (v. 2.26.0.20) to extract data from the figures. In total, 59 published papers with 210 paired observations were selected, which were defined as the productivity of each tree mixtures and corresponding monocultures (Table S1; see the distribution of the studies included in the meta-analysis in Supporting Information: Figure S1). We extracted the data of tree species identities and the relative proportions of stem density from the constituent species of each mixture.

Among the many plant functional traits linked with productivity, we selected LNC, SLA and WD for each tree species from each study for the quantification of functional diversity. The LNC and SLA represent the leaf economics functions, whereas the WD represents the wood economics function (Figure S2). These traits were selected as they are important for explaining plant ecological strategies and community processes, and are strongly related to the productivity of ecosystems (Chave et al., 2009; Díaz et al., 2016; Reich, 2014; Wright et al., 2004). When the plant functional traits were not available in the original publication, they were extracted from the TRY Plant Trait Database (Kattge et al., 2011), as well as other published datasets and literature (Table S2). Thirty-six of the 210 observations (27 of the 59 studies) lacked functional traits from the original studies.

Furthermore, we obtained the experimental stand age (SA), mean annual temperature (MAT) and mean annual precipitation (MAP) for each study. In cases where the MAT and MAP were not reported, they were extracted from a global climate database (http://www.worldclim.org/) using the geographical coordinates of the study sites. Overall, the SR ranged from two to 24, and the experimental SA ranged from 0.5 to 120 years (Table S1).

2.2 | Functional diversity and identity of species mixtures

We used FDis to represent the functional diversity of each mixture. FDis offers possibilities for formal statistical tests to compare differences in functional diversity between groups of communities through a distance-based test for homogeneity of multivariate dispersion (Anderson, 2006; Laliberté & Legendre, 2010). Multidimensional FDis and the FDis for each individual trait of each species mixture were calculated and weighted by the relative abundances of each species. The relative abundance of constituent species of each mixture was calculated by stem density or basal area. For most studies, the proportion of each species in the mixtures was equal (Table S1). The Gower dissimilarity matrix and species–species Euclidean distance matrix were employed to compute the multidimensional FDis and FDis of every single trait respectively (Laliberté et al., 2014).

The functional identity of the economics traits for each species mixture was represented by the CWM of the SLA, LNC and WD, which was calculated as the averaged trait value of each species mixture (Table S3). The FDis and CWM calculations were performed using the FD package (Laliberté & Legendre, 2010).

2.3 | Effects of diversity on productivity

The net effects of tree mixtures on productivity were calculated as the natural log-transformed response ratio (lnRR; Hedges et al., 1999):

$$\ln\mathrm{RR} = \ln\left(X_t / X_c\right), \tag{1}$$

where X_t and X_c are the observed productivity of species mixtures and the mean productivity of all monocultures corresponding to the mixtures respectively.

Subsequently, for a subset of studies with sufficient data in which both the observed productivity of each species in mixtures and monocultures could be obtained (140 paired observations from 22 studies), we partitioned the net diversity effects into two components, complementarity effects (CEs) and selection effects (SEs) following Loreau and Hector (2001):

$$\mathrm{CE} = \mathrm{N} \cdot \overline{\Delta RY_i} \cdot \overline{M_i}, \tag{2}$$

$$\mathrm{SE} = \mathrm{N} \cdot \mathrm{cov}(\Delta RY_i, M_i), \tag{3}$$

where N is the SR of a species mixture, M_i is the productivity of species i in a monoculture and ΔRY_i is the relative yield for species i in the mixture.

CE measures the mean changes in the relative yields of all species present in the mixture, whereas SE measures the covariance between the species' relative yield and their yields in monocultures (Loreau & Hector, 2001). Positive SE occurs when the acquisitive species with higher productivity in a monoculture also have a higher relative yield in a mixture. In contrast, the negative SE occurs when the conservative species with low productivity in a monoculture has a higher relative yield in a mixture. The observed values of CE and SE in various studies had different units across studies. Therefore, the CE and SE were standardized by using the CE and SE response ratio of each mixture to the mean productivity of all monocultures corresponding to the mixture, to compare the contributions of CE and SE across different studies.

