Functional trait variability and identity determine the extent of tree diversity effects on productivity: A global meta-analysis

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Abstract

Growing evidence has revealed that ecosystem productivity depends more on the functional characteristics of species than on their number. However, just how the extent of tree diversity effects on ecosystem productivity is influenced by functional trait variability and composition has been rarely tested across and within species richness levels. Employing a meta-analysis of data from 59 global scale tree diversity experiments, we examined how functional dispersion and identity determine the outcomes of tree mixture effects on productivity, both across and at given species richness levels. We found that the positive effects of tree mixtures on productivity were strengthened by the increasing multidimensional functional dispersion and the community-weighted mean of leaf nitrogen content both across, and within, two- and four-species mixtures. Our analysis provides mechanistic insights into the potent roles of functional trait attributes in determining the magnitude (and even directionality) of the biodiversity-ecosystem functioning relationship in forest ecosystems.

Introduction

Positive biodiversity-productivity relationships are a predominant pattern in global forests that are based on both observational and experimental studies (Zhang et al. 2012; Liang et al. 2016). Species richness, as a surrogate of biodiversity, has been demonstrated to increase ecosystem productivity (Diaz & Cabido 2001; Hooper et al. 2012). Traditionally, numerous biodiversity-ecosystem functioning experiments have been implemented through the manipulation of species richness to understand the mechanisms that drive this relationship (Tilman et al. 1996; Grossman et al. 2017; Huang et al. 2018). However, there has been controversy in regard to the relationship between species richness and productivity, being either positive (Grossman et al. 2017; Huang et al. 2018), insignificant, or even negative (Vila et al. 2003; Tobner et al. 2016) in forest ecosystems. Still, a deeper mechanistic elucidation of which ecological processes drive variant species richness-productivity relationships remains incomplete.

Experimental plant communities involve random assemblages of species from a species pool (Tilman et al. 1996; Grossman et al. 2017; Huang et al. 2018), 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 outcomes (Diaz & Cabido 2001; Loreau et al. 2001; Tobner et al. 2016). Species with various functional traits lead to increased niche differentiation and positive interspecific interactions, more comprehensive resource use, and improved community-level biomass production, i.e., the so called complementarity effects (Tilman et al. 1997; Cardinale et al. 2011). 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 particular productive species that dominate in mixtures (Grime 1997; Loreau & Hector 2001). However, the outcomes of various species mixtures might be influenced through the extent of trait variations, even though the species richness is constant (Tobner et al. 2016). Thus far, the functional significance of tree diversity on ecosystem productivity has been rarely tested, both across and within species richness levels.

Recent studies have confirmed that effects of biodiversity on ecosystem functioning may be predicted by the degree of functional differences between constituent species in mixtures (Heemsbergen et al. 2004; Chen et al. 2019). Functional differences might result in variable interactions between species (Heemsbergen et al. 2004). For instance, greater interspecific functional dissimilarities increase niche differentiation and facilitative interactions to enhance the usage of resources; thereby, increasing ecosystem productivity (Loreau et al. 2001; Wright et al. 2017). Functional trait dispersion (FDis) is theoretically associated with niche differentiation (Laliberte & Legendre 2010). Accordingly, we hypothesized that FDis in species mixtures would be positively associated with positive diversity effects on forest productivity, both across and within species richness levels. We expected that the positive effects of species richness on productivity were attributable to the positive association between species richness and functional dispersion. Furthermore, the effects of diversity on productivity increased with higher levels of functional dispersion, when the species richness was constant (Fig. 1).

