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Systematic distributions of interaction strengths across tree interaction networks yield positive diversity–productivity relationships

Wentao Yu[1,2] | Georg Albert[1,2,3] | Benjamin Rosenbaum[1,2] | Florian Schnabel[1,4] | Helge Bruelheide[1,5] | John Connolly[6] | Werner Härdtle[7] | Goddert von Oheimb[8] | Stefan Trogisch[1,5] | Nadja Rüger[1,9,10] | Ulrich Brose[1,2]

[1]German Centre for Integrative Biodiversity Research (iDiv) Halle-Jena-Leipzig, Leipzig, Germany

[2]Institute of Biodiversity, Friedrich Schiller University Jena, Jena, Germany

[3]Department of Forest Nature Conservation, University of Göttingen, Göttingen, Germany

[4]Systematic Botany and Functional Biodiversity, Leipzig University, Leipzig, Germany

[5]Institute of Biology/Geobotany and Botanical Garden, Martin Luther University Halle-Wittenberg, Halle (Saale), Germany

[6]School of Mathematics and Statistics, University College Dublin, Dublin 4, Ireland

[7]Institute of Ecology, Leuphana University of Lüneburg, Lüneburg, Germany

[8]Institute of General Ecology and Environmental Protection, Technische Universität Dresden, Tharandt, Germany

[9]Department of Economics, Institute of Empirical Economic Research, Leipzig University, Leipzig, Germany

[10]Smithsonian Tropical Research Institute, Ancón, Panama

Correspondence
Wentao Yu, German Centre for Integrative Biodiversity Research (iDiv) Halle-Jena-Leipzig, 04103 Leipzig, Germany.
Email: wentao.yu@idiv.de

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Abstract

Understanding the mechanisms underlying diversity–productivity relationships (DPRs) is crucial to mitigating the effects of forest biodiversity loss. Tree–tree interactions in diverse communities are fundamental in driving growth rates, potentially shaping the emergent DPRs, yet remain poorly explored. Here, using data from a large-scale forest biodiversity experiment in subtropical China, we demonstrated that changes in individual tree productivity were driven by species-specific pairwise interactions, with higher positive net pairwise interaction effects on trees in more diverse neighbourhoods. By perturbing the interactions strength from empirical data in simulations, we revealed that the positive differences between inter- and intra-specific interactions were the critical determinant for the emergence of positive DPRs. Surprisingly, the condition for positive DPRs corresponded to the condition for coexistence. Our results thus provide a novel insight into how pairwise tree interactions regulate DPRs, with implications for identifying the tree mixtures with maximized productivity to guide forest restoration and reforestation efforts.

KEYWORDS
biodiversity–ecosystem functioning, competition, facilitation, interaction network, pairwise interaction

Wentao Yu and Georg Albert contributed equally to this work.

INTRODUCTION

Forests provide a wealth of ecosystem functions and services, such as biomass production, carbon sequestration, climate regulation, water filtration and prevention of soil erosion (Quijas et al., 2012). However, globally, forests are under siege from increasing land-use conversion to agriculture, associated fragmentation, pollution and climate change (FAO, 2020). The unprecedented rate of biodiversity loss in forests could considerably compromise the capacity of the world's forests to deliver essential ecosystem functions and services (Hisano et al., 2018; Mor et al., 2021). Therefore, it is crucial to understand the consequences of species loss on the functioning and services of forest ecosystems. Over the past two decades, manipulative forest experiments have established that forests with diverse species are generally more productive than monocultures (Huang et al., 2019; Paquette et al., 2018). Nonetheless, the fundamental mechanisms giving rise to positive diversity–productivity relationships (DPRs) are still obscure.

As forests are aggregates of individual trees, interactions between tree individuals influencing the productivity of individual trees could hold the key to unlocking the mechanisms underlying positive community-level diversity–productivity relationships (hereafter: community

DPRs). Interestingly, neighbourhood diversity can enhance individual tree growth (Fichtner et al., 2017). However, the effects of neighbourhood species richness on tree growth of different tree species were idiosyncratic (Schnabel et al., 2019), hindering attempts to devise mixed forests with maximum productivity (Forrester & Bauhus, 2016). This idiosyncrasy could be attributed to the inadequacy of using sheer species richness instead of explicit pairwise interaction strengths that capture the neighbourhood effect. Eventually, the neighbourhood species composition driving the frequency and strength of competitive and facilitative interactions could thus be more important for individual tree growth than the neighbourhood diversity (Lang et al., 2012; Ratcliffe et al., 2015). This suggests that observed changes in individual tree growth could be driven by divergent interactions due to the identity and relative abundance of neighbouring trees (Potvin & Dutilleul, 2009). Consequently, varying community compositions could affect productivity via changes in tree–tree interactions at the local neighbourhood (Figure 1a), a scale at which plant interactions emerge (Trogisch et al., 2021).

