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ARTICLE

Scale-dependent diversity–biomass relationships can be driven by tree mycorrhizal association and soil fertility

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Abstract

Diversity–biomass relationships (DBRs) often vary with spatial scale in terrestrial ecosystems, but the mechanisms driving these scale-dependent patterns remain unclear, especially for highly heterogeneous forest ecosystems. This study explores how mutualistic associations between trees and different mycorrhizal fungi, i.e., arbuscular mycorrhizal (AM) vs. ectomycorrhizal (EM) association, modulate scale-dependent DBRs. We hypothesized that in soil-heterogeneous forests with a mixture of AM and EM tree species, (i) AM and EM tree species would respond in contrasting ways (i.e., positively vs. negatively, respectively) to increasing soil fertility, (ii) AM tree dominance would contribute to higher tree diversity and EM tree dominance to greater standing biomass, and that as a result (iii) mycorrhizal associations would

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exert an overall negative effect on DBRs across spatial scales. To empirically test these hypotheses, we collected detailed tree distribution and soil information (e.g., nitrogen, phosphorus, organic matter, pH) from seven temperate and subtropical AM–EM mixed forest megaplots (16–50 ha). Using a spatial codispersion null model and structural equation modeling, we identified the relationships among AM or EM tree dominance, soil fertility, tree species diversity, and biomass and, thus, DBRs across 0.01- to 1-ha scales. We found the first evidence overall supporting the three aforementioned hypotheses in these AM–EM mixed forests: (i) In most forests, with increasing soil fertility, tree communities changed from EM-dominated to AM-dominated; (ii) increasing AM tree dominance had an overall positive effect on tree diversity and a negative effect on biomass, even after controlling for soil fertility and number of trees. Together, (iii) the changes in mycorrhizal dominance along soil fertility gradients weakened the positive DBR observed at 0.01- to 0.04-ha scales in nearly all forests and drove negative DBRs at 0.25- to 1-ha scales in four out of seven forests. Hence, this study highlights a soil-related mycorrhizal dominance mechanism that could partly explain why, in many natural forests, biodiversity–ecosystem functioning (BEF) relationships shift from positive to negative with increasing spatial scale.

KEYWORDS

arbuscular mycorrhizal (AM) tree species, biodiversity–ecosystem functioning, biomass, ectomycorrhizal (EM) tree species, forest dynamics plot, soil fertility, spatial scale, tree species diversity

INTRODUCTION

Biodiversity is being lost globally (Butchart et al., 2010), and this may have negative consequences for ecosystem functioning (Cardinale et al., 2012; van der Plas, 2019). However, in most studies of the relationship between biodiversity and ecosystem functioning (BEF), especially those in forest ecosystems, the grain size of plots where biodiversity and ecosystem functions are measured is relatively small (<0.1 ha), even for studies carried out across regional (e.g., Paquette & Messier, 2011) or global extents (e.g., Liang et al., 2016). Therefore, the extent to which findings of BEF studies may scale up to inform management of "real-world" ecosystems remains debated (Manning et al., 2019; Srivastava & Vellend, 2005; Whittaker, 2010).

BEF relationships at larger scales often differ from small-scale patterns (reviewed in Gonzalez et al., 2020). For example, in large forest plots around the world, the generally positive tree diversity–biomass relationship (DBR; one important BEF relationship) found at smaller spatial scales (0.04 ha) is sometimes replaced by a negative relationship at larger spatial scales (≥0.25 ha; Chisholm et al., 2013). Positive BEF relationships at small scales are in line with theoretical expectations mostly focusing on how interspecific interactions, including niche complementarity and facilitation, may drive biomass production and stocks (Ammer, 2019; Barry et al., 2019). However, these mechanisms might be less important at large spatial scales, given the negative BEF relationships often found in natural settings (Chisholm et al., 2013; van der Plas, 2019). This raises the question as to what mechanisms drive scale-dependent shifts in BEF relationships (Thompson et al., 2018).

Here we propose a novel mycorrhiza-related mechanism for explaining the scale-dependent relationships between community diversity and ecosystem functioning (e.g., standing biomass) in heterogeneous forests. Most plant species (>80%) in terrestrial ecosystems have mutualistic associations with mycorrhizal fungi (Smith & Read, 2008; van der Heijden et al., 2015), especially with arbuscular mycorrhizal (AM) and ectomycorrhizal (EM) fungi. These two mycorrhizal associations greatly regulate belowground functional traits and niche space of plants (Bergmann et al., 2020; Peay, 2016), community diversity and ecosystem functioning (Tedersoo et al., 2020; van der Heijden et al., 1998), and, thus, BEF relationships (Ferlian et al., 2018; Luo et al., 2017; Schnitzer et al., 2011). However, a key unresolved question is whether and how the effects of mycorrhizae on plant diversity and ecosystem functioning, and hence the BEF relationships, differ among spatial scales. Furthermore, because AM and EM tree species generally play different roles in regulating forest community structure (Tedersoo et al., 2020), identifying the differential effect of AM and EM tree species on BEF relationships across scales might also be important for the conservation of the AM–EM mixed forests widely distributed in temperate and subtropical biomes (Brundrett & Tedersoo, 2018; Lu & Hedin, 2019).

Given that AM and EM fungi have distinct physiological and morphological properties (reviewed in Tedersoo & Bahram, 2019) and possess different nutrient foraging trade-offs with root networks and other soil microorganisms (Bahram et al., 2020; Chen et al., 2016), AM and EM tree species differ in nutrient acquisition strategies (Phillips et al., 2013). As a consequence, AM tree species tend to be most dominant in pH-neutral fertile soils, benefiting from their lower energetic costs in maintaining mycorrhizal symbiosis and/or higher root foraging precision than EM trees (Chen et al., 2016; Mao et al., 2019). In contrast, EM tree species have a competitive advantage in acidic infertile soil patches, partly due to the capability of EM fungi to directly access organic nutrients and their greater enzymatic capabilities (Figure 1a,b; Corrales et al., 2016; Lindahl & Tunlid, 2015; Lu & Hedin, 2019; Phillips et al., 2013). This may have important impacts on spatial patterns of tree diversity and biomass production for several reasons. First, because the majority of tree species associate with AM fungi (Brundrett, 2009), AM-associated trees account for the vast majority of the species pool for forests across biomes, especially in tropical, subtropical, and temperate regions (Brundrett & Tedersoo, 2018). Therefore, the communities dominated by AM trees are more likely to contain more species than EM-dominated communities assembled by fewer EM tree species. Second, AM tree species often possess strong conspecific negative density dependence or negative plant–soil feedback (Bennett et al., 2017; Jiang et al., 2021; Pu et al., 2022), promoting species coexistence and thus improving species diversity in AM-dominated communities (Tedersoo et al., 2020). These facts support the hypothesis that communities with more AM trees (i.e., AM-dominated) tend to possess higher species diversity, which has been proposed by Allen et al. (1995) and supported by recent empirical studies (e.g., Gerz et al., 2016; Jiang et al., 2021; Mao et al., 2019; Yan, Bongers, et al., 2022; also see Deng et al., 2023 for new nutrient-acquiring strategy perspective). However, since some other studies did not find evidence that AM-dominated communities are more diverse (Bahram et al., 2020; Carteron et al., 2022), this hypothesis still needs to be tested by more empirical studies especially including data across spatial scales, such as the present study. Contrary to AM-associated tree species, EM-associated tree species (e.g., *Tilia*, *Quercus*, and *Pinus*) often dominate the forest canopy because of their large size and/or high abundance, due to positive conspecific and con-mycorrhizal density dependence (Averill et al., 2022; Bennett et al., 2017; Chen et al., 2019; Jiang et al., 2021), resulting in greater biomass and/or basal area content (Jiang et al., 2021; Luo et al., 2023; Mao et al., 2019). Together, these findings predict that in AM–EM mixed forests, quadrats in fertile soils should contain more AM trees and thus possibly higher diversity, while quadrats in infertile soils contain more EM trees and thus greater biomass (Figure 1a,b).

We expect that the aforementioned patterns (Figure 1a,b) exert a consistently negative effect on the DBRs across scales, which weakens the positive DBRs found at smaller scales (e.g., <0.1 ha; Figure 1c) while driving a negative DBR at larger scales (e.g., >0.1 ha; Figure 1d). At smaller scales, we expect that many processes that can drive positive DBRs (e.g., biotic or abiotic facilitation and the effect of stem density) would play a key role, and then positive DBRs will still be prevalent (Barry et al., 2019; Chisholm et al., 2013). However, because trees in more species-poor EM-dominated quadrats are generally larger than those in more species-rich AM-dominated quadrats, we do not expect this positive relationship to be strong. That is, AM and EM tree dominance affect quadrat tree diversity and biomass in contrasting directions, which weakens positive DBRs. In this case, the observed DBR should be less positive than the DBR of a randomly assembled community where soil-related changes in the tree mycorrhizal dominance are excluded (Figure 1c; and see the null model test in what follows).

