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Research

Tree mycorrhizal associations mediate soil fertility effects on forest community structure in a temperate forest

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Summary

- Soil fertility influences plant community structure, yet few studies have focused on how this influence is affected by the type of mycorrhizal association formed by tree species within local communities.
- We examined the relationship of aboveground biomass (AGB) and diversity of adult trees with soil fertility (nitrogen, phosphorus, organic matter, etc.) in the context of different spatial distributions of arbuscular mycorrhizal (AM) and ectomycorrhizal (EM) trees in a temperate forest in Northeast China.
- Diversity showed a positive trend along the soil fertility gradient driven mostly by a positive relationship between AM tree abundance and soil fertility. By contrast, the AGB showed a negative trend along the soil fertility gradient driven mostly by a negative relationship between EM tree AGB and soil fertility. Furthermore, the opposite trend in the AGB and tree species diversity along the soil fertility gradient led to an overall negative diversity–biomass relationship at the 50-m scale but not the 20-m scale.
- These results suggest that tree mycorrhizal associations play a critical role in driving forest community structure along soil fertility gradients and highlight the importance of tree mycorrhizal associations in influencing how the diversity–ecosystem function (e.g. biomass) relationships change with soil fertility.

Introduction

As the main resource provider for plants, soils can greatly influence plant community structure by altering the community composition (Ehrenfeld *et al.*, 2005; John *et al.*, 2007). Traditional field studies have suggested that soil fertility could account for the spatial patterns of plant diversity (e.g. Huston, 1980; Perroni-Ventura *et al.*, 2006; Shirima *et al.*, 2016), biomass or productivity (e.g. Laurance *et al.*, 1999; Delgado-Baquerizo *et al.*, 2017; van der Sande *et al.*, 2018), and species distributions or community composition in natural communities (Swaine, 1996; John *et al.*, 2007; Baldeck *et al.*, 2013). However, as an important biotic component of soil environments, soil microbes also can contribute to the formation of plant diversity and biomass patterns (van der Heijden *et al.*, 2008; Bever *et al.*, 2010). For instance, recent experimental studies have recognized soil microbes as an unappreciated but important driver of classical plant diversity–productivity (or biomass) patterns (e.g. Maron *et al.*, 2011; Schnitzer *et al.*, 2011; Luo *et al.*, 2017). In field studies, Johnson *et al.* (2018) also found that the symbiosis between trees and different mycorrhizal fungi potentially influenced the spatial patterns of tree species in a forest community. Thus, both soil fertility and soil microbes might contribute to plant community structure *in situ*, especially given that the symbiosis between land plants and mycorrhizal fungi has continued for *c.* 400 Myr (Smith & Read, 2008).

Trees usually form two main types of mycorrhizal associations: arbuscular mycorrhizal (AM) associations with fungi in the Glomeromycota subphylum, and ectomycorrhizal (EM) associations with fungi mostly in the Ascomycota and Basidiomycota phyla (Wang & Qiu, 2006; Brundrett, 2009; also see Martin *et al.*, 2018). An increasing number of studies have focused on the differences in nutrient cycling (e.g. Phillips *et al.*, 2013; Averill *et al.*, 2014; Sulman *et al.*, 2017; Liu *et al.*, 2018; Zhu *et al.*, 2018) and nutrient foraging strategies (e.g. Cheng *et al.*, 2016; Chen *et al.*, 2018) between AM and EM trees derived from their associated fungi. For instance, using a novel modelling framework, Sulman *et al.* (2017) found significant differences in both the soil carbon (C) and nitrogen (N) contents in response to a switch in mycorrhizal dominance (AM- to EM-dominance or vice versa), highlighting the differences in belowground processes under AM- vs EM-dominated plots. Few of these studies, however, further considered the relationship between the dominant type of mycorrhizal association and the plant community

patterns (e.g. diversity and biomass), and consequently, there is still a gap between these emerging studies and traditional studies in community ecology that have considered only the interaction between plant community composition and soil fertility.

Tree mycorrhizal associations can greatly mediate forest community patterns because AM and EM tree communities have different species composition properties ('AM or EM tree community' represents all tree species associated with AM or EM fungi in a local community). Generally, EM tree communities contain fewer species (Brundrett, 2009), but many of these species (e.g. Fagaceae and Pinaceae) achieve local dominance with a greater biomass in natural communities (Corrales *et al.*, 2016). For instance, EM associations could facilitate monodominance by producing changes in the rhizosphere (Connell & Lowman, 1989; Audet, 2012; Sulman *et al.*, 2017; Zhu *et al.*, 2018) or N cycling (Phillips *et al.*, 2013; Corrales *et al.*, 2016; see Lang & Polle, 2011 and Zhu *et al.*, 2018 for temperate forests, and see Rosling *et al.*, 2016 for phosphorus (P) cycling). Conversely, AM tree communities include more species (Brundrett, 2009) and potentially contribute to the maintenance of highly diverse communities (Hart *et al.*, 2003; van der Heijden *et al.*, 2008; Moora & Zobel, 2010). Therefore, tree communities that associate with different types of mycorrhizal fungi potentially impact different community patterns (i.e. biomass and diversity).