The effect size and subsequent inferences were contingent on how individual observations were weighted in a particular meta-analysis (Chen et al., 2019). Weightings that were based on sampling variances might assign extreme importance to a few individual observations (which consequently caused the average lnRR to be determined by a small number of studies). We employed the number of replications, as similar to previous studies (Ma & Chen, 2016; Pittelkow et al., 2014), for weighting the lnRR, CE and SE of each observation in this study:

$$W_r = (N_c \times N_t) / (N_c + N_t), \tag{4}$$

where W_r is the weight of each observation, N_c and N_t are the numbers of replications of monocultures and mixtures respectively.

2.4 | Data analysis

We examined how the FDis and CWM in tree mixtures were associated with the SR in mixtures using Model II regression with the LMODEL2 package (Legendre, 2015). We initially tested the extent to which the FDis and CWM impacted the mixture effects on productivity across SR levels by constructing different models. Each constructed model included a single fixed effect, which included multidimensional FDis, FDis for each individual trait and CWM of each individual trait, respectively. Subsequently, to reduce the SR effects, we tested how FDis and CWM determined the tree mixture effects within two-, three- and four-species levels respectively. These three SR levels contained the largest number of observed mixtures (i.e. 119, 24 and 49 respectively) in this meta-analysis. Because of the spatial correlation of experimental study sites and the non-independence of multiple observations within the same study, we included the spatial variance structure in the residuals and the 'study' as a random factor in each model. We initially constructed the nonlinear mixed effect models to test the impacts of the FDis of tree mixtures on productivity across SR levels using an asymptotic regression model, as the biodiversity–productivity relationships were found to be in the form of general positive concave-down in most real-life cases (Liang et al., 2016). However, the estimates and p values of the parameters indicated that the functional diversity and lnRR did not follow the nonlinear positive concave-down relationship very well in this study (see Table S4).

Subsequently, we compared the linear, loglinear and quadratic responses of lnRR by individually including each predictor with the random effect of 'study' in a linear mixed effects model to assess the assumption of linearity between lnRR and the predictors. The linear and loglinear models yielded lower Akaike information criterion (AIC) values than quadratic models (Table S5). Moreover, as the AIC differences were <2 between linear and loglinear mixed models in most cases, we selected the linear models, which were the simplest among the three alternatives. The linear mixed effect model was constructed using Equation (5):

$$\ln \mathrm{RR} \sim \beta_0 + \beta_1 \cdot x_i + \mathrm{Corr}(\varepsilon_{ij}, \varepsilon_{ij'}) + \pi_{\mathrm{study}} + \varepsilon_{ij}, \tag{5}$$

where x_i are the multidimensional FDis, FDis and CWM of each individual trait respectively; β, $\mathrm{Corr}(\varepsilon_{ij}, \varepsilon_{ij'})$, π_{study} and ε_{ij} are the regression coefficient associated with a single predictor, spatial correlation structure in the residuals, the random effect of 'study' and sampling error respectively. The random effect accounted for autocorrelation between observations within the same study. Further, we assessed how FDis and CWM determined the CE and SE using the same linear mixed effect model. Overall, there were 32 linear mixed effect models in this study, including seven models for across SR levels, 21 models for within SR levels and four models for CE and SE across SR levels.

To examine whether the effects of FDis on lnRR change across the temperature and precipitation gradients, we tested the effects of MAT or MAP and their interactions with FDis on lnRR. We construct the mixed effect model by adding the terms of MAT and 'FDis × MAT', or MAP and 'FDis × MAP' as fixed factors to Equation 5, respectively. Furthermore, we also tested whether the effects of FDis on lnRR were affected by SA by adding SA and the interaction term of 'FDis × Stand age' to Equation 5.

There were several methods used for the measurement of forest productivity in the original studies (Table S6). The influence of productivity measurement method on the effects of tree mixtures on productivity was also tested. We found no significant effects of productivity measurement methods ($F = 0.60$, $df = 11$, $p = 0.82$), and when analysed by individual methods, none of the lnRRs was significantly different from zero (Figure S3). In addition, the FDis still had a significant effect on lnRRs when the method was considered as a random factor ($F = 20.38$, $df = 1$, $p < 0.001$, $R^2_m = 0.05$, $R^2_c = 0.23$). Therefore, the productivity measurement method did not influence the magnitude of diversity effects on productivity in this study.