As spatial scale increases, it is increasingly unlikely that species within a quadrat directly interact, so we do not expect that large-scale diversity would directly affect standing biomass. Instead, other processes driving nonrandom species compositions, such as the soil-related changes in mycorrhizal dominance, may increasingly influence the relationship between plant diversity and standing biomass in a negative way (Mao et al., 2019). Because quadrats in infertile soils often contain more EM trees (i.e., EM-dominated) and, thus, greater biomass and lower tree diversity than quadrats in fertile soils, a negative relationship between tree diversity and standing biomass along a soil fertility gradient is expected ("all trees" in Figure 1d). Therefore, we predict DBRs at larger spatial scales (predominantly negative) to differ from those at smaller scales (predominantly positive) in abiotically heterogeneous AM–EM mixed forests. In other words, while changes in mycorrhizal dominance are expected to weaken DBRs (i.e., decrease positive DBRs or even make DBRs negative) across scales, the effects may be

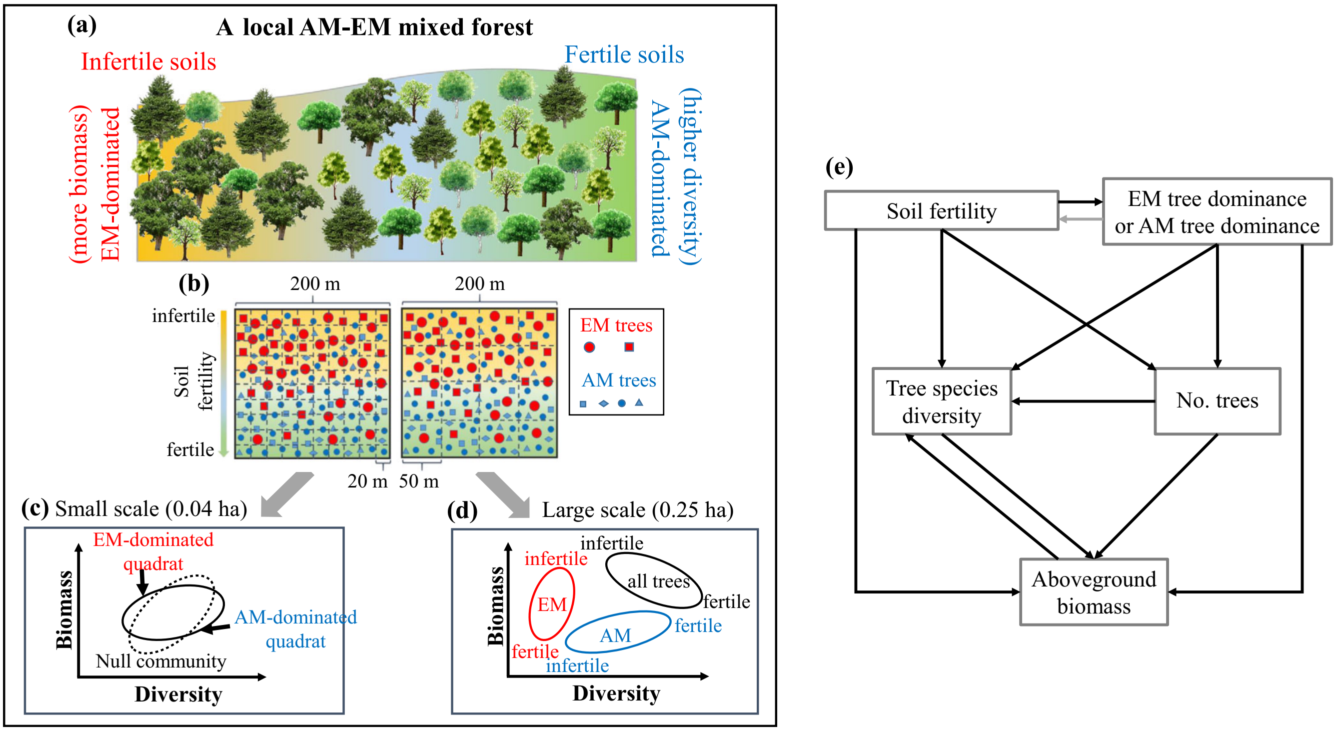


FIGURE 1 The *mycorrhizal dominance* mechanism about how soil fertility-related changes in tree mycorrhizal dominance (i.e., arbuscular mycorrhizal [AM]-dominated vs. ectomycorrhizal [EM]-dominated) modulate the relationship between tree diversity and standing biomass at different spatial scales (i.e., quadrat size) within local AM–EM mixed forests. (a) Representation of expected forest community located in heterogeneous soil environment (background color [yellow: infertile soil; green: fertile soil]), which contains two EM tree species (dark green) and four AM tree species (light green). In this forest, EM trees are mainly distributed in infertile soil (EM-dominated), while AM trees are mainly distributed in more fertile soils (AM-dominated). Because the EM tree community (sensu Mao et al., 2019: "EM tree community" represents all tree species associated with EM fungi in a local community) contains bigger trees and the AM tree community includes more and smaller tree species, the spatial patterns of AM and EM tree species lead to the spatial variation of tree diversity and biomass along the soil fertility gradient. (b) One 200 × 200-m^2 plot abstracted from the forest described by panel (a), where the color of the point represents types of mycorrhizal association (red: EM tree community; blue: AM tree community), and the shape and size of points represent different tree species and tree size, respectively. Under this scenario, the tree diversity–biomass relationship (DBR) should be less positive at the smaller spatial scales, e.g., 0.04 ha—panel (c), that is, the observed DBR (the solid ellipse) should be less strongly positive than the null DBR (the dashed ellipse), where the mycorrhizal dominance effect is excluded. At the larger but still local scales, e.g., 0.25 ha—panel (d), since most tree species are AM-associated, we expect that AM tree communities mainly determine tree diversity and thus range more widely along the diversity axis. Meanwhile, EM tree communities mainly affect quadrat biomass and thus range most widely along the biomass axis. As a result, the observed DBRs for all trees should be negative along the soil fertility gradient. (e) The conceptual structural equation modeling to test how selected abiotic (here soil fertility) and biotic factors (mycorrhizal dominance and number of trees) contribute to tree diversity and biomass. Because the DBRs might be nonlinear, we used the ellipses rather than lines to outline the overall DBR patterns in panels (c) and (d).

scale-dependent to some extent. For example, if increased species richness in AM-dominated quadrats is partly driven by abiotic heterogeneity, then one might expect that AM or EM tree dominance would primarily increase or decrease species richness mainly at larger scales. As a result, the negative effects of mycorrhizal dominance on DBRs would be stronger at larger spatial scales, thus partly explaining why DBRs shift from positive to negative with increasing spatial scale.

In this study, we integrated detailed soil information and adult tree data within seven large forest dynamics plots (16–50 ha) distributed in temperate and subtropical regions where both AM and EM symbioses are common (Table 1). To systematically evaluate the aforementioned predictions (Figure 1) in these AM–EM mixed forests, we used a spatial codispersion null model and structural equation modeling (SEM) to test the following three hypotheses across 0.01–1 ha scales. Hypothesis I: There is a positive relationship between AM tree dominance and soil fertility across scales and, hence, a negative relationship between EM tree dominance and soil fertility. Hypothesis II: AM tree dominance has a positive effect on tree species diversity and a negative effect on biomass, while EM tree dominance has exactly the reverse effects.

TABLE 1 Forest plot characteristics only including adult trees ≥10 cm in their diameter at breast height (i.e., dbh ≥ 10 cm).

Forest plots, with plot dimensions and latitude/longitude	Province/state and country	Year[a]	Forest type	Variables	All trees	AM trees	EM trees
FL (600 × 500 m^2; 48.08° N, 129.12° E)	Heilongjiang, China	2009	Temperate mixed coniferous broadleaf forests	No. trees	11,242	2213 (19.7%)	8249 (73.4%)
				Biomass (Mg/ha)	149.66	8.27 (5.5%)	135.06 (90.2%)
				No. species	25	11 (44%)	11 (44%)
CBS (500 × 500 m^2; 42.38° N, 128.08° E)	Jilin, China	2014	Temperate mixed coniferous broadleaf forests	No. trees	10,287	4179 (40.6%)	5550 (54.0%)
				Biomass (Mg/ha)	298.66	87.81 (29.4%)	187.19 (62.7%)
				No. species	30	17 (56.7%)	10 (33%)
TRC (400 × 400 m^2; 38.52° N, 90.56° W)	Missouri, USA	2013	Temperate broadleaf deciduous forests	No. trees	4848	1293 (26.7%)	3555 (73.3%)
				Biomass (Mg/ha)	315.69	19.73 (6.2%)	295.96 (93.8%)
				No. species	35	22 (62.9%)	13 (37.1%)
SCBI (400 × 600 m^2; 38.89° N, 78.15° W)	Virginia, USA	2008	Temperate broadleaf deciduous forests	No. trees	8004	4034 (50.4%)	3970 (49.6%)
				Biomass (Mg/ha)	283.69	156.27 (55.1%)	127.41 (44.9%)
				No. species	52	31 (59.6%)	21 (40.4%)
DHS (400 × 500 m^2; 23.17° N, 112.51° E)	Guangdong, China	2005	Subtropical broadleaf evergreen forests	No. trees	12,945	7801 (60.3%)	3568 (27.6%)
				Biomass (Mg/ha)	265.70	92.39 (34.8%)	158.43 (59.6%)
				No. species	118	108 (91.5%)	4 (3.4%)
TTS (500 × 400 m^2; 29.81° N, 121.78° E)	Zhejiang, China	2008	Subtropical broadleaf evergreen forests	No. trees	14,967	10,345 (69.1%)	4459 (29.8%)
				Biomass (Mg/ha)	70.95	43.76 (61.7%)	26.74 (37.7%)
				No. species	107	89 (83.2%)	12 (11.2%)
HSD (1000 × 500 m^2; 23.27° N, 111.53° E)	Guangdong, China	2013	Subtropical broadleaf evergreen forests	No. trees	37,968	27,995 (73.7%)	9459 (24.9%)
				Biomass (Mg/ha)	347.50	155.76 (44.8%)	190.43 (54.8%)
				No. species	148	124 (83.8%)	20 (13.5%)

Abbreviations: AM, arbuscular mycorrhizal; CBS, Changbaishan; DHS, Dinghushan; EM, ectomycorrhizal; FL, Fenglin; HSD, Heishiding; SCBI, Smithsonian Conservation Biology Institute; TRC, Tyson Research Center; TTS, Tiantongshan.

[a] The time when the census data were collected in our studied forests.

As a consequence, Hypothesis III: DBRs shift from positive to negative with increasing spatial scale in these forests, and this scale-dependent pattern mainly results from the changes in mycorrhizal dominance along the soil fertility gradients.