The local neighbourhood is characterized by the focal tree and the pairwise tree interactions with all of its immediate neighbours, forming an intricate local interaction network. The productivity of individual trees can be
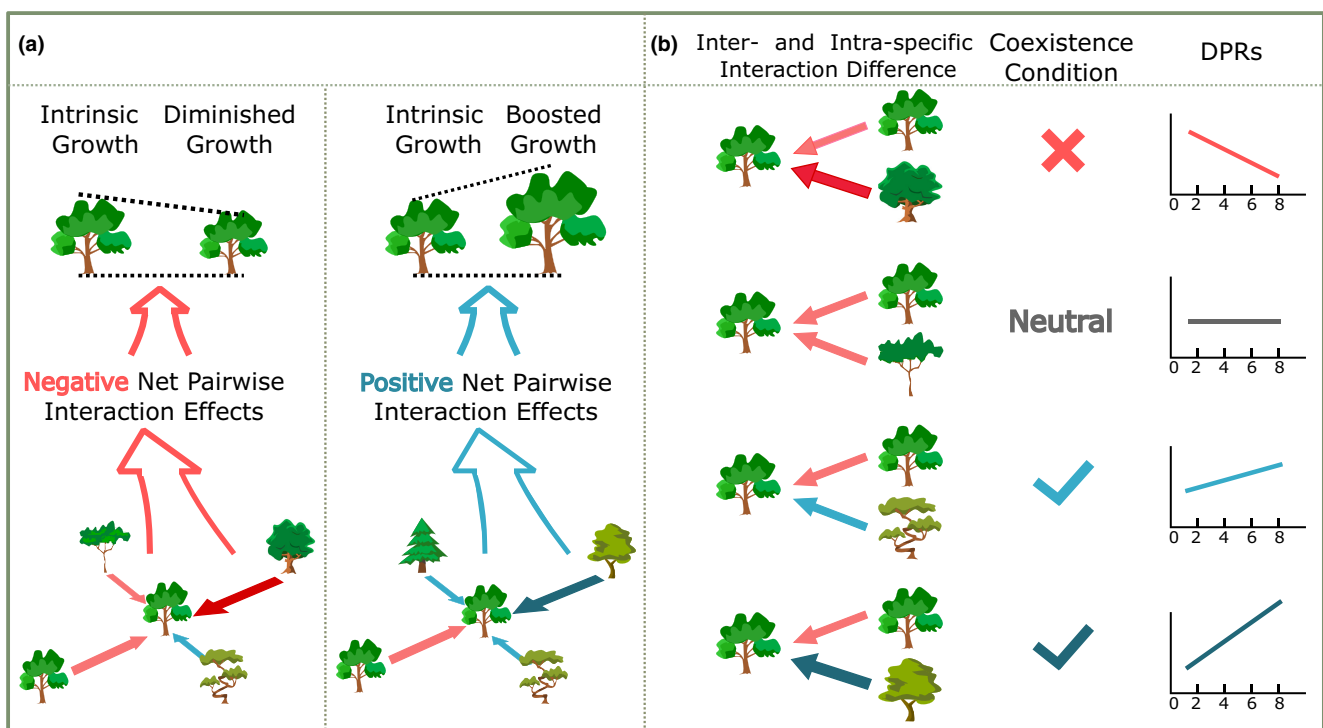

FIGURE 1 Conceptual illustration of mechanisms through which local neighbourhoods can affect (a) individual tree productivity and (b) diversity–productivity relationships (DPRs). Red and blue colour denote negative and positive interaction strength, respectively, with the degree of shading indicating the magnitude of interactions. (a) The same species richness in the neighbourhood but different species compositions can either diminish or promote the productivity of individual trees through the combined net interaction effects determined by pairwise interactions. (b) Demonstrates the hypothesized link between conditions for species coexistence and DPRs. The mean difference between inter- and intra-specific interactions in a diverse community could be negative, neutral and positive, corresponding to negative, neutral and positive DPRs.

boosted by the dominance of positive (e.g. facilitation) over negative (e.g. resource competition) interactions in the network depending on diversity, size, density and identity of its neighbours (Callaway & Walker, 1997). Conversely, the productivity of individual trees can also be decreased by the dominance of negative over positive interactions. By extension, the interaction network composed of all the pairwise tree interactions in the community should impact productivity at the community scale unless their aggregation is a zero-sum game. Consequently, the nature and intensity of interactions in the network could play a key role in determining community DPRs. This species-pair specificity is thus particularly pertinent to unravelling general patterns of interactions and their role in inducing community DPRs (Trogisch et al., 2021). Specifically, positive effects of tree diversity on community productivity require that inter-specific interaction strengths are weakly negative, or even positive, compared to intra-specific interaction strengths that govern monoculture productivity, which is similar to conditions for coexistence (Figure 1b; Chesson, 2000).

Despite the attempts made to explore diversity effects at the neighbourhood scale, studies focused on pairwise tree interactions are scarce (but see Sapijanskas et al., 2013). This scarcity finds an explanation in the thorny issues hampering the discovery of above-mentioned mechanisms. Firstly, resolving multiple pairwise tree interactions of a focal tree demands a specific experimental design that ensures the systematic representation of all pairwise tree interactions across a diversity gradient including monocultures. Secondly, the typically low replication of pairwise tree combinations and the simultaneous effects of multiple pairwise interactions on focal tree productivity impose serious challenges on statistical models. Therefore, to make the link to productivity, we are missing systematic interaction-network approaches to investigate characteristics of the interaction network, such as the distribution of positive and negative interactions among different tree species pairs and the difference between inter- and intra-specific interactions. An in-depth knowledge of pairwise tree interactions underpinned by concomitantly operating mechanisms, that is, competition and facilitation, with an interaction-network perspective would greatly advance our mechanistic understanding of diversity effects at the community scale.

Here, we used annual tree growth data spanning 7 years from a large-scale biodiversity–ecosystem functioning (BEF) experiment (Bruelheide et al., 2014). The random planting scheme of the experiment yielded sufficient pairwise tree interaction data. Moreover, equal distances between planted trees allow us to adequately assess interactions between all immediate tree neighbours. We partitioned individual tree growth into the intrinsic growth rate and effects of interactions with its immediate neighbours. We started with describing the allometric relationship between intrinsic growth rates and tree biomass (*null model*; Enquist et al., 1999).