The effects of plant mixtures on productivity are also driven by the functional identities of species mixtures, which represent the characterized functional strategies for resource acquisition of species assemblages (Mokany et al. 2008). Acquisitive species with significant production investments in their stems and leaves have higher efficiencies in terms of resource acquisition and utilization, than conservative species (Reich 2014; Diaz et al. 2016). High productivity associated with acquisitive traits in mixed communities have been matched with high productivity in corresponding monocultures (Mokany et al. 2008). Moreover, the functional characteristics of species determine the intensity of the interactions between constituent species in plant communities along abiotic stress gradients (Maestre et al. 2009). The varied intensities of species interactions, therefore, can lead to different outcomes in terms of community-level productivity (Lusk et al. 2008; Fichtner et al. 2017). Additional available resources allow for the improved realization of niche differentiation in communities dominated by acquisitive traits (Sterck et al. 2011; Baez & Homeier 2018). Alternatively, in stressed or resource-limited environments, conservative traits dominate and interspecific facilitation tends to be stronger, as predicted by a stress-gradient hypothesis (Prado-Junior et al. 2016). Therefore, it may be anticipated that the positive effects of species mixtures on productivity are contingent on the community-weighted means (CWM) of acquisitive traits (Fig. 1). Further, the trajectory of the influence of the CWM indirectly reflects the relative strength of its effects on niche differentiation versus interspecific facilitation.

Here, we aimed to investigate how functional differences and identity determine the various outcomes of tree mixture effects on ecosystem productivity, both across and within species richness levels. We conducted a global meta-analysis based on 210 paired observations of tree mixtures and corresponding monocultures from 59 tree diversity experiment studies (Fig. 1). We collected data on specific leaf area, leaf nitrogen content, and wood density of the selected species for each observation to determine whether FDis and the CWM of acquisitive traits of species mixtures might be positively associated with positive diversity effects on forest productivity, both across and within species richness levels.

Material and Methods

Data collection

We conducted a survey of suitable studies using ISI Web of Science and Google Scholar, and cited references in relevant publications, up to September 01, 2019. 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: (1) studies contained at least one mixture treatment with corresponding monocultures, (2) all productivity and names of the species in each mixture and corresponding monocultures could be extracted directly from the text, tables, and/or figures, (3) the proportion of constituent species in each mixtures could be extracted or be calculated, (4) 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 GetData Graph Digitizer (v. 2.26.0.20) to extract data from the figures. In total, 59 published papers with 210 paired observations of aboveground productivity for tree mixtures and corresponding monocultures were selected. We extracted the data of tree species identities and the relative proportions of stem density from the constituent species of each species mixture.

We also obtained the plant functional traits, including leaf nitrogen content (LNC), specific leaf area (SLA), and wood density (WD) for each tree species from each study. 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) and other published datasets and literature. The LNC and SLA represent the leaf economics functions, whereas the WD represents the wood economics function (see Fig. S1 in Supporting Information).

Furthermore, we obtained the experimental duration, 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 species richness ranged from two to 24, and the experimental duration ranged from 0.5 to 120 years (Table S1). We performed a principal component analysis (PCA) of the MAT and MAP and extracted the first principal component (representing 82.69% of total inertia) to represent the climate condition of each study (Fig. S2).

Functional dispersion and functional identity of species mixtures.

We used functional dispersion (FDis) to represent the functional dissimilarities between the co-occurring species of each mixture. FDis opens possibilities for formal statistical tests for comparing differences in functional diversity between groups of communities through a distance-based test for homogeneity of multivariate dispersion (Anderson 2006; Laliberte & Legendre 2010). FDis was unaffected by species richness and could handle any number of traits (Laliberte & Legendre 2010). Most of the mixtures included in this study contained only two tree species. Multidimensional FDis, as well as the FDis for each individual trait of each species mixture were calculated 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 each species mixture was represented by the community-weighted mean (CWM) of the SLA, LNC, and WD, which was calculated as the averaged trait value of each species mixture (see details in Table S2). The FDis and CWM calculations were conducted using the *FD* package (Laliberte & Legendre 2010).

Data analysis

The effects of tree mixtures on productivity were calculated as the natural log-transformed response ratio ($\ln RR$) (Hedges et al. 1999):

$\ln RR = \ln(X_{\text{t}} / X_{\text{c}})$ (1)

where X_{t} and X_{c} are the observed productivity of species mixture and the mean productivity of all monocultures corresponding to the mixture, respectively.