MATERIALS AND METHODS

Study sites and tree species information

Seven large forest plots (16–50 ha) located in Asia and North America were utilized in this study (Table 1), including four temperate forest plots with latitude ranging from 38.52° N to 48.08° N (i.e., Fenglin [FL], Tyson Research Center [TRC], Changbaishan [CBS], and Smithsonian Conservation Biology Institute [SCBI]) and three subtropical forests with latitude ranging from 23.17° N to 29.81° N (i.e., Tiantongshan [TTS], Dinghushan [DHS], and Heishiding [HSD]). All living trees within these plots with diameter at breast height (dbh) ≥ 1 cm were tagged, identified, measured, and mapped following the CTFS-ForestGEO protocol (Anderson-Teixeira et al., 2015). Given that adult trees (dbh ≥10 cm) greatly contribute to community structure (especially biomass carbon) and that the spatial distributions of AM and EM saplings are associated with the mycorrhizal type of adult trees (Johnson et al., 2018), we conducted our analyses only with adult tree data sets, as in previous studies (e.g., Chisholm et al., 2013). For the 25-ha TRC forest plot (Spasojevic et al., 2014), we only used the central 16-ha (400 × 400-m^2) section because detailed soil information and tree censuses were only carried out in the central 20-ha (480 × 420-m^2) section (LaManna et al., 2016), and the remaining part cannot be divided into 100 × 100-m^2 quadrats. For the same reason, we only used the rectangular 24-ha (400 × 600-m^2) part of the 25.6-ha SCBI forest plot (Bourg et al., 2013) to conduct our analyses. The final data set contained between 20 and 150 tree species in each forest plot (Table 1).

Tree mycorrhizal association

According to the strong phylogenetic conservatism of mycorrhizal trait (Brundrett & Tedersoo, 2018), we assigned the mycorrhizal association for each tree species based on their taxonomic information (mostly at species and genus levels) referring to the available literature (>40 literature items; see Mycorrhizal types.xlsx [Mao et al., 2023a]). Most of the included tree species have consistent mycorrhizal association information in the available global data sets, including Akhmetzhanova et al. (2012), Soudzilovskaia et al. (2020, 2022), Wang and Qiu (2006), and website sources such as http://mycorrhizas.info/index.html. To avoid incorrect conclusions resulting from the misdiagnosis of mycorrhizal types (Brundrett & Tedersoo, 2019), some tree species were classified as AM–EM associations (e.g., *Ulmus japonica*) and not included in the AM or EM community because there were contradictory reports of their mycorrhizal association or they were reported as forming dual-mycorrhizal associations (Guo et al., 2008; Teste et al., 2020). Some tree species, all with few individuals, were weakly AM-associated or facultative AM-associated species (e.g., *Myrica*), which we classified as AM species. Despite this, some species might still be misdiagnosed (see Mycorrhizal types.xlsx [Mao et al., 2023a] for details). To test the sensitivity of our results to the misdiagnosis of mycorrhizal types, we also conducted a robustness test for the DBR results after reassigning the mycorrhizal types for these uncertain species (see the *Data analyses* section for details). In total, over 85% of all tree species, containing over 90% of aboveground biomass in each forest plot, were classified as either AM- or EM-associated in our primary analyses (Table 1).

Tree diversity and biomass information

In this study, tree diversity and biomass were measured as species richness and aboveground biomass, respectively. We selected species richness because it is an easily interpreted and the most widely used index to represent species diversity in scale-dependent BEF studies (Chisholm et al., 2013). Specifically, species richness for each quadrat at each sampling scale was calculated by summing the number of tree species with at least one individual (dbh ≥10 cm) in the quadrat. Tree aboveground biomass (AGB) was calculated using available species-specific (Ali et al., 2018; Mao et al., 2019) or generic allometric regression equations (Chave et al., 2014) based on previous studies. Only for the SCBI forest plot did we calculate the AGB based on detailed allometric equations for most tree species in the allodb package (Gonzalez-Akre et al., 2022). AGB stocks strongly varied among these forests, ranging from 70.95 Mg/ha in TTS to 347.50 Mg/ha in HSD (Table 1), which was consistent with previous studies (Ali et al., 2018; Chisholm et al., 2013).

Soil information

We collected data on soil nitrogen (N), phosphorus (P), potassium (K), soil organic matter and carbon content, and soil pH in the upper soil layer (0–10 cm, where the majority of available nutrients and root biomass are concentrated), based on available studies with the assistance of the principal scientists in these forest plots (LaManna et al., 2016; Shen et al., 2016; Wang et al., 2012; see Appendix S1: Section S1 for a detailed description). Due to differences in soil analysis protocols, the soil data sets were not uniform among these plots but contained at least four soil variables (Appendix S1: Table S1). The ordinary kriging method was used to get the soil variable data at a scale of 0.01 ha (Wang et al., 2012). Then we conducted a principal component analysis for these data sets and used the first principal component (PC1), which described over 45% of soil variation for most forest plots to map the soil fertility gradient (Appendix S1: Figure S1). For TTS and HSD, we focused on both PC1 and the second principal component (PC2) because the PC2 in these two forest plots mainly described the soil P information, which was relatively low in content (Appendix S1: Table S1) and thus might limit the tree distribution patterns (Fang et al., 2017). Finally, we obtained the soil fertility gradient at 0.04-, 0.25-, and 1-ha scales by averaging the soil fertility values of 0.01-ha quadrats. Note that we used both PC1 and PC2 variables (Appendix S1: Figure S1) in the SEM analyses.

Data analyses

To test the scale dependence of DBRs and how these scale-dependent DBRs are driven by mycorrhizal associations and soil fertility, we first divided each forest plot into nonoverlapping quadrats at four spatial grains: $10 \times 10\ \mathrm{m}^2$ (0.01 ha), $20 \times 20\ \mathrm{m}^2$ (0.04 ha), $50 \times 50\ \mathrm{m}^2$ (0.25 ha), and $100 \times 100\ \mathrm{m}^2$ (1 ha), respectively. Given the differences in plot size (16–50 ha) of our studied forests, there were 1600–5000, 400–1250, 64–200, and 16–50 quadrats at 0.01-, 0.04-, 0.25-, and 1-ha scales, respectively. We then quantified the quadrat information about soil fertility, mycorrhizal dominance, species richness, AGB, and number of trees at all scales to test our three hypotheses. Mycorrhizal dominance was quantified using both the proportion of AM tree individuals (i.e., *AM tree dominance*) and the proportion of EM tree AGB (i.e., *EM tree dominance*) in each quadrat, given that AM tree communities contained more trees (relative to their AGB contribution), while EM tree communities contained larger trees and, thus, greater biomass in most forests (Table 1; Appendix S1: Figure S2).

Hypothesis I—Relationship between mycorrhizal dominance and soil fertility

Our first objective was to test Hypothesis I that with increasing soil fertility, AM tree species would become more dominant at the cost of EM tree species. Given the diverse heterogeneity of soil fertility in these forests (Appendix S1: Figure S1) and the possibility of spatial autocorrelation, we used the codispersion method to test the relationship between AM or EM tree dominance and soil fertility. Codispersion analysis is a nonparametric approach to quantifying spatial covariation of two or more spatially explicit variables (Cuevas et al., 2013), which can directly detect the magnitude of studied relationships at different directions and distances. The details about the codispersion method and the examples for result interpretation can be found in Appendix S1: Section S2 and Buckley et al. (2016). In brief, the codispersion coefficient of AM tree dominance and soil fertility for each spatial lag (i.e., distance between quadrats) is computed as their semi-cross-variogram divided by the square root of the semivariograms for each of them (Buckley et al., 2016). In general, the value of the codispersion coefficient ranges from −1 to 1, where positive (negative) values represent positive (negative) covariation between studied variables, and the strength of the covariation increases with the increasing absolute value of the codispersion coefficient. Following Buckley et al. (2016), we used the Epanechnikov kernel function to smooth the spatial variation surface of the two data sets (i.e., AM or EM tree dominance data set, soil fertility data set), and the kernel bandwidth was set equal to the dimension of the studied quadrat (e.g., 20 m for a $20 \times 20\text{-m}^2$ quadrat).

Overall, we expected a positive covariation between AM tree dominance and soil fertility and a negative covariation between EM tree dominance and soil fertility across scales of 0.01–1 ha (Figure 1). To verify the significance of covariation between AM or EM tree dominance and soil fertility, we performed a null model test of the codispersion analysis under a scenario in which trees are randomly assembled within the plot. Specifically, we permutated the entire community of AM trees and EM trees, respectively, in a random distance and direction, and then combined the new AM and EM tree communities into one null community (i.e., a mycorrhiza-dependent toroidal shift model; Appendix S1: Figure S3). We repeated this process 199 times to generate 199 null communities using the spatstat package in R (Baddeley & Turner, 2005). Theoretically, in these randomly assembled communities, the AM and EM tree species are distributed independently with respect to each other and the soil fertility gradients (Wiegand & Moloney, 2014), so the soil-related changes in AM or EM tree dominance were removed. Then, using these 199 null community data sets, we conducted a codispersion analysis as described earlier for the observed data sets and compared the observed patterns with the 199 null patterns. Specifically, we first used our observed codispersion value minus the expected value (i.e., mean values) of the 199 simulated results at each spatial lag to get a new codispersion map showing whether observed relationships were more positive or negative than the null relationships. Then the observed value was compared with the 195th and fifth null values at each spatial lag, and we deemed the observed relationship significantly differed from the expected relationship at $p < 0.05$ when the observed value ≥195th or ≤ fifth null value (i.e., a two-tailed test).

Hypothesis II—Effect of mycorrhizal dominance on tree species diversity and biomass

Our second objective was to test Hypothesis II, that AM tree dominance has a positive effect on tree species diversity and a negative effect on biomass, while EM tree dominance has exactly the reverse effects. Specifically, we conducted a SEM analysis to test how AM and EM tree dominance affected species richness and AGB when accounting for other biotic (i.e., number of trees) and abiotic factors (i.e., soil fertility; Figure 1e). We included "number of trees" as one of the SEM variables because many empirical studies (e.g., Chisholm et al., 2013) and theoretical mechanisms (e.g., more-individual hypothesis; Storch et al., 2018) have highlighted the importance of "number of trees" in driving BEF relationships. Given the ongoing debate on the causal relationship between biomass production and tree diversity (e.g., Craven et al., 2020), both directions were checked when we parameterized the SEMs, and the final direction was determined by the best fitted model. While we are aware of reciprocal relationships between soil fertility and AM or EM tree dominance (i.e., plant–soil feedback; Bennett et al., 2017; van der Putten et al., 2016), we presented the results about the direction "soil fertility (both PC1 and PC2)" → "AM or EM tree dominance" because this direction was more relevant to our proposed framework (Figure 1). Given that there were only 16–50 independent quadrats at the 1-ha scale within each forest, we mainly conducted the SEM analysis at scales of 0.01–0.25 ha to ensure a sufficient sample size to build the SEM paths.