Considering the sensitivity of the results to the use of TRY traits or site-specific traits, we compared whether the magnitude of effect sizes of the FDis and CWMs on lnRR from the site-specific dataset differed from the lnRR derived from the full dataset. We conducted the analysis using restricted maximum likelihood estimation with the NLME package (Pinheiro et al., 2020). All analyses were performed in R 3.6.1 (R Core Team, 2019).

3 | RESULTS

The effects of tree mixtures on productivity (lnRR) were significantly increased with the multidimensional FDis across SR levels ($p < 0.001$; Figure 2a). There were positive relationships between SR and each of the FDis, and the lnRR (Table S7; Figure S4). Notably, the lnRR varied substantially within two-, three- and four-species levels (Figure S4b), and increased with multidimensional FDis within two- and four-species mixtures ($p < 0.001$, $p = 0.01$ respectively; Figure 2a; Table S8). Moreover, the lnRR increased with the FDis of LNC across SR levels ($p = 0.01$; Figure 2b), within two- and four-species mixtures ($p = 0.03$, $p = 0.01$ respectively; Figure 2b). The lnRR also increased with the FDis of SLA ($p = 0.05$; Figure 2c) and WD ($p = 0.001$; Figure 2d) across SR levels; however, they only exhibited the significant effect of FDis of WD within two- and four-species mixtures ($p = 0.002$, $p = 0.04$ respectively; Figure 2d).

The lnRR increased significantly with the CWM of the LNC both across SR levels ($p = 0.02$; Figure 3a) and within two- and four-species mixtures ($p = 0.003$, $p = 0.03$ respectively; Figure 3a; Table S9). The lnRR also marginally increased with the CWM of SLA across SR levels ($p = 0.05$; Figure 3b) and within four-species mixtures ($p = 0.08$; Figure 3b). Among the correlated CWM of the WD, LNC and SLA (Table S10), the CWM of the SLA and WD had weaker impacts on the tree mixture effects on productivity than that of the LNC (Figure 3). A comparison of the effect sizes of the FDis and CWMs on the lnRR from the site-specific dataset and the full dataset revealed that the functional diversity effects with the site-specific dataset had similar effect sizes with the results of the full dataset (Figure S5). Only the effects of the CWM of WD within three-species mixtures became significantly negative when we used the site-specific dataset.

Further, we found that the CE was positively correlated with increasing multidimensional FDis ($p = 0.02$; Figure 4a); however, selection effects did not (Figure 4b). The CWM of LNC had a significant positive influence on the complementarity effect ($p = 0.01$; Figure 4c), but a marginally negative influence on the selection effect ($p = 0.09$; Figure 4d).