Interactions with neighbouring trees were described by the sum of each pairwise tree interaction between a tree and its immediate neighbours. Each unique pairwise tree interaction is characterized by a species-specific interaction coefficient (*pairwise interaction model*; Kirwan et al., 2009), all of which constitute the tree–tree interaction network. Alternatively, if the strengths of pairwise tree interactions do not hinge on species identities, an average interaction coefficient is sufficient (*neutral model*). We then set out to test: (H1) species-specific pairwise tree interaction coefficients are necessary to accurately predict individual tree growth; (H2) inter-specific interaction coefficients should be systematically higher (i.e. if negative then of smaller magnitude, or if positive, then larger) than intra-specific interaction coefficients. In the light of acquired empirical interaction matrices, we performed simulation experiments by perturbing the interaction matrices to test (H3) this non-random distribution of coefficients across inter- and intra-specific interactions leads to the emergence of positive DPRs at the community level.

MATERIALS AND METHODS

General overview

To test the necessity of pairwise interactions in determining individual tree productivity, we formulated three models, (1) a *null model* without interactions, (2) a *neutral model* that assumes interactions are independent of the species involved, and (3) a *pairwise interaction model* that incorporates species identity. We employed a Bayesian approach for model fitting given its capacity of capturing complex and non-linear relationships among numerous variables. The specific experimental design of BEF China enabled us to examine interactions between various tree species over a 7-year time series with sufficient replicates. Lastly, we carried out simulation experiments based on the empirical interaction coefficient matrices to unravel the specific characteristics in the distribution of interaction coefficients in shaping positive diversity–productivity relationships.

Experimental design

We used data from site A (29.125° N, 117.908° E) of the BEF-China tree diversity experiment, which is located in southeast subtropical China (29.08°–29.11° N, 117.90°–117.93° E) between 105 and 275 m above sea level with an average slope of 27.5°. The major forest type is subtropical evergreen broad-leaved forest with Cambisols, Regosols and Colluvisols being the predominant soil types in the area (Scholten et al., 2017). The mean annual temperature is 16.7°C, whereas the mean precipitation is 1821 mm per year (Yang et al., 2013).

We used data from 155 study plots ($25.8 \times 25.8 \,\text{m}^2$) to analyse two independent data sets. The two data sets had no overlap in species (Supporting Information S1) and were well replicated. Each spanned a diversity gradient ranging from monocultures to 2, 4 and 8 species mixtures. Species compositions were randomly assigned to plots following a 'broken-stick' design. Within plots, species were planted randomly. All species were equally represented along the diversity gradient. In March 2009, each plot was planted with 400 1–2-year-old tree saplings (20×20 individuals) with equal distance of 1.29 m in horizontal projection. During the first year, dead samplings were replanted. Plots were weeded regularly. See Bruelheide et al. (2014) for more details about the experimental design.

Tree data

To avoid edge effects, we focused our analyses on plots' core areas of 6×6 trees for monocultures and 2-species mixtures and 12×12 trees for 4- and 8-species mixtures. For trees within core areas, species identity, stem diameter and tree height were recorded once per year over the 7-year study period (2010–2016). We defined the inner trees of the core areas as focal trees (Figure S1). For each focal tree, the location and identity of its eight neighbouring trees were recorded. One sample for the model fitting consists of one focal tree and its immediate neighbouring trees in a given year. Above-ground biomasses of each tree were calculated by multiplying above-ground volume and species-specific wood densities measured in comparative study plots near the BEF-China experiment (Kröber et al., 2014). Above-ground wood volume of each tree was calculated by multiplying tree basal area by tree height with a form factor of 0.5 to account for discrepancies between actual tree volume and the volume of a cylinder (Fichtner et al., 2020). In the case of missing biomass data of one or more neighbouring trees in a certain year, the sample was removed from the data set. Annual biomass growth rates were calculated as the biomass difference between two consecutive years. Trees that exhibited negative growth rates in consecutive years, most likely due to measurement errors, were excluded to avoid problems with statistical convergence. In the end, 1948 and 1352 focal trees of data set 1 and 2 from 74 and 81 plots, respectively, were included in this study, totalling 7700 and 4585 data points over the 7-year study period.

Pairwise interaction model

We decomposed the observed individual growth rate into its intrinsic growth rate and interactions with its immediate neighbouring trees, assuming the effects of higher order interactions are negligible (Simberloff, 1982). Metabolic theory predicts the relationship between intrinsic growth rate and body mass can be described by a three quarter power allometric scaling. It is predicated on the assumption that the metabolic rate of an organism is constrained by the rates of resources uptake across surfaces and rates of nutrient distribution through branching networks of vessels within the organism (West et al., 1999).

Here, we employed this allometric relationship between biomass and intrinsic growth rate while retaining the flexibility of the exponent to test the validity of three quarter scaling in metabolic theory, which formed our *null model* described by:

$$B_{t+1,i} - B_{t,i} = \beta_{s(i)}\, B_{t,i}^{\theta} * \left(1 + \varepsilon_p + \varepsilon_{ps} + \varepsilon_t + \varepsilon_{ts}\right) \quad (1)$$

where $B_{t,i}$ and $B_{t+1,i}$ denote the biomass of tree i in year t and $t+1$ respectively. Following metabolic theory, $\beta_{s(i)}$ is a species-specific coefficient, whereas θ is a general exponent for allometric scaling. We accounted for plot effects and annual environmental changes by incorporating them as random effects ($\varepsilon_p, \varepsilon_t$), and species-specific random effects ($\varepsilon_{ps}, \varepsilon_{ts}$) allow tree species to respond differentially to similar environmental conditions.