Prior to analyses, species richness and AGB were log-transformed, and all other predictors were standardized to have a mean of 0 and a standard deviation of 1 in order to improve the interpretability of regression coefficients (i.e., *Z*-score standardization; Schielzeth, 2010). To construct the initial SEM structure, we selected all possible paths among these variables (Figure 1e) and parameterized them at each scale in each plot. Then, to test other possible reduced models sharing the same causal structure with the initial model, we eliminated nonsignificant paths one by one and compared the overall performance of the model fit between reduced models and the initial model. The performances of the structural equation models were determined by several criteria: (i) $p > 0.05$ in chi-square test; (ii) the standardized root mean square residual was less than 0.05; (iii) Bentler's comparative fit index was larger than 0.9; and (iv) the root mean square error of approximation was less than 0.05. Finally, we selected the best model from all satisfactory models by their Akaike Information Criterion (AIC) value. The indirect effects of the predictors in the final model (i.e., soil PC1, soil PC2, number of trees, and EM tree dominance or AM tree dominance) were calculated by multiplying the coefficients of all paths linking these variables to tree diversity or AGB, and the total effects equaled the sum of all direct and indirect effect coefficients (Appendix S1: Tables S2 and S3). Note that we retained both species richness and AGB in all final structural equation models even if their paths were nonsignificant. We did this for two reasons. First, these models can better show how AGB and tree diversity affected each other when accounting for other variables, which is important given the focus of our study on DBRs. Second, all these models had good performance in all criteria and were thus adequate.

Hypothesis III—Effect of tree mycorrhizal dominance together with soil fertility on scale-dependent DBRs

Our third objective was to test Hypothesis III, that soil fertility-related shifts in the dominance of AM- versus EM-associated tree species contribute to the scale dependence of DBRs. To this end, as a first step, we quantified the relationship between quadrat AGB (dependent variable) and species richness (independent variable) at multiple spatial scales (0.01–1 ha), using generalized least squares (GLS) methods. The quadrat species richness and AGB were log-transformed prior to analysis. Following Chisholm et al. (2013), these paired data sets (i.e., log [AGB]–log [species richness]) were used to fit the linear models with and without a spherical autocorrelation structure to detect the DBR while accounting for spatial autocorrelation. In this case, the *slope* and *intercept* of the final linear model quantify the effect of tree species richness on AGB based on the nonlinear power function form: $\mathrm{AGB} = \mathrm{Exp}\,(intercept) \times (\text{species richness})^{slope}$ (Chisholm et al., 2013; Liang et al., 2016). We then compared the AIC of the separate models and selected the model with the lowest AIC score as the optimal model (Appendix S1: Table S4). Finally, the parameters of the optimal models were extracted to show the DBR at different scales. Given the generally hump-shaped relationships between species richness and biomass production (Fraser et al., 2015), it is worth noting that the positive or negative DBRs in our study showed positive or negative relationships within the data range observed.

Second, we conducted a codispersion null model analysis to test how DBRs were influenced by soil-related changes in AM and EM tree dominance at each scale and thereby how mycorrhizal associations influenced the scale dependence of DBRs. Here, we repeated the codispersion null model analysis introduced earlier when testing Hypothesis I. We first quantified the covariation patterns between species richness and AGB in each observed community (i.e., spatial DBRs, which showed the DBRs in different directions and distances). Then, 199 null communities were created in which associations between soil fertility and tree mycorrhizal dominance were removed (Appendix S1: Figure S3), and the spatial DBRs were quantified in each null community. Finally, we compared the observed DBRs with those expected (i.e., generated by null model) DBRs across scales using the same procedure as described earlier when testing Hypothesis I. This allowed us to verify (1) whether, at each scale, observed DBRs were negatively affected by soil-related changes in mycorrhizal dominance (i.e., whether the expected DBRs were less negative and/or more positive than the observed DBRs); and (2) whether this negative effect was strong enough to explain the scale dependence of DBRs (i.e., whether the scale dependence of DBRs observed in these forests disappeared in the null communities).

Finally, we conducted a robustness test to assess the sensitivity of our analyses to the misdiagnosis of mycorrhizal types. To this end, we reassigned the species with insufficient genus-level mycorrhizal evidence or facultative AM-associated type (i.e., "AM–NM" type in Mycorrhizal types.xlsx [Mao et al., 2023a]) as "Other," and these species were not included in the AM or EM community in our sensitivity analysis. For the species with contradictory reports (i.e., AM vs. EM), we reassigned their mycorrhizal types opposite to the recommended types in our primary analysis (e.g., AM → EM). For some trees without species information that were identified as "sp" (e.g., *Fraxinus* sp in Mycorrhizal types.xlsx [Mao et al., 2023a]), we also reassigned their mycorrhizal type as "Other" in the robustness test. In total, we found that mycorrhizal associations of 68 out of the 415 studied species needed to be reassigned in the robustness test, which contained many rare species accounting for 10.96% of total biomass and 13.68% of total abundance. Using this reassigned data set, we conducted the codispersion null model analysis and checked the mycorrhizal dominance effects on scale-dependent DBRs again.

All statistical analyses were performed in R version 3.6.1 (R Core Team, 2019), and the SEM test was performed using the lavaan package (Rosseel, 2012).

RESULTS

Across our study plots, AM tree species represented 44%–92% of species versus 4%–44% for EM tree species. AM trees ranged from 20%–74% of the total numbers of individuals, compared to 25%–74% of individuals that belong to EM-associated species. Also, AM trees accounted for 6%–62% of the total biomass, versus 38%–94% for EM trees (Table 1). Thus, as expected, there were more AM tree species in these forests, while EM tree species contained more large trees and greater biomass (Appendix S1: Figure S2), except in the SCBI and TTS forest plots. There were obvious soil fertility gradients in our study plots, where the more fertile soils often contained more nitrogen, phosphorus, and other nutrients and were pH-neutral in most cases (Appendix S1: Figure S1; PC1).

Hypothesis I: Relationships between mycorrhizal dominance and soil fertility

We used the codispersion method to test the spatial covariation between AM or EM tree dominance and soil fertility. The results indicated that AM tree dominance (in abundance) showed a consistent positive covariation (i.e., detecting a significant positive signal in more than half spatial lags) with soil fertility, while EM tree dominance (in AGB) had a negative covariation with soil fertility across scales in five forests, but not in two of the subtropical forests (i.e., TTS and HSD; Figure 2; Appendix S1: Figure S4). That is, in most forests, the AM-dominated quadrats mainly occurred in fertile soils

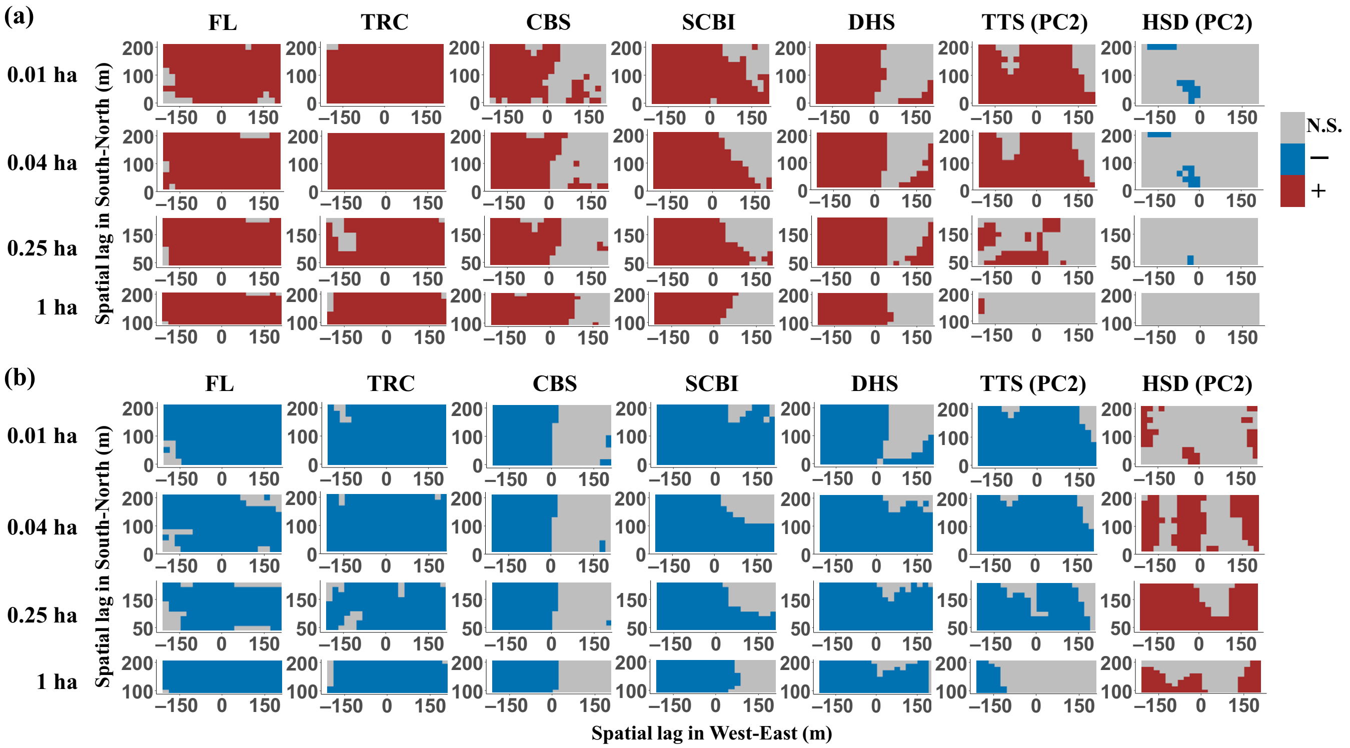


FIGURE 2 Codispersion results for covariation between AM tree dominance (a) or EM tree dominance (b) and soil fertility at different scales in seven study plots. The color of each cell represents a significant positive (brown), negative (blue), or insignificant covariation (gray) at $p < 0.05$ in the corresponding spatial lag (Appendix S1: Figure S4). The spatial lag represents the distance over which in corresponding directions a covariation pattern is measured. See Appendix S1: Figure S4 for the more detailed results including the soil first principal component (PC1) results in TTS and HSD. Abbreviations: CBS, Changbaishan; DHS, Dinghushan; FL, Fenglin; HSD, Heishiding; SCBI, Smithsonian Conservation Biology Institute; TRC, Tyson Research Center; TTS, Tiantongshan.

and EM-dominated quadrats tended to occupy the infertile soils, which supported our Hypothesis I. In TTS, however, the significant covariation between mycorrhizal dominance and soil fertility was only observed when using soil PC2 (mainly about soil P content and pH; Appendix S1: Figure S1) at scales smaller than 0.25 ha (Figure 2). In HSD, there was no obvious relationship between mycorrhizal dominance and soil fertility at multiple scales (Figure 2; Appendix S1: Figure S4).