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

$W_{\text{r}} = (N_{\text{c}} \times N_{\text{t}}) / (N_{\text{c}} + N_{\text{t}})$ (2) where W_{r} is the weight of each observation, and N_{c} and N_{t} are the numbers of replications of monocultures and mixtures, respectively.

We examined how the FDis and CWM in tree mixtures were associated with the species richness 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 effect on productivity across the species richness levels. Subsequently, we tested how they determined the tree mixture effect within two-, three- and four-species mixtures, respectively. These three species richness levels contained the largest number of mixtures in this meta-analysis. The linear-mixed effect model was constructed using Eqn. (3):

$\ln \text{RR} \sim \beta_0 + \beta_1 \bullet x_i + \pi_{\text{study}} + \varepsilon_{\text{ij}}$(3)

where x_i are the species richness in mixtures, multidimensional FDis, FDis and CWM of each individual trait, respectively; β, π_{species} and ε_{ij} are regression coefficients, the random effect of "study", and sampling error, respectively. The random effect accounts for autocorrelation between observations within the same study. We conducted the analysis using maximum likelihood estimation with the *lme4* package (Bates et al. 2015). All analyses were performed in R 3.6.1 (Team 2019).

Results

There was a positive relationship between the species richness in mixtures and plant functional dispersion, with the majority of the FDis variations being within two-, three-, and four-species mixtures ($P = 0.049$; Fig. 3a, Table S3). Although the effects of the tree mixtures on productivity (lnRR) significantly increased with the species richness in mixtures ($P < 0.001$; Fig. 3b), there were still large variations within two-, three-, and four-species mixtures.

There were significant positive effects of multidimensional FDis on lnRR both across the species richness levels ($P < 0.001$; Fig. 4a), and within two- and four-species mixtures ($P = 0.02$,$P = 0.004$, respectively; Fig. 4a, Table S4). Further, the lnRR increased with the FDis of LNC across species richness levels ($P=$ 0.02; Fig. 4b), as well as within four-species mixtures ($P = 0.01$, respectively; Fig. 4b). The effects of tree mixtures on productivity also increased with the FDis of SLA ($P = 0.01$; Fig. 4c) and WD ($P = 0.003$; Fig. 4d) across the species richness levels; however, they exhibited a significant effect of FDis of WD within only four-species mixtures ($P = 0.02$; Fig. 4d).

The lnRR also increased with the CWM of the LNC both across the species richness levels ($P = 0.04$; Fig. 5a) and within two- and four-species mixtures ($P = 0.02$, $P = 0.03$, respectively; Fig. 5a, Table S5). The lnRR also increased with the CWM of SLA across the species richness levels ($P = 0.11$; Fig. 5b) and within four-species richness mixtures ($P = 0.04$; Fig. 5b). Among the correlated CWM of the WD, LNC, and SLA (Table S6), the CWMs of SLA and WD had weaker impacts on the tree mixture effects on productivity than that of the LNC (Fig. 5c).

Discussion

This meta-analysis explicitly revealed that both functional trait variability and identity influenced the effects of tree mixtures on forest productivity, both across and within species richness levels of tree mixtures in experimental tree communities at a global scale. Specifically, we found that the functional dispersion of tree mixtures increased the extent of the positive mixture effects on productivity overall, and within the two- and four-species mixtures. Moreover, the CWM of acquisitive traits of species mixtures enhanced the positive effects of mixtures on forest productivity. Our findings offer novel insights into the importance of plant functional 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 segregated functional aspects from species richness to test the effects of functional diversity or individual traits involved in tree productivity (Tobner et al. 2016; Grossman et al. 2017). The previous studies