Then, the interaction effect between the focal tree and its neighbouring tree was factored in as the product of the interaction coefficient α and the biomass of the neighbouring tree with a scaling exponent. This assumes that the interaction strength scales with body size since larger trees seize disproportionately more resources relative to their size (Freckleton & Watkinson, 2001). Additionally, the exponent of the biomass of the neighbouring tree allowed us to test whether the scaling relationship is linear (exponent = 1) or non-linear. If the species identities of interacting trees have no bearings on the interaction strength, an average interaction coefficient (which is identical across species) would suffice, resulting in the *neutral model* which is described as follows:

$$B_{t+1,i} - B_{t,i} = \beta_{s(i)}\, B_{t,i}^{\theta} * \left(1 + \varepsilon_p + \varepsilon_{ps} + \varepsilon_t + \varepsilon_{ts}\right) + \alpha_{ave} \sum_{j \in n_i} B_{t,j}^{b}$$

$$(2)$$

where the α_{ave} represents an average interaction coefficient and $B_{t,j}$ denotes the biomass of neighbouring tree j in year t with a scaling exponent b. n_i denotes the set of neighbouring trees, which could be smaller than eight trees due to mortality.

Contrary to Equation (2), if the identity of the neighbouring trees is necessary for accurately characterizing individual tree productivity, then a *pairwise interaction model* is needed, which can be expressed by:

$$B_{t+1,i} - B_{t,i} = \beta_{s(i)}\, B_{t,i}^{\theta} * \left(1 + \varepsilon_p + \varepsilon_{ps} + \varepsilon_t + \varepsilon_{ts}\right) + \sum_{j \in n_i} \alpha_{s(i),s(j)} B_{t,j}^{b}$$

$$(3)$$

where the interaction coefficient $\alpha_{s(i),s(j)}$ encapsulates the effects of species $s(j)$ of tree j on species s(i) of tree i. Specifically, the interaction coefficient represents the net effect of both facilitation and competition. A positive coefficient indicates stronger facilitation than competition, whereas a negative coefficient suggests stronger competition than facilitation or exclusive competitive interactions. When $s(i) = s(j)$, $\alpha_{s(i),s(j)}$ stands for the intra-specific interaction coefficient, while $s(i) \neq s(j)$, $\alpha_{s(i),s(j)}$ represents the inter-specific interaction coefficient. We tested different formulations of the random effect structure and found that the formulation in which only intrinsic growth rates were affected generally fitted best (Supporting Information S3). Distances between focal tree and neighbouring trees were not considered in our study, because in plots where the spacing is well controlled, additional spatial information may not improve the performance of the model to characterize tree–tree interactions (Biging & Dobbertin, 1995).

We fitted the *null, neutral* and *pairwise interaction* models to the two independent empirical data sets using the Rstan package in R version 4.2. To ensure that it is theoretically possible to estimate unique parameters given the data and our model structure, we performed a parameter identifiability analysis (Supporting Information S4; Guillaume et al., 2019). Each model was fitted using three Markov chains and 4000 iterations with 2000 as warm-up. To ensure that the HMC sampler effectively explored the parameter space and the model convergence, we graphically checked the trace plots of Markov chains and the R-hat metric (Gelman et al., 2013). We used posterior predictive checks to inspect the goodness-of-fit for each model via visually comparing the predictions from the model to the observed data. Bayesian leave-one-out cross-validation (LOO-CV) was chosen to evaluate the model performance based on its out-of-sample predictive ability (Vehtari et al., 2015). The set of models fitted with two independent data sets allowed us to robustly evaluate the model performances.

Reshuffling the interaction coefficient matrix

To uncover the specific characteristics in the tree–tree interaction network that are responsible for positive diversity–net interaction relationships, we performed simulation experiments on the interaction coefficient matrix obtained from the pairwise interaction model. The resultant interaction matrices from reshuffling the empirical interaction matrix were considered as simulated communities. We defined the second term in Equation (3) as the net interaction effect, which can directly boost or diminish the growth of individual trees. We first reshuffled the whole interaction

coefficient matrix to test whether the estimated interaction coefficient matrix could have emerged by chance. We then investigated how the difference between inter- (off-diagonal elements in the interaction matrix) and intra-specific (diagonal elements) interaction coefficients shaped the DPRs by constraining the reshuffling to the off-diagonal and diagonal elements respectively. For each scenario, we sampled 1000 times. With the generated interaction coefficient matrices under each scenario, we computed the net interaction effects and productivity for each focal tree using Equation (3). We then scaled up the individual-based effects to the community level by summing up Equation (3) for multiple individuals i of the community and examined the diversity–net interaction and community DPRs using the last year growth, thereby establishing the link between the diversity effect at the local level and the diversity effect at the community level (Supporting Information S5). We hypothesized that the inter-specific interaction strengths should be weaker, if negative, or positive than the intra-specific interactions for a positive DPR to emerge. To test this hypothesis, we calculated the mean difference of inter- and intra-specific interaction for each of the randomly reshuffled matrices (unconstrained) and tested for the relationship between the difference in inter- and intra-specific interactions and the slopes of the emerging DPRs.