Hypothesis II: Effect of mycorrhizal dominance on tree species diversity and biomass

We conducted a SEM test to clarify how AM and EM tree dominance affected species richness and AGB when controlling for other factors (i.e., soil fertility and number of trees). All the final models had good performance in statistical criteria, and the selected variables explained over 20% of the variation in AGB or species richness in most forests (Appendix S1: Figure S5). When combining the significant paths of these structural equation models into one integrated SEM framework, we found that EM tree dominance (quantified by EM tree AGB proportion) had negative effects on tree diversity and positive effects on biomass, but not at all the studied scales (Figure 3b). In contrast, AM tree dominance (quantified by AM tree abundance proportion) positively affected tree diversity and negatively affected biomass across scales of 0.01–0.25 ha (Figure 3a) after controlling for other factors (i.e., soil fertility and number of trees; direct and total effects in Appendix S1: Table S2). All these SEM results supported our Hypothesis II, that AM tree dominance contributes to higher tree diversity and EM tree dominance contributes to greater standing biomass.

We also found nonlinear relationships between AM tree dominance and tree diversity or biomass, especially at scales of 0.01–0.04 ha (Appendix S1: Figure S6). These indicated that tree diversity was not always maximized in quadrats with maximal AM tree dominance at smaller scales, although in the majority of cases the greatest tree diversity was found in quadrats with above-average AM tree dominance. Similarly, standing biomass was not maximized in quadrats with minimal AM tree dominance at smaller scales. Nevertheless, in the four forests with a scale-dependent DBR (i.e., TRC, CBS, SCBI, and DHS; Figure 4), tree diversity and biomass showed opposite trends along the AM tree dominance gradient (Appendix S1: Figure S6). Therefore, at least in those four forests, these opposite trends (regardless of nonlinearity) supported our Hypotheses II about the opposite effects of mycorrhizal dominance on tree diversity and biomass.

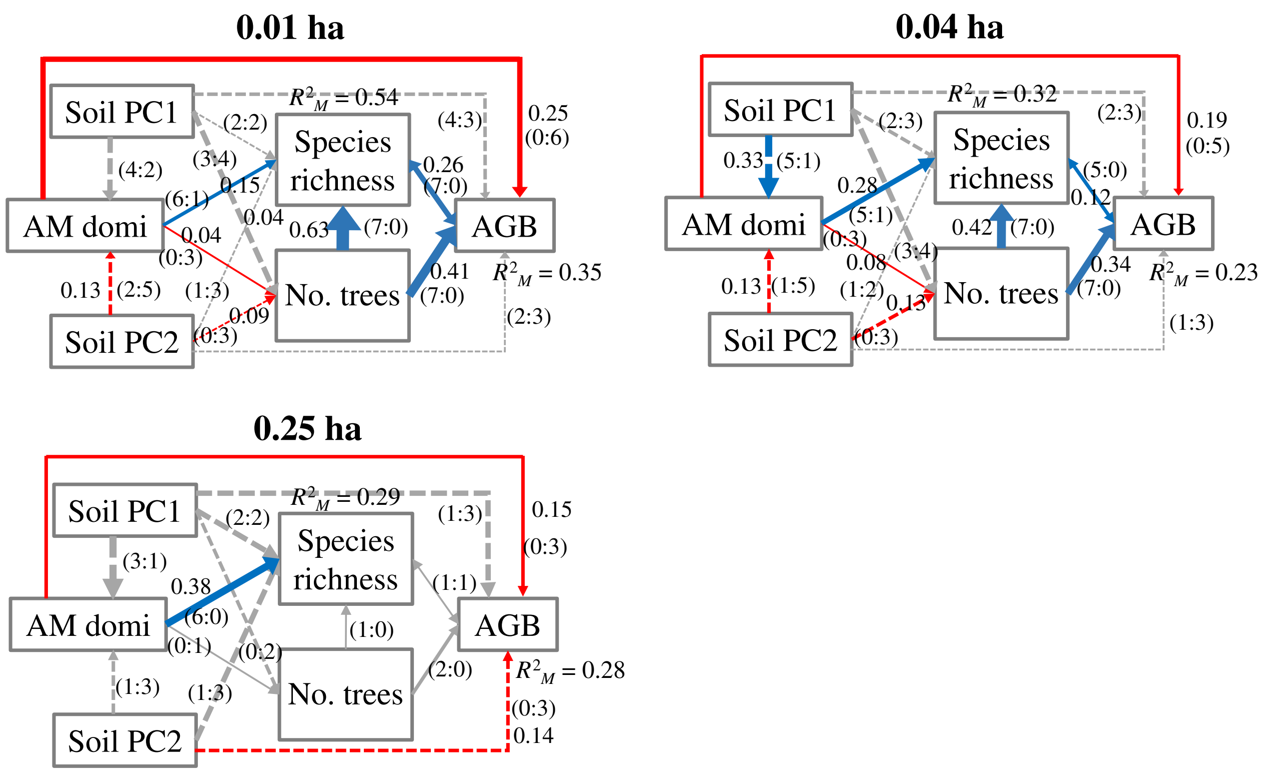
For other factors, the SEM results suggested that number of trees had a very strong positive effect (mean standardized coefficients >0.4; Figure 3; Appendix S1: Tables S2 and S3) on both species richness and AGB at scales of 0.01 and 0.04 ha but not at the 0.25-ha scale. Finally, soil factors defined by the first two principal components (i.e., soil PC1 and soil PC2) had significant direct and indirect effects (via the number of trees and mycorrhizal dominance) on AGB and species richness across scales (Figure 3; Appendix S1: Figure S5), and many indirect effects were stronger than direct effects (Appendix S1: Tables S2 and S3).

Hypothesis III: Effect of tree mycorrhizal dominance together with soil fertility on scale-dependent DBRs

The DBRs depended on the spatial grain size in most of the forests studied (Figure 4; Appendix S1: Table S4). Specifically, species richness showed a significant positive relationship with standing biomass at the 0.01-ha scale in all forest plots (log-transformed linear models: $p < 0.05$). At the 0.04-ha scale, relationships between species richness and standing biomass were mixed across sites. Finally, at the 0.25- and 1-ha scales, relationships were negative or nonsignificant at $p < 0.05$ in most forests (Figure 4). In four out of seven studied AM–EM mixed forests (i.e., TRC, CBS, SCBI, and DHS), as expected (Figure 1c,d), there were obvious positive-to-negative shifts in DBRs with increasing spatial scale. The codispersion results further verified that these positive-to-negative DBRs were spatially stationary within these four forests, as the codispersion values between species richness and AGB in these forests were consistent in nearly all directions and distances (Figure 5a).

When removing the directional changes in AM and EM tree dominance along the soil fertility gradient (Figure 2) using a mycorrhiza-dependent toroidal shift model (Appendix S1: Figure S3), we found that the negative covariation between species richness and AGB (i.e., negative DBR) originally observed in those four forests at scales >0.04 ha disappeared (Figure 5a,b). This suggests that the negative large-scale DBRs observed in these forests were mainly attributed to changes in mycorrhizal dominance. Notably, a significant negative effect of changes in mycorrhizal dominance on DBRs at multiple scales was directly affirmed by comparing the observed covariation with expected covariation of 199 randomized communities ($p < 0.05$; Figure 5c). These results are robust to the uncertainties of mycorrhizal assignation because very similar patterns were observed in a sensitivity analysis with mycorrhizal type-reassigned data set