emphasized that a particular combination of functional attributes (e.g., deciduous and shade-intolerant species, high leaf-nitrogen, and calcium) (Tobner et al. 2016; Grossman et al. 2017; Huang et al. 2018), or shade tolerance heterogeneity between constituent species (Zhang et al. 2012), caused the observed species diversity effect. However, these researches also demonstrated that functional diversity *per se* could not explain the additional variation in ecosystem productivity across communities at a given species richness level. Beyond such conventional wisdom, our meta-analysis revealed that both functional dispersion and identity in tree mixtures determined the extent of diversity effects on productivity across and within the species richness levels. Our results, therefore, provided evidence that increased functional diversity should enhance ecosystem functioning through the coincidental dominance of influential species, or through niche partitioning (Tilman et al. 1997; Diaz & Cabido 2001; Loreau et al. 2001).

The degree of functional differences between species drive the effects of plant mixtures on ecosystem productivity, due to niche partitioning and positive interactions between constituent species at the community level (Tilman et al. 1997; Diaz & Cabido 2001; Loreau & Hector 2001). Plant leaf and wood economics traits are associated with plant resource acquisition, shade tolerance, hydraulic transport, mechanical support, and carbon storage (Reich 2014). Communities consisting of species with contrasting leaf and wood economics traits caused niche differentiation with respect to the utilization of light and water and facilitative interactions (Fichtner et al. 2017; Baez & Homeier 2018), which might increase the community-level acquisition and efficient use of light and water (Anderegg et al. 2018; Huang et al. 2018). Species-diverse mixtures with higher FDis, in turn, enhances the efficacy of resource use in mixtures due to recourse niche differentiation (Tilman et al. 1997; Cardinale et al. 2011), thereby improving ecosystem productivity (Flynn et al. 2011). Moreover, we found that increasing FDis resulted in higher productivity, even at a given species richness level. These outcomes suggested that trees in the communities with the same number of species that occupied various positions in the leaf and wood economics spectrum, increased the efficacy of resource utilization, and tended to promote forest productivity.

Consistent with our hypothesis, we found that the higher CWM of LNC increased the positive effects of species mixtures on productivity, which indicated the important role of the N-acquisitive strategies involved in diversity effects for improving forest productivity (Fig. 4). The functional characteristics of plant species determined the interactions between constituent species in plant communities along abiotic stress gradients (Maestre et al. 2009). In this study, mixtures dominated by acquisitive species were found at experimental sites with warmer climates and higher precipitation (Fig. S3). Additional available resources allowed for intense species interaction caused by effective light acquisition of fast-growing species, and hence niche differentiation in communities (Bertness & Callaway 1994; Callaway et al. 2002). These interactive processes appeared to be more intense in mixtures that included acquisitive plants compared with conservative mixtures, which consequently improved the effects of mixtures on productivity (Tobner et al. 2016; Fichtner et al. 2017). It is noted that the impacts of species mixtures on productivity were enhanced with the CWM of leaf nitrogen but independent of wood density (Sakschewski et al. 2015). Wood density correlates to a large number of structural characteristics of wood plants (Chave et al. 2009), and species with high wood density generally represent the conservative-end of the fast-slow plant economics spectrum (Reich 2014). Communities being characterized by great CWM of wood density reflect the coincidental dominance of slow growing species for maintaining ecosystem productivity. In such case, the interactive processes should be weak in mixtures that dominated by slow growing plants, which consequently cannot enhance the effects of mixtures on productivity.

In conclusion, our meta-analysis integrated the functional differences of species between global scale tree diversity experiments and investigated how functional trait variability and identity determined the outcomes of tree mixture effects on ecosystem productivity. Our results revealed that the effects of tree mixtures on productivity increased with the functional dissimilarity of the leaf and wood economics traits, and the community-weighted mean of leaf nitrogen content overall and within the two- and four- species mixtures. These results revealed the key role of the functional dispersion and composition of species mixtures toward explaining the variations in the effects of plant mixtures on ecosystem productivity, both across and within the species richness levels. We anticipate that our analysis will stimulate future inquiries into the role of functional traits in the diversity-productivity relationships.