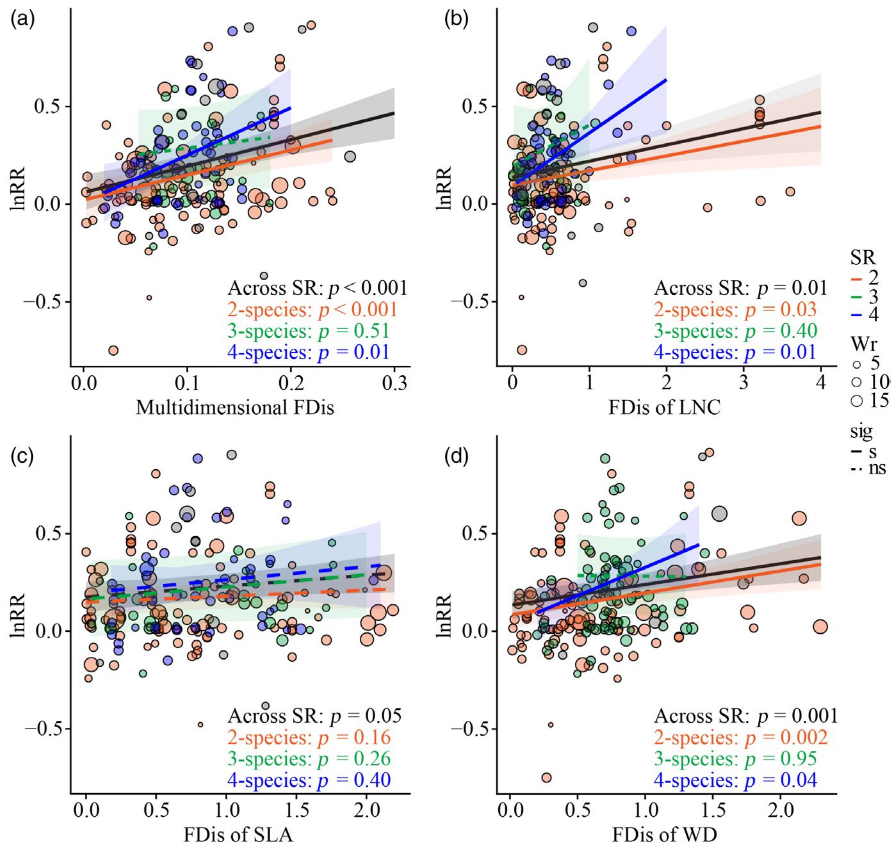


FIGURE 2 Relationships between the effects of tree mixtures on productivity (lnRR) with functional dispersion across and within species richness levels. (a) Multidimensional functional dispersion (FDis). (b–d) FDis of leaf nitrogen content (LNC), specific leaf area (SLA) and wood density (WD). Black, orange, green and blue lines represent the mixed effects model fits across species richness levels, within two-, three- and four-species mixtures respectively. Solid and dashed lines indicate significant ($p < 0.05$) and non-significant ($p > 0.05$) relationships respectively. Curves with their 95% confidence intervals (shaded) were estimated by regressions with corresponding levels of significance (p). The sizes of the circles represent the relative weights of corresponding observations

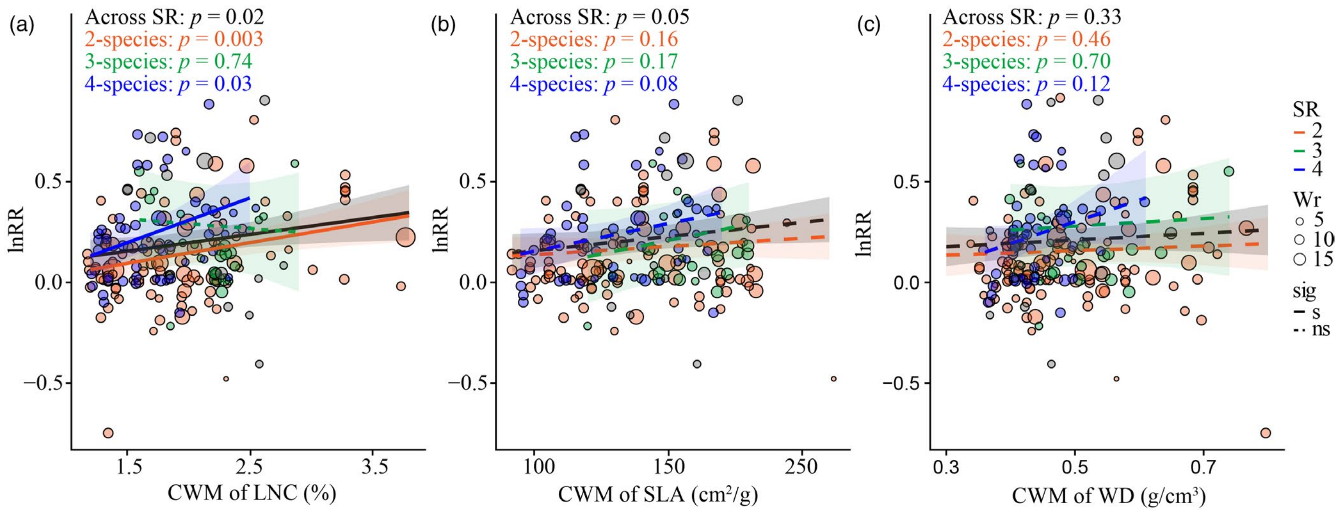
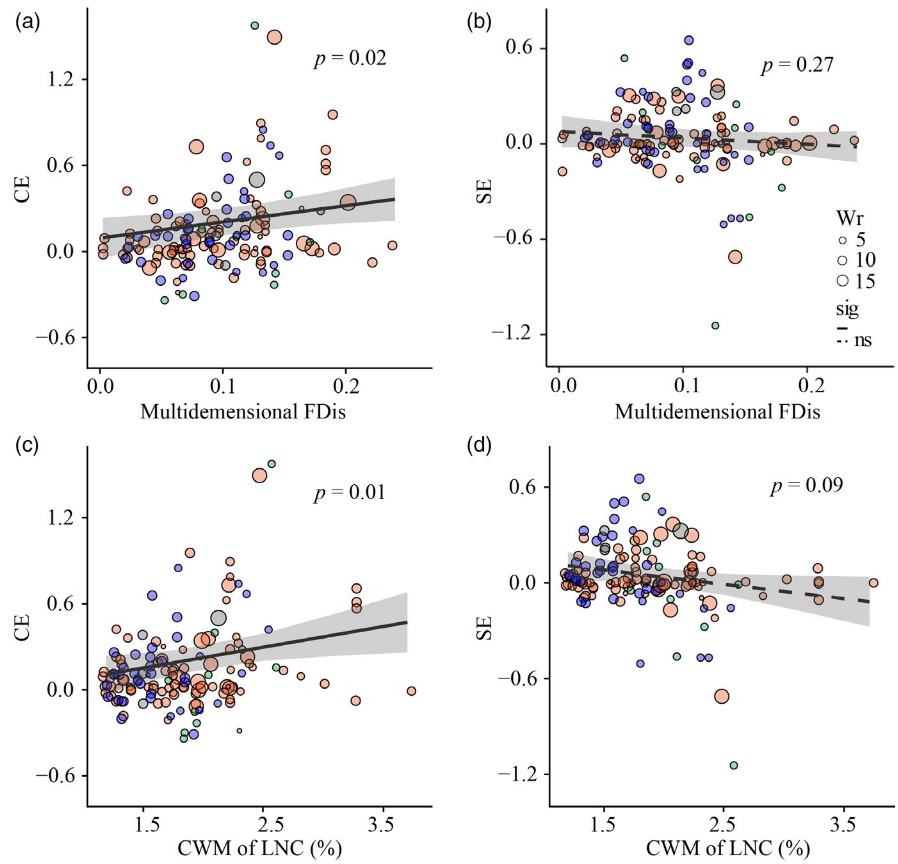