(a) AM tree dominance case



(b) EM tree dominance case

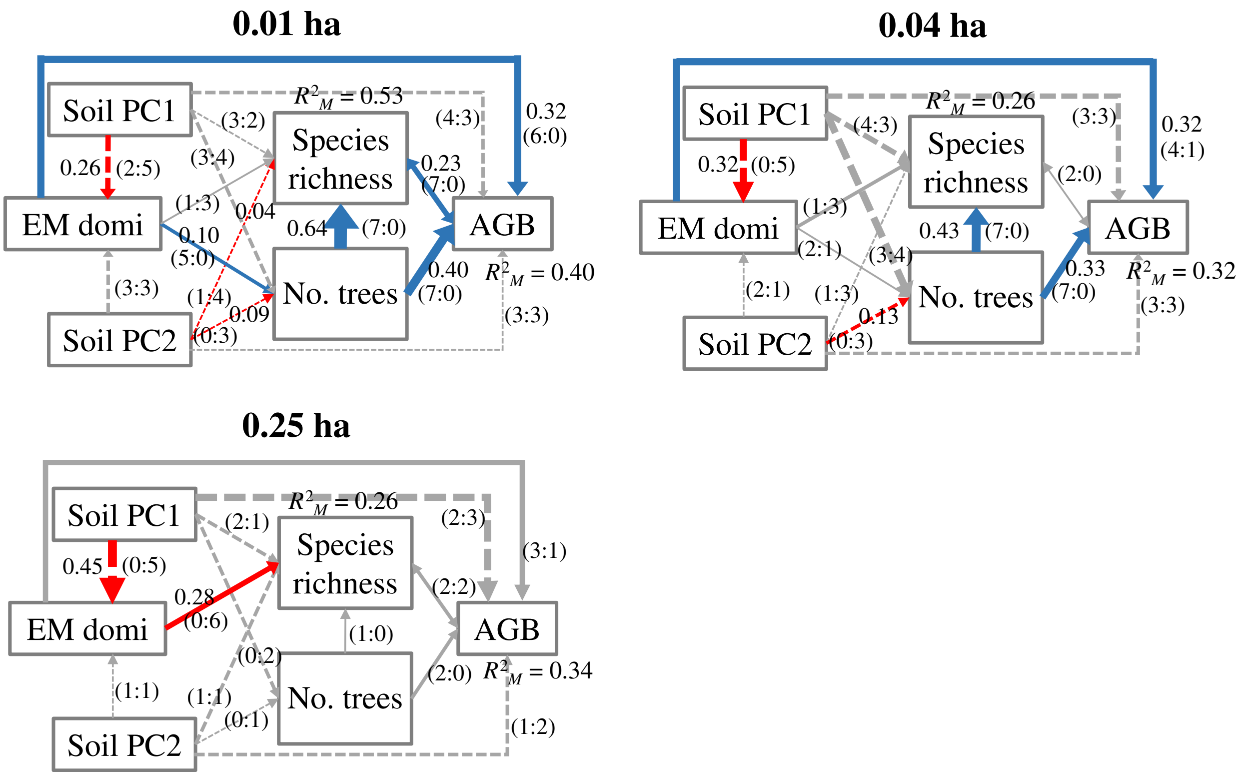


FIGURE 3 Legend on next page.

(Appendix S1: Figure S7). All these findings support our Hypothesis III that the soil-related changes in mycorrhizal dominance weakened the positive DBRs at smaller scales while driving a negative DBR at larger scales (Figure 1c,d), even though many negative effects at larger scales were nonsignificant at $p < 0.05$ (Figure 5c).

As visible evidence, the soil-related DBR patterns for AM, EM, and all trees (Figure 1d) were directly observed in those four plots with a positive-to-negative shift in DBRs (i.e., TRC, CBS, SCBI, and DHS; Appendix S1: Figure S8). In contrast, there was no soil-related DBR pattern in the other three plots (i.e., FL, TTS, and HSD; Appendix S1: Figure S8) without a positive-to-negative shift in DBRs (Figures 4 and 5). Together, this further suggested that in those four forests, the positive-to-negative shifts in DBRs with increasing spatial scale were mainly attributed to the soil-related changes in mycorrhizal dominance.

DISCUSSION

Our study provides the first evidence for our hypotheses that in AM–EM mixed forests, the soil-related changes in mycorrhizal dominance negatively affect DBRs across scales and, thus, underpin negative DBRs especially at larger scales (Figure 1). In particular, we found that EM tree dominance decreased along the soil fertility gradient, while AM tree dominance increased along the local soil fertility gradient in most studied forests (Figure 2). Moreover, AM tree dominance generally affected quadrat tree diversity and biomass in contrasting directions when controlling for other factors (Figure 3; Appendix S1: Figure S5), with positive effects on tree diversity and negative effects on biomass. Together, the changes in AM and EM tree dominance along the soil fertility gradient exert an overall negative effect on the DBRs across spatial scales (Figure 5), which weakens the positive DBRs at scales of 0.01–0.04 ha while driving negative DBRs at scales of 0.25–1 ha, thereby causing positive-to-negative shifts in DBRs across scales within some forests (Figure 4).

Relationships between mycorrhizal dominance and soil fertility: Temperate versus subtropical forests

Experimental and observational evidence is mounting that AM and EM tree species have contrasting responses to differences in soil fertility, which is consistent with our Hypothesis I for AM–EM mixed forests. For instance, both species-focused (e.g., *Oreomunnea mexicana* and *Gilbertiodendron dewevrei*; Corrales et al., 2016; Hall et al., 2020) and community-focused studies (Mao et al., 2019; Weemstra et al., 2020) have found that EM tree dominance increases (or AM tree dominance decreases) with decreasing soil fertility, in line with the mechanism of mycorrhizal-associated nutrient economy (Corrales et al., 2016; Phillips et al., 2013). Recently, regional observations also gave support to the superiority of EM-dominated forests in infertile soils (Lu & Hedin, 2019; Peay, 2016), but these patterns may depend on forest type (Gomes et al., 2019). In this study, we examined the relationships between mycorrhizal dominance and soil fertility in seven forests belonging to three forest types (Table 1). In four temperate forests (i.e., temperate mixed coniferous broadleaf forests (FL and CBS) and temperate broadleaf deciduous forests (TRC and SCBI)), AM tree dominance has a significant positive relationship with soil fertility, while EM tree dominance possesses a negative relationship with soil fertility across scales of 0.01–1 ha. By contrast, there is a weaker signal in subtropical forests compared with temperate forests on the relationship between mycorrhizal dominance and soil fertility because the significant and scale-consistent patterns were only observed in one (i.e., DHS) out of three subtropical broadleaf evergreen forests.

There are multiple possible causes of the aforementioned differences between temperate and subtropical forests. In general, the response of mycorrhizal dominance to soil fertility should originate from the physiological and functional differences between AM and EM symbionts (e.g., exudation, enzyme activities, associated root traits; Bergmann et al., 2020; Tedersoo & Bahram, 2019), through

FIGURE 3 Significant paths in structural equation modeling test for the seven forest plots. The mycorrhizal dominance is represented by AM tree dominance (AM domi; a) or EM tree dominance (EM domi; b). The arrow thickness is proportional to the “mean effects” between variables defined by the average of the absolute values of significant (at $p < 0.05$) standardized coefficients in corresponding paths across forests (Appendix S1: Figure S5). The numbers in parentheses show how many positive and negative effects in corresponding paths were significantly detected in our SEM analysis (positive: negative; Appendix S1: Figure S5). The color of each path represents the difference in frequency of positive versus negative effects, with blue representing at least three more positive effects than negative effects and red representing at least three more negative effects than positive effects. The italic numbers around the blue and red paths show their “mean effects.” R^2_M values are the average of the R^2 for species richness or aboveground biomass (AGB) in individual SEM results across the seven forests. The bidirectional arrows between species richness and AGB indicate there are paths in both directions in our best-fitted models. We used the dashed lines to represent the effects of Soil PC1 and Soil PC2 because the soil variables used to conduct these two principal components were different across forests (Appendix S1: Figure S1, Table S1).

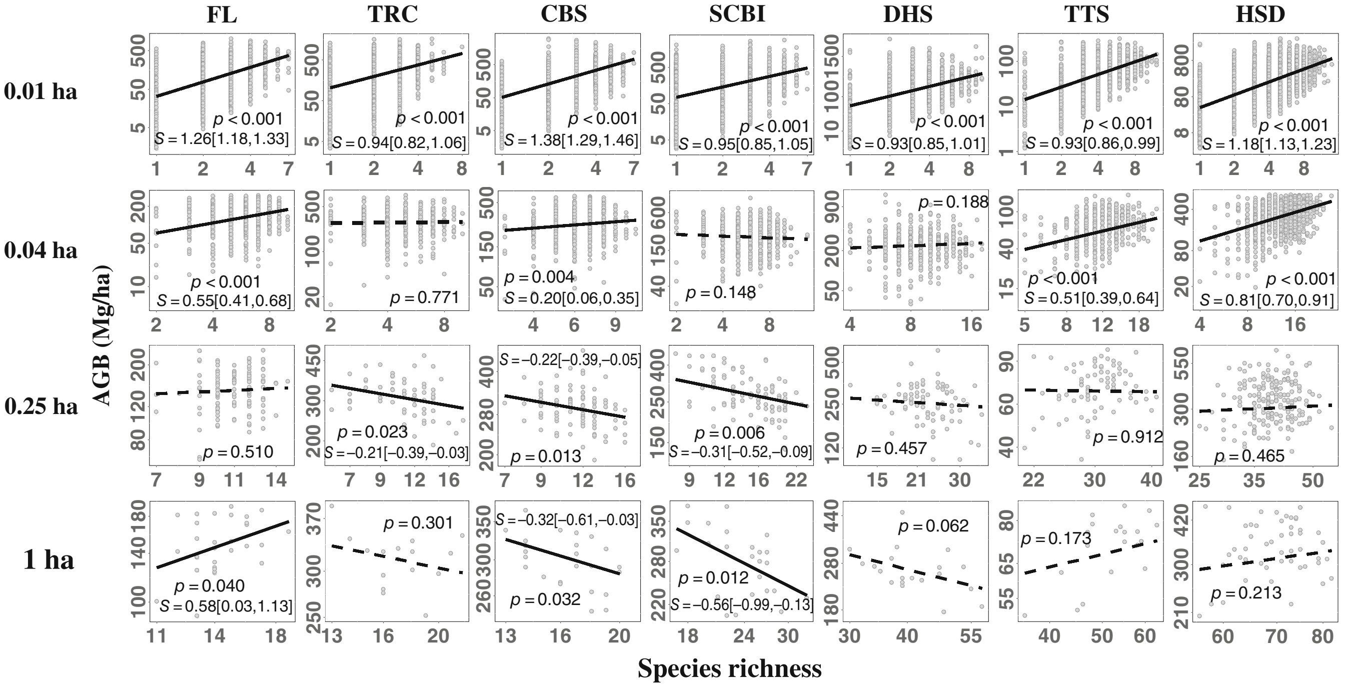


FIGURE 4 Log-transformed linear relationship between aboveground biomass (AGB) and species richness. The abbreviations of the seven forest plots are consistent with Figure 2. The lines show the fitted linear models using generalized least-squares methods, and dashed lines represent statistically insignificant slopes ($p \geq 0.05$; Appendix S1: Table S4). The slope with 95% CIs (only for significant models) and *p*-value of fitted models are presented. The points represent the information of AGB and species richness in each quadrat (see *Materials and Methods* section for the number of quadrats at each scale). Abbreviations: CBS, Changbaishan; DHS, Dinghushan; FL, Fenglin; HSD, Heishiding; SCBI, Smithsonian Conservation Biology Institute; TRC, Tyson Research Center; TTS, Tiantongshan.