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Figure legends

Figure 1 | Conceptual diagram of how functional trait dispersion and identity influences the tree mixture effect on productivity, both across and within species richness levels. (A) Mixtures (representing by circles) consisting of different species are distributed along the gradient of species richness in mixtures (SR), functional dispersion (FD), and functional identity (from conservative to acquisitive). The blue area (a) demonstrates species mixtures with increasing FDis or acquisitive strategies across the SR levels. Alternatively, the green area (b) demonstrates species mixtures with low variation of FDis or acquisitive strategies across the SR levels. The red area demonstrates species mixtures with increasing FDis or acquisitive strategies at a constant SR level. (B) The different lines are our predictions according to the different situations in panel A.

The blue line (a) assumes a positive relationship between lnRR and SR with increasing FDis or acquisitive strategies. The green dashed line (b) assumes a nonsignificant relationship between lnRR and SR, with a low variation of FDis or acquisitive strategies. The red line (c) assumes a positive relationship between lnRR with increasing FDis or acquisitive strategies at a constant SR level.

Figure 2 | Global distribution of the 59 studies included in the meta-analysis.

Figure 3 | Relationship between species richness with plant functional dispersion (a) and with the tree mixture effects on productivity (b). Dashed and solid blue lines are non-significant and significant mixed-effects models fit across all studies, respectively. Light blue bands represent 95% confidence intervals. The sizes of the circles represent the relative weights of corresponding observations. Curves with their 95% confidence interval (shaded) were estimated by partial regressions, with corresponding levels of significance (P). All numerical variables were natural log-transformed.

Figure 4 | Relationship between the tree mixtures on productivity (lnRR) with multidimensional functional dispersion (a), and with single trait dispersion (b-d). Blue lines are mixed-effects models fit across species richness levels. Light blue bands represent 95% confidence intervals. Red, green, and yellow lines are mixed-effects models fit within two-, three-, and four-species mixtures, respectively. The sizes of the circles represent the relative weights of corresponding observations. Curves with their 95% confidence interval (shaded) were estimated by partial regressions with corresponding levels of significance (P). All numerical variables were natural log-transformed.

Figure 5 | Relationship between the effects of tree mixtures on productivity with the CWM of species mixtures. (a) Leaf nitrogen content (LNC). (b) Specific leaf area (SLA). (c) Wood density (WD). Blue lines represent mixed-effects models fit across species richness levels. Light blue bands represent 95% confidence intervals. Red, green, and yellow lines are mixed-effects models fit within two- , three-, and four-species mixtures, respectively. The sizes of the circles represent the relative weights of corresponding observations. Curves with their 95% confidence interval (shaded) were estimated by partial regressions with corresponding levels of significance (P). All numerical variables were natural log-transformed.