RESULTS

Model fitting and model performance

To assess the importance of explicitly modelling pairwise tree interactions, we compared the *pairwise interaction* model (i.e. the model assigning specific interaction parameters to all tree species pairs) with a *null model* without interactions and a neutral model where interaction terms are constant across species (i.e. interactions are neutral concerning species identities).

All models showed good convergence with R-hat values of 1.0 for almost all estimates (Figure S3). Across both data sets, the *pairwise interaction model* was invariably ranked the best in terms of its predictive power (Table 1). In the parameter identifiability analysis, all parameters of the pairwise interaction models were accurately retrieved using simulated data with relatively low deviations between the estimated and assigned true values (Figure S2). In the *pairwise interaction model*, the estimated allometric scaling exponent of the intrinsic growth term was 0.80 and 0.81 for data set 1 and data set 2 respectively (Table 1). The interaction strength scaled sublinearly with the biomass of the neighbouring tree, with exponents of 0.19 and 0.14 for the two data sets (Table 1).

	Model	elpd_diff	se_diff	Allometric exponent θ	Exponent of neighbouring tree's biomass b
Data set 1	Pairwise	0	0	0.80 (0.78, 0.81)	0.19 (0.14, 0.24)
	Null	−63.80	46.89	0.77 (0.76, 0.78)	—
	Neutral	−64.37	45.35	0.78 (0.77, 0. 80)	0.13 (0.09, 0.35)
Data set 2	Pairwise	0	0	0.81 (0.79, 0.83)	0.14 (0.10, 0.18)
	Null	−47.77	41.40	0.82 (0.80, 0.83)	—
	Neutral	−55.15	41.05	0.81 (0.80, 0.83)	0.21 (0.03, 0.55)

TABLE 1 Comparison of the *null* (Equation 1), *neutral* (Equation 2) and *pairwise interaction model* (Equation 3) and their predictions of the allometric exponent, θ, intrinsic biomass growth and the scaling exponent, b, for the effect of the neighbouring tree's biomass.

Note: Model fit is evaluated by elpd_diff (expected log pointwise predictive density difference), with lower values indicating poorer fit, se_diff is its standard deviation and quantifies uncertainty and scaling exponents are characterized by their mean and 90% credible interval.

The estimates of interaction coefficients

We tested for the differences between inter- and intra-specific interaction strengths in the full interaction coefficient matrices from both data sets. The estimates of interaction coefficients in the pairwise model showed values ranging from −1.23 to 2.81 and − 1.44 and 1.56 for data set 1 and data set 2 respectively (Figure 2a,b, see Figure S4a,b for data set 2). Note that negative and positive values imply negative and positive interactions respectively. Out of the 64 interaction coefficients estimated, about half (data set 1: 33; data set 2: 32) had 90% credible intervals that did not overlap with zero, indicating that those interaction effects were significantly positive or negative (Figures S5 and S6). Interestingly, we noticed that the two interaction coefficients between specific tree pairs (effects of species i on j and j on i) were neither reciprocal nor inverse in magnitude (Figure 2c), which is mirrored by the links with different thickness or/and colour between the connecting species, depicted in the network (Figure 2b). From the two interaction networks in data sets 1 and 2, we found that the majority of the tree–tree interactions were positive, with an incidence of 67.2% (43/64) and 51.6% (33/64) respectively. When separating intra- (diagonal values in Figure 2a) and inter-specific (off-diagonal values in Figure 2a) coefficients, a similar trend emerged from the two independent model fittings, with the mean inter-specific interactions being consistently larger than mean intra-specific interactions (Figure 2d, see Figure S4d for data set 2). Statistically, inter- and intra-specific interaction strengths can be considered to be sampled from different distributions for both data sets because the inter-specific interaction strengths were on average larger than the intra-specific interaction strengths, with a posterior probability of 100% and 90% for data sets 1 and 2 respectively (Figure S7). These results demonstrate two related patterns: (1) inter-specific interaction strengths were generally weaker, if negative, than intra-specific interaction strengths, and (2) inter-specific interactions even tended to be positive, whereas intra-specific interactions were on average negative.

Effect of inter- and intra-specific interaction strengths on community DPR

Reshuffling the whole interaction coefficient matrix gave us a wide variety of relationships between net interactions and diversity, ranging from negative to neutral and positive (Figure 3a, unconstrained, see Figures S8 and S10 for data set 2). Compared to the positive relationship observed in the empirical data (Figure 3a, green lines), the average across all the simulated communities led to a flat line of both mean community net interaction and productivity with respect to diversity (Figure 3a, unconstrained, blue lines). This suggests that the empirical emergence of the positive relationship does not arise from a random distribution of interaction strengths across the matrix. In contrast, reshuffling the intra- and inter-specific interactions in their respective subsets greatly constrained the relationships between community mean productivity and diversity to be positive (Figure 3a, constrained). This indicates that the pattern of inter-specific interactions being less negative than intra-specific interactions largely explains why community DPRs are positive. Likewise, when we analysed how the difference between mean inter- and intra-specific interactions from the unconstrained reshuffling related to the slopes of the DPRs, we found that positive difference between mean inter- and intra-specific interactions led to positive community DPRs and vice versa (Figure 3b). Collectively, these results indicate the significance of the difference in sign as well as magnitude of the inter- and intra-specific interactions in determining the direction and strength of DPRs.