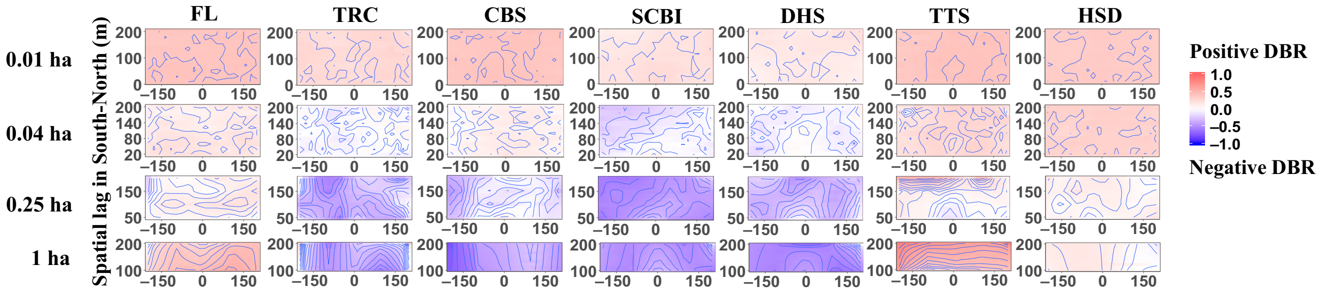
which AM and EM tree species adapt and modulate surrounding soil conditions (Yan, Freschet, et al., 2022). However, because of the differences in climate properties (e.g., temperature, precipitation), environment context (e.g., N limitation vs. P limitation), and species pools (e.g., deciduous vs. evergreen) (Keller & Phillips, 2019; Netherway et al., 2021; Seyfried et al., 2021; Steidinger et al., 2019), the physiological and functional properties of AM and EM tree species might be different between temperate and subtropical/tropical ecosystems. For instance, although great functional differences between AM and EM groups have been reported in temperate and boreal ecosystems, such as plant nutrient traits (acquisitive vs. conservative), leaf litter and fine root decomposition rates, and soil acid–base chemistry, these differences do not necessarily occur in subtropical and tropical ecosystems (Averill et al., 2019; Keller & Phillips, 2019; Lin et al., 2022; See et al., 2019; Seyfried et al., 2021). Consequently, the relationship between mycorrhizal dominance and soil fertility should be more robust in temperate compared with subtropical forests.

Other site properties not considered in our analyses (e.g., topography, disturbance, stand age) could also have contributed to the mixed patterns in our subtropical forests, although this still needs more site-specific evidence. In the 50-ha HSD plot, for instance, the environmental filtering effect defined by topographical and soil variables is not obvious, because AM and EM tree species are more likely to co-occur in root neighborhoods of each other rather than separately distribute in habitat patches (Luo et al., 2021). Alternatively, the mixed AM–EM patterns along soil gradients in these subtropical forests might result from AM versus EM partitioning of different nutrients (e.g., N and P) or nutrient sources (e.g., inorganic vs. organic) in the same soil patches (Lin et al., 2018; Liu et al., 2018). Nevertheless, to further understand the distribution patterns of AM and EM tree species (and thus their relative dominance) within local forests, future studies should compare the effect of soil conditions (both resource content and resource composition [e.g., N:P]) and other abiotic factors in temperate and subtropical forests separately.

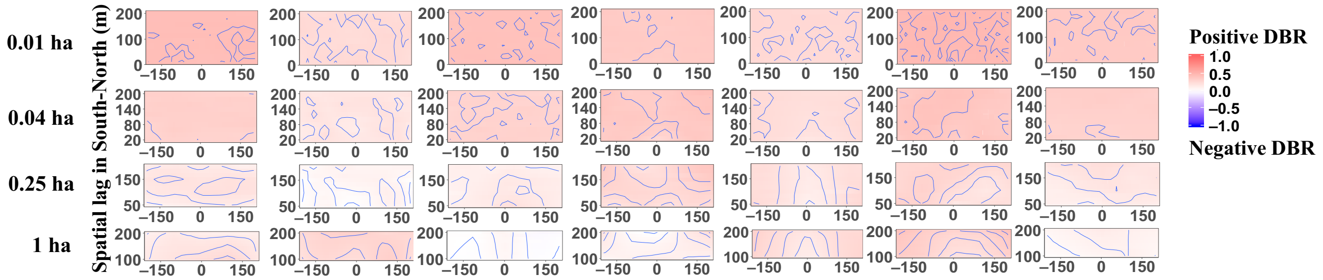
Effect of tree mycorrhizal dominance on community diversity and standing biomass

In most studied forests, we found that AM tree dominance had a positive effect on tree diversity and a negative effect on biomass, while EM tree dominance had exactly the reverse effects (Figure 3). This finding supported our

(a) Observed spatial DBRs



(b) Spatial DBRs without mycorrhizal dominance effect (null results)



(c) Mycorrhizal dominance effect (observed − null)

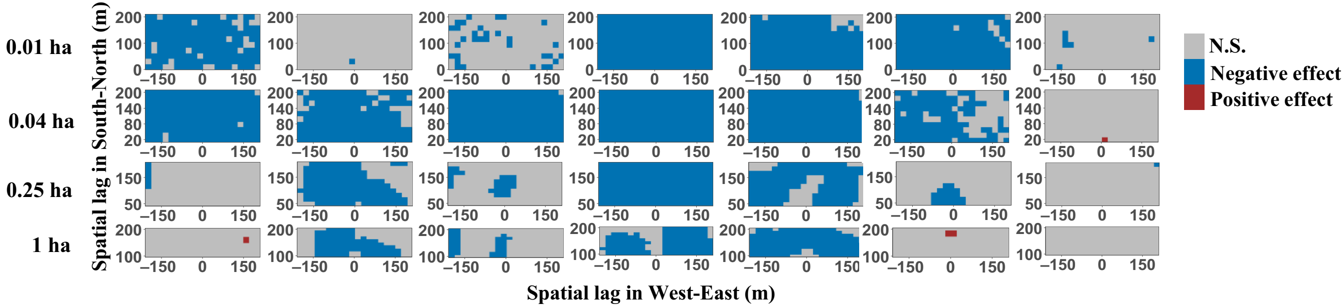


FIGURE 5 Codispersion results for the covariation between species richness and aboveground biomass. The abbreviations of the seven forest plots are consistent with Figure 2. (a) The observed results for each forest and the color of each cell represent whether observed covariation is positive (i.e., positive DBR; red) or negative (i.e., negative DBR; blue). (b) The expected results of null forests (199 times) where soil-related changes in the tree mycorrhizal dominance are excluded, and the color of each cell represents the same meaning as in panel (a). (c) Significance test for mycorrhizal dominance effect using observed—null results, where the color of each cell represents whether the observed covariation is significantly more positive (i.e., positive effect, brown) or more negative (i.e., negative effect, blue) at the $p < 0.05$ level relative to the null expectation of the 199 null communities. Abbreviations: CBS, Changbaishan; DBR, diversity–biomass relationship; DHS, Dinghushan; FL, Fenglin; HSD, Heishiding; SCBI, Smithsonian Conservation Biology Institute; TRC, Tyson Research Center; TTS, Tiantongshan.

Hypothesis II about the opposite effects of AM or EM tree dominance on tree diversity and standing biomass across scales, although the strength of these effects varied across forests and scales (Appendix S1: Figure S5). Interestingly, we found a scale-dependent effect of EM tree dominance (in AGB) on tree diversity in most forests, that is, an insignificant (direct effects; Figure 3b) or even positive effect (total effects in Appendix S1: Table S3) at the 0.01-ha scale and a negative effect at the 0.25-ha scale (Figure 3b). In contrast, the effects of AM tree dominance (in abundance) on tree diversity and biomass are scale-independent (Appendix S1: Table S2). Thus, in these forests, the proportion of individuals (rather than AGB) of AM versus EM tree species has a consistent effect on both tree diversity and standing biomass across scales, although the scale-dependent diversity effects of EM tree dominance were also expected. Nevertheless, increasing EM tree dominance in AGB had a very strong positive effect on quadrat biomass in many forests (mean standardized coefficients >0.4; Appendix S1: Table S3), supporting our prediction that mainly EM tree species would determine standing biomass (Figure 1).

It is worth noting that we mainly assessed the linear effects of tree mycorrhizal dominance on tree diversity and biomass after considering soil fertility and number of trees. We did this because (1) both soil fertility and number of trees are important drivers of tree diversity and biomass production (Chisholm et al., 2013; van der Sande et al., 2018); (2) this allowed us to compare the effects of mycorrhizal dominance with the effects of other factors on tree diversity and biomass and, thus, DBRs, which is important given the focus of our study on DBRs (see subsequent discussion). However, given the general unimodal relationships between mycorrhizal dominance and tree diversity or biomass especially at smaller scales (Appendix S1: Figure S6), the linear models we used may have underestimated some nonlinear variation of the mycorrhizal dominance effects on tree diversity and biomass (Carteron et al., 2022).

Despite these nonlinear relationships, we observed overall opposite trends between tree diversity and biomass along the AM tree dominance gradient in four forests with a positive-to-negative shift in DBRs (i.e., TRC, CBS, SCBI, and DHS) but not in the other three forests (Appendix S1: Figure S6). Thus, in these four forests, the opposite effects of AM tree dominance on tree diversity and biomass (Hypothesis II) greatly contribute to the negative effects of mycorrhizal dominance on DBRs (Hypothesis III; Figure 5c), which supports the linkage between our Hypotheses II and III. Given the different contributions of AM and EM tree species to ecosystem functions (e.g., carbon stocks) and community diversity in global forests (Soudzilovskaia et al., 2019; Steidinger et al., 2019; Zhong et al., 2021), future studies should continue to assess the effects of tree mycorrhizal dominance on community diversity and ecosystem functions.