Figure 1

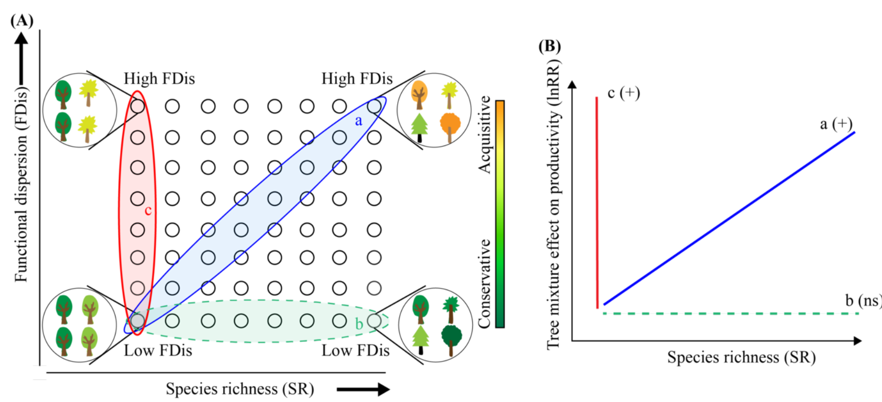

Figure 2

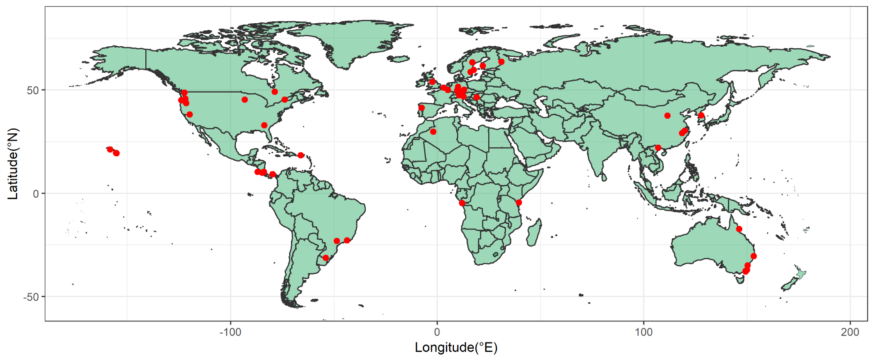

Figure 3

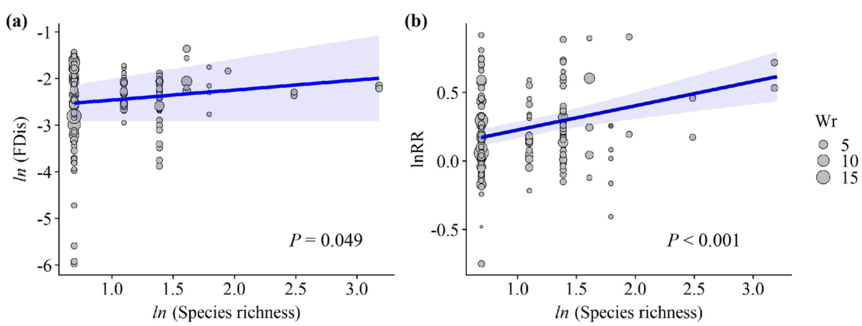

Figure 4

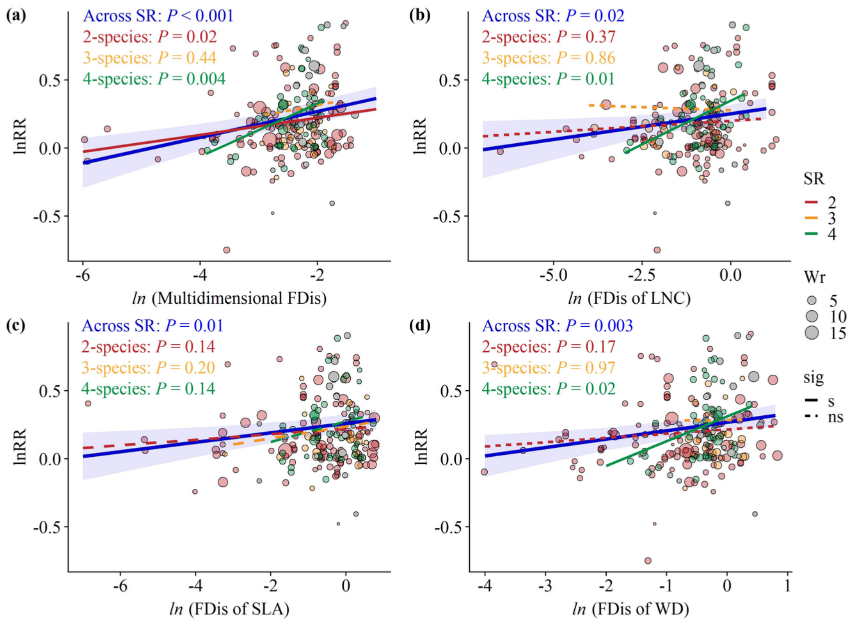

Figure 5