DISCUSSION

Employing a unique data set on the growth rates over 7 years of 3300 tree individuals and a novel modelling approach, we obtained two full interaction networks. We found that (1) pairwise interactions in our model are essential for predicting tree growth, (2) the species interaction network is dominated by positive over negative interactions and (3) the positive difference between
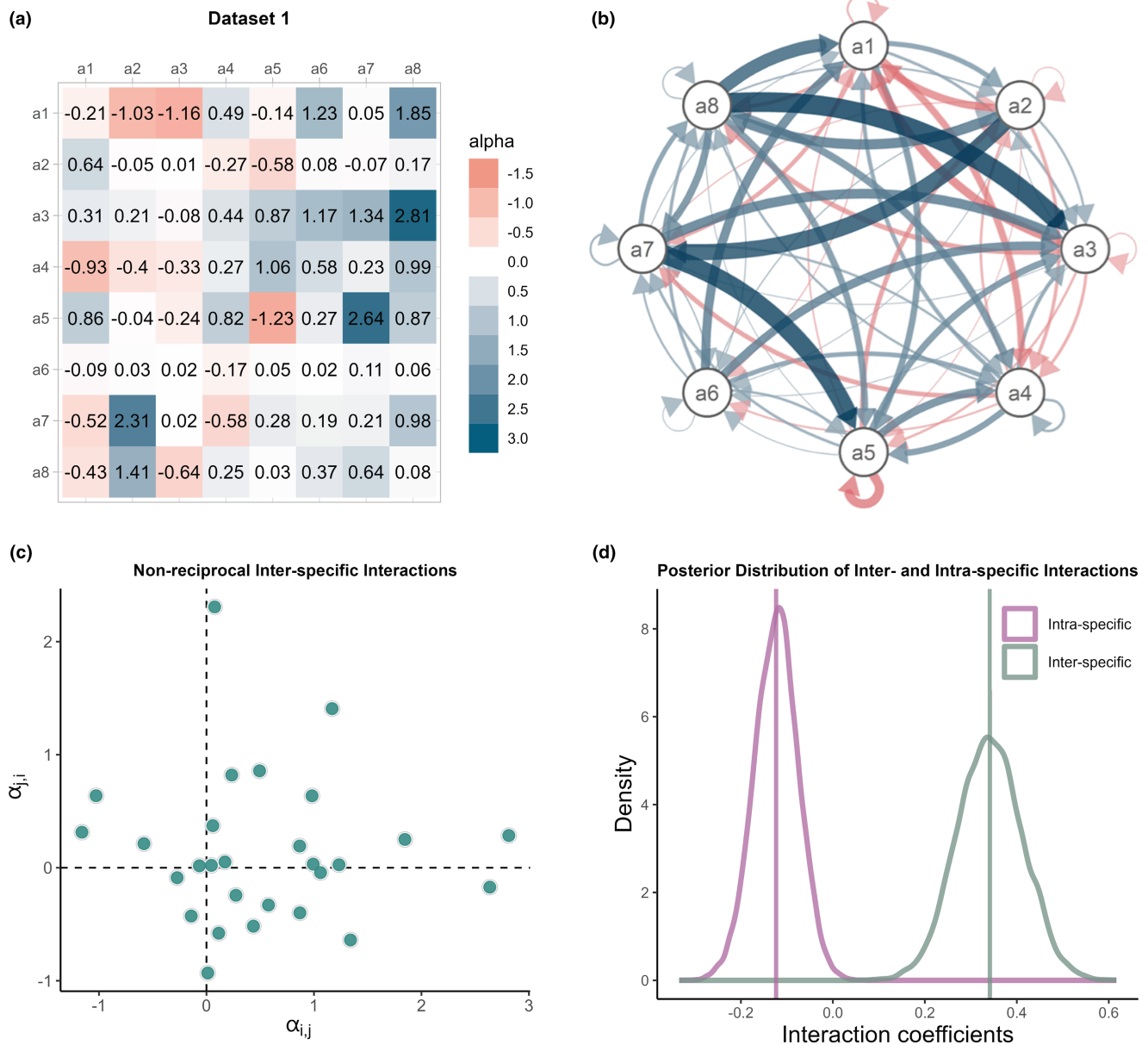
FIGURE 2 Inter- and intra-specific interaction coefficients obtained by fitting the pairwise interaction models (Equation 3) with empirical data. (a) Shows empirical interaction coefficient matrices, that is, row a1 and column a4 denotes the interaction coefficient $\alpha_{1,4}$, representing the effect that species 4 has on species 1. (b) Depicts the empirical interaction network with blue and red colour denoting positive and negative interaction coefficients respectively. The thickness and colour saturation correspond to the absolute magnitude and direction of interaction coefficients respectively. The arrows point to the species which is affected by the connecting species. (c) Demonstrates that there is no pattern between the two interaction coefficients of a specific tree pair. (d) Depicts the posterior distribution of the average of intra- (pink) and inter-specific (green) interaction strengths with the solid lines denoting the mean values respectively.

mean inter- and intra-specific interaction strength in the community is a critical determinant of the empirically observed positive community diversity–productivity relationships (DPRs). Taken together, our results illuminate the role that the pairwise interactions play in regulating community DPRs. The knowledge of tree–tree interaction networks also has great implications for forest restoration and reforestation efforts. It opens the door to the optimal design of forest mixtures that can maximize productivity, which is an important ecosystem function and positively related to multifunctionality (Baeten et al., 2019).