FIGURE 3 Relationships between the effects of tree mixtures on productivity (lnRR) with the community-weighted mean (CWM) of economics traits across and within species richness levels. (a) Leaf nitrogen content (LNC), (b) Specific leaf area (SLA) and (c) Wood density (WD). Black, orange, green and blue lines represent the mixed effects model fits across species richness levels, within two-, three- and four-species mixtures respectively. Solid and dashed lines indicate significant ($p < 0.05$) and non-significant ($p > 0.05$) relationships respectively. Curves with their 95% confidence intervals (shaded) were estimated by regressions with corresponding levels of significance (p). The sizes of the circles represent the relative weights of corresponding observations

FIGURE 4 Relationships between the multidimensional functional dispersion (FDis) and the community-weighted mean (CWM) of LNC with complementarity effect (CE) and selection effect (SE). (a,b) Multidimensional FDis versus CE and SE, respectively. (c,d) CWM of LNC versus CE and SE, respectively. Solid and dashed lines indicate significant ($p < 0.05$) and non-significant ($p > 0.05$) relationships respectively. Curves with their 95% confidence intervals (shaded) were estimated by regressions with corresponding levels of significance (p). The sizes of the circles represent the relative weights of corresponding observations



4 | DISCUSSION

This meta-analysis explicitly revealed that the diversity and identity of economics traits determined the effects of tree mixtures on forest productivity, both across and within SR levels of tree mixtures in experimental tree communities at a global scale. Specifically, we found that the FDis of tree mixtures increased the positive mixture effects on productivity overall, and within the two- and four-species mixtures. The CWM of acquisitive traits of species mixtures also enhanced the positive effects of mixtures on forest productivity.

Both the FDis and the CWM of acquisitive traits, especially the leaf nitrogen, of species mixtures were positively associated with the complementarity effect. Our findings offer novel insights into the importance of plant economics traits in determining the magnitude (and even directionality) of the biodiversity–productivity relationships that have been under debate for more than two decades.