Understanding scale-dependent BEF patterns via mycorrhizal functions: *Mycorrhizal dominance* mechanism

Although recent biodiversity experiments suggested that mycorrhizal functions can drive the positive BEF patterns in different ecosystems (Deng et al., 2023; Dietrich et al., 2023; Ferlian et al., 2018; Luo et al., 2017; Schnitzer et al., 2011), these findings were obtained under highly controlled environmental conditions and might not be informative for BEF observations in field studies (Hagan et al., 2021). Given the scale-dependent property of BEF patterns in natural forests (Chisholm et al., 2013), the fact that most mycorrhiza-related BEF studies have been conducted at one individual scale (actually often at scales smaller than 0.1 ha) limits the practical value of mycorrhizal functions for managing “real-world” forests (Manning et al., 2019).

Our study contributes to filling these knowledge gaps by proposing our main hypothesis that in AM–EM mixed forests, the changes in mycorrhizal dominance along soil fertility gradients can exert a negative effect on the DBRs across spatial scales (Figure 1). Overall, there are two remarkable findings relevant to this hypothesis. First, we found a positive-to-negative shift in DBRs, and we found that this shift mainly occurred at scales between 0.04 and 0.25 ha. Because previous global studies focusing on tree diversity–biomass and productivity relationships also found the same shift at scales between 0.04 and 0.25 ha (Chisholm et al., 2013), we propose that future BEF observations in forest ecosystems should cover a corresponding range of spatial grain sizes (Gonzalez et al., 2020). Further, by breaking the directional change in mycorrhizal dominance along the soil fertility gradient while controlling for the effect of other important ecological processes (e.g., dispersal limitation; Wiegand et al., 2017), the mycorrhiza-dependent toroidal shift model (Appendix S1: Figure S3) confirmed that these positive-to-negative shifts in DBRs can be explained by the negative effects of soil-related changes in mycorrhizal dominance, which supported our Hypothesis III. The finding that the negative effects of mycorrhizal dominance on DBRs were consistent across scales is particularly surprising given that our null model randomizes species co-occurrence patterns. In real-world communities, species that coexist are expected to be better able to partition resources than random species combinations (HilleRisLambers et al., 2012) and, hence, to give rise to complementarity effects that often drive positive DBRs (Cardinale et al., 2007). Hence, one might expect that originally positive DBRs would disappear in null models where communities are randomly assembled. Our findings that, instead, DBRs in null communities are more positive or less negative than in observed communities (Figure 5) therefore suggest strong negative effects of mycorrhizal dominance, across scales. Unlike other mycorrhiza-related BEF studies that mostly suggested a positive effect of mycorrhizal associations on BEF relationships (e.g., Dietrich et al., 2023; Ferlian et al., 2018), we presented the first multiscale evidence for the negative effect of mycorrhizal dominance on BEF relationships, which we propose as a novel *mycorrhizal dominance* mechanism (Figure 1). However, we acknowledge that as a new explanation for the observed scale-dependent BEF relationships, this mycorrhizal dominance mechanism still needs more sequent studies to be fully tested (see following *Discussion* section).

Second, to further assess the extent to which the mycorrhizal associations determined the observed DBRs across scales, we compared the effect of mycorrhizal dominance (together with soil fertility) with the effects of other factors (i.e., number of trees or stem density effect in Chisholm et al., 2013). Overall, the SEM results suggested that at small spatial scales (0.01 and 0.04 ha), the number of trees should be more important than mycorrhizal dominance in driving both tree diversity and AGB (Figure 3) and, hence, driving the positive DBR (Chisholm et al., 2013). This is partly because each individual positively contributes to total AGB, and abundance may promote diversity via a statistical or sampling effect at the scales where a tree community is far from being saturated by species (Appendix S1: Figure S9a; Fung et al., 2020; Godlee et al., 2021). Actually, many previously described mechanisms (e.g., complementarity and selection effect) that can drive positive BEF relationships mainly work at small spatial scales (Luo et al., 2019). When the spatial scale is larger than 0.04 ha, however, AGB and tree diversity and number of trees have relatively low variation (i.e., coefficient of variation <50%; Appendix S1: Figure S9b), so that more individuals do not necessarily translate to increased AGB or diversity (Figure 3). Instead, the factors determining species distribution (e.g., soil fertility) and species attributes (e.g., mycorrhizal association and tree size) are more influential in determining BEF patterns at larger scales (Luo et al., 2019; Mao et al., 2019; Mensah et al., 2020; Figure 5). Therefore, the mycorrhizal dominance effect should be a relatively minor driver at smaller scales and a major determinant at larger scales of DBRs (and maybe other BEF relationships) in AM–EM mixed forests.

Beyond effects driven by mycorrhiza highlighted in this study, our study may also yield insights on other processes driving the scale dependence of DBRs. Interestingly, we found that mycorrhizal dominance had negative effects on DBRs across spatial scales, due to opposite effects on species richness and biomass. Thus, factors other than mycorrhiza that drive species richness and biomass production in opposite ways might also drive scale-dependent patterns in DBRs. For example, invasive plant species typically have higher growth rates than native species (van Kleunen et al., 2010), so they have the ability to promote biomass production. At the same time, they negatively affect plant diversity, and these negative effects are strongest at small spatial scales (Powell et al., 2013). This suggests that in communities where invasive plant species play a key role, they may also negatively affect DBRs, particularly at smaller spatial scales, and this negative effect will be weakened with increasing spatial scale. As a result, the DBRs in these communities should be less positive or more negative than the null expectation at smaller spatial scales compared with larger spatial scales. We therefore welcome future studies that test these predictions.

There are also some findings inconsistent with the mycorrhizal dominance effects proposed in this study that could be resolved by future experimental and theoretical studies. For instance, because the dominant AM tree species (i.e., *Liriodendron tulipifera*) greatly contributes to biomass (43.7%) in the SCBI forest (Bourg et al., 2013), in this plot, AGB is mainly determined by AM tree species (Table 1; Appendix S1: Figure S2). This challenges our assumption that EM tree species mainly determine the AGB patterns (Figure 1), possibly because the warmer climate, N deposition, and the relative fertile soils stabilize and strengthen the predominance of AM tree species at this site (Anderson-Teixeira et al., 2015; Jo et al., 2019). Furthermore, given that SCBI is a secondary forest with the majority of dominant canopy trees having established around 1900 following a history of mixed land uses (Bourg et al., 2013), this might also be related to the land-use history. Nevertheless, the directional changes in AM and EM tree dominance along the soil fertility gradient in the SCBI (Figure 2) still greatly contribute to the positive-to-negative trends in DBR with increasing spatial scale (Figure 5), suggesting a strong effect of mycorrhizal dominance. Given this exception, we deem our framework (Figure 1) a potential, but not universally applicable, scenario regarding the mycorrhizal dominance mechanism, and we call for subsequent theoretical studies to propose more alternative scenarios to complete this mechanism. Also, more detailed knowledge about the biological processes (e.g., plant resource economics strategies; Weemstra et al., 2020) determining the relationship between mycorrhizal dominance and soil fertility will be particularly necessary for future experimental studies in AM–EM mixed forests, because we found that the forests without this relationship (e.g., HSD) often had no signal of mycorrhizal dominance effect and, thus, no positive-to-negative shift in DBRs across scales (Figures 2 and 5).

Despite these remaining questions, our study represents one key step toward a cross-scale empirical understanding on the ecological effects of changes in AM and EM tree dominance on forest ecosystems, together with some recent regional-scale studies focusing on the mycorrhizal dominance effect on tree diversity (Carteron et al., 2022) and stable states of the forest mycobiome (Averill et al., 2022). All these findings are especially relevant due to increases in AM tree dominance at the expense of decreasing EM tree dominance in some regions (e.g., North America), under ongoing climate change and anthropogenic impacts (Averill et al., 2018; Jo et al., 2019). Furthermore, recent studies have reported that current carbon-focused conservation schemes might fail to protect some biodiversity hotspots in both temperate and tropical forests (Ferreira et al., 2018; Sabatini et al., 2019). In our study, we found that forests located in fertile soils had different diversity and biomass properties compared to those located in nearby infertile soils (Appendix S1: Figure S8), partly due to opposite soil fertility effects on (or response to) AM and EM tree dominance. Hence, we propose to develop site-specific forest conservation projects (e.g., carbon-focused vs. biodiversity-focused) that prioritize in situ feedbacks among plants, soil organisms, and abiotic soil conditions (Gottschall et al., 2022; Pugnaire et al., 2019).

CONCLUSIONS

Our findings support the idea that scale-dependent DBRs are common in abiotically heterogeneous forests with a mixture of AM and EM tree species. We introduced a novel mechanism related to soil-related changes in the relative dominance of AM- and EM-associated tree species that in part helps understand these scale-dependent relationships. Although we only focused on temperate and subtropical forests in this study, mixed forests dominated by both AM and EM trees are also common in some tropical regions (e.g., forests in central Africa and southeast Asia; Lu & Hedin, 2019), and there is evidence that AM- and EM-dominated tropical forests sometimes differ in soil fertility (Corrales et al., 2016, 2018). Thus, regardless of the biome, future forest management and BEF studies should pay more attention to the coupling effects of soil conditions and tree mycorrhizal associations.

AUTHOR CONTRIBUTIONS

Xugao Wang and Zikun Mao conceived the study. Kristina J. Anderson-Teixeira, Norman A. Bourg, Chengjin Chu, Zhanqing Hao, Guangze Jin, Juyu Lian, Fei Lin, Buhang Li, Wenqi Luo, William J. McShea, Jonathan A. Myers, Guochun Shen, Xihua Wang, En-Rong Yan, Ji Ye, Wanhui Ye, and Zuoqiang Yuan collected the data on forest censuses and soil information. Zikun Mao and Adriana Corrales identified the mycorrhizal association types of tree species. Zikun Mao, Fons van der Plas, Adriana Corrales, and Xugao Wang wrote the first draft and carried out most statistical analyses. All authors contributed to revisions of the manuscript.

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CONFLICT OF INTEREST STATEMENT

The authors declare no conflicts of interest.

DATA AVAILABILITY STATEMENT

The data sets (Mao et al., 2023a) supporting the results are available in the Dryad digital repository at https://doi.org/10.5061/dryad.612jm646w. R codes (Mao et al., 2023b) to perform the data analyses are archived in Zenodo at https://doi.org/10.5281/zenodo.7549401.

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SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

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