The consistent results from two independent data sets strongly suggest that the identity of neighbours is an indispensable factor in shaping individual tree productivity. In a field experiment with subtropical trees, it was observed that the species identity of neighbouring samplings is an important determinant of sapling growth (Lang et al., 2012). Furthermore, a population-level analysis of European forests showed that the identities of neighbouring trees drive the variation in community-level productivity (Baeten et al., 2019). Studies at the neighbourhood scale usually characterized the local
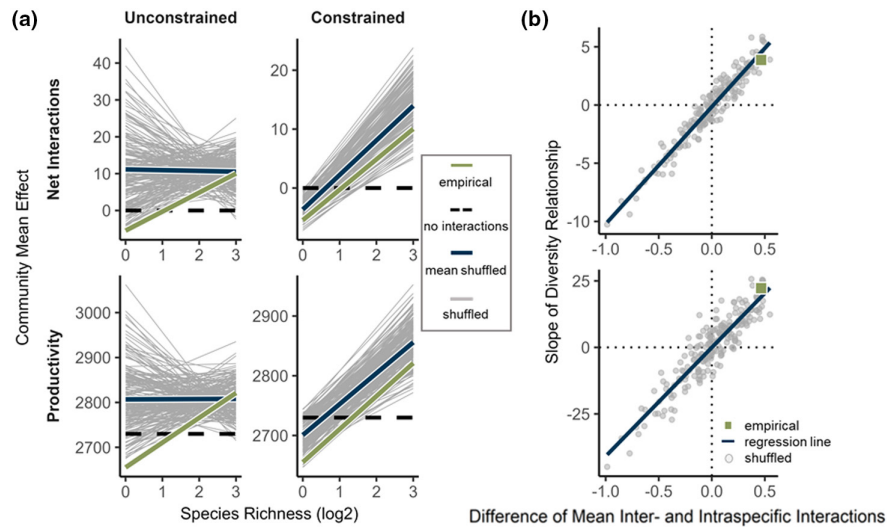
FIGURE 3 Consequences of simulated perturbations of the empirical interaction matrices for (a) simulated diversity–net interaction (top) and diversity–productivity (bottom) relationships at the community level under two different scenarios: completely random reshuffling of interaction matrix (unconstrained) and reshuffling within inter- and intra-specific interactions (constrained), and (b) the relationship between the difference between inter- and intra-specific interactions and the slopes of the simulated diversity–net interaction and diversity–productivity relationships (slopes of the grey lines in subfigure (a), unconstrained scenario). Green lines and squares show the relationships derived from empirical interaction matrices (Figure 1a,b). Grey lines and dots show the results of simulated reshuffling of these interaction matrices (i.e. keeping the values but changing their position in the matrix) with blue lines showing their average. Here, randomly selected 200 simulated communities out of 1000 (Figure S9) are shown in the figures for readability.

neighbourhood by the size of neighbouring trees (e.g. the total basal area of neighbouring trees) and the richness of neighbouring species (Pretzsch & Schütze, 2009; Schnabel et al., 2019). Their results showed that neighbourhood diversity and competition are central for regulating community productivity. Using BEF experimental data from tropical forests, Sapijanskas et al. (2013) found that the inclusion of pairwise interactions through the neighbours' litter production in addition to shading improved the prediction of individual tree growth. Our model takes a phenomenological approach, assuming that the pairwise interaction term captures the total impact of competitive and facilitative interactions between distinct species pairs. The sum of pairwise interaction effects of the focal tree then constitutes the net interaction effect, which captures the overall local neighbourhood interaction effects, allowing for scaling up to the interaction effects at the community level. This model framework thus not only permits the discernment of the pairwise interactions, but also provides a means to decipher the mechanisms through which local pairwise interactions shape the DPRs.

Surprisingly, we found that positive interaction coefficients were dominant in the interaction networks. The high frequency of positive interactions suggests the presence of facilitative processes among trees, which include both abiotic facilitation and indirect biotic facilitation (Barry et al., 2019; Wright et al., 2017). In addition, the positive interaction coefficients indicate that the facilitative effects are not offset by negative competition. Our findings therefore contrast recent studies that suggest competition to be the prevalent form of plant–plant interactions

(Adler et al., 2018; Yang et al., 2022), with only about 25% of the recorded interactions being positive. Generally, the ecological literature postulates that positive interactions are prevalent in stressful environments (stress gradient hypothesis; Brooker, 2006; Callaway, 2007). In moderately or weakly stressful environments, positive interactions are thought to be generally outweighed by the negative effects of competition which are larger in magnitude (Brooker & Callaghan, 1998). This could have repercussions on community DPRs. For instance, the positive slope of the community DPRs diminished from boreal to subtropical forests, which feature less stressful conditions compared to boreal forests (Wu et al., 2015). Our results from a subtropical tree diversity experiment show that positive interactions eclipse competition in the majority of interactions, leading to the positive community DPRs. We ascribe this discrepancy primarily to the fact that prior studies with a focus on positive interactions usually used isolated species pairs (Brooker et al., 2008) and investigated how the strength of positive interactions changes from stress-free to an extremely stressful environment rather than examining the relative importance of positive interaction and competition across species in diverse communities.

Moreover, our results also point to a potential mismatch between two paradigms in the literature. On one hand, the predominance of negative inter-specific interactions, and on the other hand, positive community DPRs. Based on our empirical analysis and simulations, we show that positive community DPRs require that inter-specific interaction strengths are on average higher (and often positive) than intra-specific interaction strengths. While a

dominance of weakly negative inter-specific interactions cannot be completely ruled out, these results also suggest that the occurrence or dominance of positive inter-specific interactions, as in our study, makes the occurrence of positive DPRs much more likely. Our results thus highlight the significance of understanding the relative importance and intensity of pairwise tree interactions, which drive positive community DPRs through a predominance of positive local interactions.