To date, a few experimental studies have provided mechanistic insights into whether functional diversity per se could explain the diversity effects on productivity across communities at a constant SR level (Grossman et al., 2017; Tobner et al., 2016; Williams et al., 2017). Several studies emphasized that a particular combination of functional attributes (e.g. deciduous and shade-intolerant species, high leaf nitrogen and calcium; Grossman et al., 2017; Huang et al., 2018; Tobner et al., 2016), or shade tolerance heterogeneity between constituent species (Zhang et al., 2012), caused the observed species diversity effect. Williams et al. (2017) showed that crown complementarity explained the overyielding of species mixtures among communities of the equivalent number of species. Our global meta-analysis not only corroborated the findings of these individual studies, but also revealed that both the functional diversity and identity in tree mixtures determined the extent of tree mixture effects on productivity across and within SR levels, through the enhanced complementarity effects. Therefore, our study provided evidence that interspecific trait variability rather than richness alone played a critical role in determining the plant diversity effects on ecosystem productivity through the coincidental dominance of influential species or through niche partitioning (Díaz & Cabido, 2001; Loreau et al., 2001; Tilman et al., 1997).

The degree of functional differences between species drives the effects of plant mixtures on ecosystem productivity due to enhanced complementarity effects, arising from niche partitioning and facilitation between constituent species at the community level (Díaz & Cabido, 2001; Loreau & Hector, 2001; Tilman et al., 1997). Plant leaf and wood economics traits correlate with plant resource acquisition, shade tolerance, hydraulic transport, mechanical support and carbon storage (Reich, 2014). Communities consisting of species that occupy various positions in the leaf and wood economics spectrum support niche differentiation with respect to the utilization of light and water and facilitative interactions (Baez & Homeier, 2018; Fichtner et al., 2017), which might increase the community-level acquisition and usage of light and water (Anderegg et al., 2018; Huang et al., 2018). In turn, species-diverse mixtures with higher FDis enhance the efficiency of resource use in mixtures due to recourse niche differentiation (Cardinale et al., 2011; Tilman et al., 1997), thereby improving the impacts of plant diversity on ecosystem productivity (Flynn et al., 2011).

Moreover, we found that FDis in species mixtures was positively associated with positive diversity effects on forest productivity even at a given SR level. Our finding highlights the importance of niche differentiation at the level of within SR for increasing ecosystem productivity (Williams et al., 2017). However, as suggested by our analysis, the effect of niche differentiation on community productivity for a given species mixture was more strongly determined by the multidimensional than by the univariate FDis. It was reasonable that multidimensional trait axes represent more dimensional resource niches (Laliberté & Legendre, 2010); thus, accurately linking with the effects of plant mixtures on ecosystem productivity. It was noted that the effects of tree mixtures on productivity for both multidimensional and univariate FDis were not significant within three-species mixtures in this analysis. This was likely related to the insufficient samples, that is, only 24 observations.

Interestingly, we found that both diversity and the higher CWM of LNC increased the positive effects of species mixtures on productivity. This indicates that leaf economics traits, and especially LNC, are involved in the diversity effects towards the improvement in forest productivity. The functional characteristics of plant species determine the interactions between constituent species in plant communities (Maestre et al., 2009). Leaf nitrogen content is one of the important physiochemical characteristics of leaf photosynthesis and plant growth, as nitrogen is integral to the proteins of the photosynthetic machinery that is responsible for the capture of CO_2 and light interception (Leuning et al., 1995). Fast-growing species with high leaf nitrogen exhibit greater light harvesting, photosynthetic capacities and carbon uptake (Reich, 2014). The effective light acquisition of communities dominated by species on the 'fast' end of the spectrum allows for intense species interactions; hence, niche differentiation or facilitation in communities (Bertness & Callaway, 1994; Brooker et al., 2008; Butterfield et al., 2013; Callaway & Walker, 1997), which consequently drives improved complementary productivity (Fichtner et al., 2017; Hisano & Chen, 2020; Tobner et al., 2016). The positive impacts of the diversity of economics traits and the CWM of LNC on the complementarity effect in this study could be interpreted as evidence of this pattern (Figure 4). Furthermore, the negative relationship between the CWM of LNC with selection effects suggests that species with relatively lower productivity in monocultures dominate species mixtures resulting from species complementarity, including resource partition or facilitation (Cardinale et al., 2007).