Our results reveal that interaction strength scales sublinearly with the biomass of the neighbouring tree with the exponents between 0 (size-independent) and 1 (linearly proportional to biomass), reflecting the differing capacity of plants competing for resources. While there is a general agreement that competition scales with size (Coomes & Allen, 2007), the exact way how positive interactions scale with size is not known. For instance, plants with deep roots can make water available to plants with shallow roots through hydraulic lift (Emerman & Dawson, 1996) and some plant species can shelter their direct neighbours from harsh microclimate conditions by physically mediating wind, heat or light (Wright et al., 2017). As is the case of competition, those positive interactions likely scale with the size of the neighbouring tree, with larger trees providing more readily accessible water or a more suitable microclimate (Gillerot et al., 2022). Furthermore, negative and positive interactions could scale with the size of the neighbouring tree differentially, resulting in a non-linear scaling for the net interaction. Thus, the scaling relationship between positive interaction and the size of the neighbouring trees is worth further exploration.

Our analyses of the interaction networks showed that the difference between mean inter- and intra-specific interactions is positive, which is consistent with findings of a global synthesis study (Adler et al., 2018). A field study on forests in Borneo (Stoll & Newbery, 2005), which found a differential effect of conspecific versus heterospecific neighbours, with conspecific neighbours reducing the growth of the focal tree considerably more than heterospecific neighbours, also indirectly supports our results. The magnitude and direction of competitive interactions within the network can either boost or diminish the individual growth rates. Consequently, the characteristics of the competitive network among species could be central for determining the community DPRs (Hooper et al., 2005). Our results corroborate this notion and expand the competitive network to a general interaction network which incorporates the effect of often overlooked positive interactions, demonstrating that the positive difference between inter- and intra-specific interactions is a key driver for the emergence of positive community DPRs.

This finding also echoes with the general principle of coexistence theory, which predicts that intra-specific competition should be stronger than inter-specific competition for stably coexisting species. The mechanisms underlying coexistence are frequently invoked to explain how and why mixtures outperform monocultures and

there certainly is, to some extent, correspondence between coexistence and BEF studies (Turnbull et al., 2013). Loreau (2004) provided a theoretical proof that a stably coexisting mixture would inevitably overyield and create a positive net diversity effect. Hence, when inter-specific competition is on average less intense than intra-specific competition, it is indicative of the presence of complementarity. As this pattern of interaction strengths is a prerequisite for avoiding competitive exclusion and fostering species coexistence, it may provide an explanation for the dominance of positive diversity effects in diversity–productivity studies. By establishing the connection between coexistence theory and BEF studies in an interaction network context, our research therefore offers novel insights into the preconditions for positive community DPRs.

In addition, our results show that the positive community DPRs become steeper as the difference between inter- and intra-specific interaction increases in magnitude. This finding could have practical implications for forest restoration and reforestation as it implies the possibility of selecting an optimal composition of tree species from local pools to maximize productivity. For instance, communities with species that are more complementary in their ecological strategies or more likely to engage in positive interactions may yield steeper DPRs. In this sense, the interaction coefficients in our model quantitatively reflect the ecological strategies of species pairs, paving the way to relate functional traits to the productivity. Functional traits linking essential biological processes to biotic interactions can act as common currency (Kunstler et al., 2016; Westoby & Wright, 2006). Substituting species identities with functional traits in our model would allow us to uncover universal relationships between functional traits and biotic interactions that could be generalized from the few species studied to the range of species that make up natural forests. Thus, combining our interaction-strength networks, with a functional trait approach, would not only improve our ability to predict the effects of tree diversity loss on forest ecosystem functioning, but also allow the selection of species mixtures with optimal performance for restoring forests worldwide.

In our *pairwise interaction model*, the interaction strength scales with the biomass of the neighbouring tree, reflecting an intensified interaction strength over time as the biomass of the neighbouring tree increased over the years (Reich et al., 2012). With data spanning a longer period becoming available, it could be profitable to explicitly examine the temporal variation in pairwise interactions. We accounted for environmental heterogeneity using plots and years as random factors and allowing interactions between them and species identity. Given the large number of plots with randomly assigned species and species compositions, it is not likely that the interactions were confounded with the variations in the abiotic environment (Healy et al., 2008). This interpretation is supported by Kröber et al. (2015) and Fichtner et al. (2018), whose

findings demonstrated that environmental heterogeneity explained only 4% variation of crown width growth rate and 2.5% variation of above-ground wood production in the BEF-China experiment respectively. Nonetheless, environmental conditions likely modify interactions when they are not accounted for through experimental designs. Previous studies showed that plant interactions exhibited differential responses across environmental gradients, in which the combination of specific species pairs and the stress type could play major roles (Soliveres et al., 2015). Thus, further research should consider identifying environmental factors that influence plant interactions.

AUTHOR CONTRIBUTIONS

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PEER REVIEW

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DATA AVAILABILITY STATEMENT

All the data and code used for the model fitting, simulation studies and visualization in this study are openly available on Zenodo https://doi.org/10.5281/zenodo.8403556.

ORCID

Wentao Yu https://orcid.org/0000-0001-9711-4247
Georg Albert https://orcid.org/0000-0001-5007-2043
Benjamin Rosenbaum https://orcid.org/0000-0002-2815-0874
Florian Schnabel https://orcid.org/0000-0001-8452-4001
Nadja Rüger https://orcid.org/0000-0003-2371-4172
Ulrich Brose https://orcid.org/0000-0001-9156-583X

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