It is noted that the impacts of species mixtures on productivity are enhanced with the CWM of leaf nitrogen but independent of WD (Sakschewski et al., 2015). Wood density correlates with a significant number of structural characteristics of woody plants (Chave et al., 2009), where species with high WD generally represent the conservative-end of the 'fast–slow' plant economics spectrum (Reich, 2014). Communities characterized by a high CWM of WD reflect the coincidental dominance of slow-growing species for maintaining ecosystem productivity. In such cases, the interactive processes should be weak in mixtures that are dominated by slow-growing plants, which consequently cannot enhance the effects of mixtures on productivity (Hisano & Chen, 2020). However, the significant negative effect of the CWM of wood density in three-species mixtures using the site-specific dataset suggests that the responses of plant wood traits to environmental conditions might modify the plant functional diversity effects on productivity. One limitation in this study is that we did not test the influences of intraspecific functional variability on the plant diversity and productivity relationship due to the lack of sufficient individual-level trait measurements across and within study sites. It is worth to address how the functional traits covary with environmental gradients to further drive the diversity effects in the future (Cadotte, 2017; Laughlin, 2014). Furthermore, we considered only three important functional traits in this analysis. Future studies can include more traits to test how these mechanisms influence other types of ecosystem functions (Mori et al., 2017).

Our results also indicate that climate mediates tree mixture effects on productivity, and the relationships between the diversity of economics traits and tree mixture effects on productivity increase with higher precipitation (Figure S6). When water availability increases, the competitive interactions involving light or nutrients will become more intense; thus, the complementarity effect will be enhanced to improve the uptake or use efficiency of light and/or nutrients (Ammer, 2019; Hisano & Chen, 2020; Jactel et al., 2018). However, some other studies have demonstrated the unimodal diversity–productivity relationship (the so-called 'hump-or bell-shaped' curve) across climatic gradients (Fei et al., 2018; Grime, 1973; Loreau et al., 2001). The hump-shaped pattern may be caused by the shifting strength of species interactions from facilitation in sites with low resource availability to competitive exclusion in sites with high resource availability (Grime, 1973; Michalet et al., 2010; Wright et al., 2017). In addition, atmospheric nitrogen deposition also alters the leaf economic investment strategies of species, their competitive or facilitative interactions, and indirectly influences the ecological process of plant communities (Bauer et al., 2001; Verma & Sagar, 2020). Accordingly, we speculate that the diversity of leaf economics traits provides a promising window for understanding how contemporary changes in the global nitrogen cycle and climate interact with tree diversity to influence productivity in forest ecosystems.

Furthermore, the relationship between functional diversity and species mixture effects on productivity was not affected by SA in this study (Figure S7a). The non-existent interactive effects of SA might be attributed to the fact that most experiments were in the early successional stage (~10 years; Figure S7b). It has been shown that functional diversity increases when forests experience self-thinning and succession (Lohbeck et al., 2012); we, therefore, argue that our findings may even become more pronounced through strengthened complementarity as tree diversity experiments age (Cardinale et al., 2007; Reich et al., 2012; Zhang et al., 2012).

In conclusion, our meta-analysis integrated the functional differences of species across global-scale tree diversity experiments and investigated how the diversity and identity of economics traits determined the outcomes of tree mixture effects on ecosystem productivity. Our results showed that the effects of tree mixtures on productivity increased with the functional dissimilarity of the leaf and wood economics traits, and the CWM of LNC overall and within two- and four-species mixtures. Both the FDis and the CWMs of acquisitive traits of species mixtures had positive influences on the complementarity effect. These results reveal the key roles of the FDis and composition of species mixtures towards explaining the variations in the effects of plant mixtures on ecosystem productivity, both across and within SR levels. We anticipate that our analysis will stimulate future inquiries into the role of plant economics traits in diversity–productivity relationships.

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AUTHORS' CONTRIBUTIONS

L.-T.Z., E.-R.Y and H.Y.H.C. designed the study; L.-T.Z., D.-F.B., X.-C.F. and M.A. collected the data; L.-T.Z. and S.R.B. analysed the data. All the authors contributed to the writing of the manuscript (L.-T.Z. wrote the first draft).

PEER REVIEW

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DATA AVAILABILITY STATEMENT

The list of papers used in this meta-analysis can be found in the Data Sources section and in Table S1 of the Supporting Information. The database supporting the results are available from the Dryad Digital Repository https://doi.org/10.5061/dryad.2jm63xsn8 (Zheng et al., 2021).

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SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section.

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