Trees associated with different mycorrhizal fungi also can have different soil preferences in natural communities. Mycorrhizal fungi help plants take up a large proportion of soil nutrients, especially N and P (van der Heijden *et al.*, 2008; Audet, 2012). The different abilities of AM and EM fungi for nutrient uptake could potentially lead to different soil preferences between AM and EM trees. Specifically, EM trees tend to perform better in infertile soils because some EM fungi are better at taking up N and P directly from organic sources than AM fungi (Peay, 2016; Chen *et al.*, 2018; Liu *et al.*, 2018). However, AM trees have usually shown a competitive advantage in relatively fertile soils, benefiting from their higher root foraging precision and lower energetic costs in maintaining mycorrhizal symbiosis (Connell & Lowman, 1989; Chen *et al.*, 2016, 2018; Cheng *et al.*, 2016). Interestingly, recent studies have found that plots dominated by AM trees differed in their nutrient retention and cycling from plots dominated by EM trees (Phillips *et al.*, 2013; Sulman *et al.*, 2017), and thus, the different soil preferences between AM and EM trees may be derived from the soil-resource competition between them in a local community. Although the soil preferences of AM and EM trees have been recognized (e.g. Connell & Lowman, 1989; Phillips *et al.*, 2013; Corrales *et al.*, 2016; Peay, 2016), few studies have specifically examined how the different performances of AM and EM trees change along a local soil fertility gradient in natural communities and further influence local plant community structure (Lekberg & Helgason, 2018; Martin *et al.*, 2018) – thus, the spatial patterns of plant diversity and biomass.

If the soil preferences truly differ between AM and EM trees, we expect that trees with different mycorrhizal associations will show different trends along the soil fertility gradient within a local community: thus, AM-associated tree species will perform better in fertile soils, whereas EM-associated tree species will perform better in infertile soils (Hypothesis I (HI) and see Fig. 1a; 'perform better' means a greater dominance, with a higher number of trees, a higher species richness, or a greater biomass per unit area). In addition, because most rare species form AM associations (Connell & Lowman, 1989; Corrales *et al.*, 2016) and contain the majority of species in plant communities (McGill *et al.*, 2007; Brundrett, 2009), a higher diversity within a plant community could be associated with a higher abundance of AM trees (see Heegaard *et al.* (2013) and Leitão *et al.* (2016) for the contribution of rare species to community diversity at a local scale). By contrast, more abundant or dominant tree species form EM associations (Corrales *et al.*, 2016), thus, in a plant community, the total tree biomass will be highly correlated with the biomass of EM trees resulting from a greater biomass of dominant species. Thus, we expect that the community diversity will show a positive trend, whereas the biomass will show a negative trend along a local soil gradient moving from low to high fertility (Hypothesis II (HII) and see Fig. 1b,c). Significantly, recent reviews (e.g. Ammer, 2019) and experimental studies (e.g. Luo *et al.*, 2017) have suggested that both soil fertility and soil biomes could mediate diversity–ecosystem function relationships in forest ecosystems. In this context, we also wanted to determine whether the spatial patterns of plant diversity and biomass driven by tree mycorrhizal associations along the soil fertility gradient (Fig. 1) could affect the diversity–biomass relationship in local communities.

We tested the above hypotheses within a 25 ha plot with a detailed soil map and precise spatial information for trees ≥ 10 cm in their diameter at breast height (dbh ≥ 10 cm, adult trees) in a temperate forest. We used generalized least squares methods to examine the overall trends in the aboveground biomass (AGB) and diversity for all trees, AM trees and EM trees, respectively, along the soil fertility gradient (Chisholm *et al.*, 2013; LaManna *et al.*, 2016). Then, we used codispersion analysis (Buckley *et al.*, 2016) to test the spatial information of these patterns and tested HI and HII using null models. Finally, we evaluated whether the contrasting trends in biomass and diversity along the soil fertility gradient contributed to the diversity–biomass relationship in the local community. All of the above analyses were conducted at both 20-m and 50-m scales to test for the effect of scale on these spatial patterns and to compare the scale problem of traditional diversity–biomass relationships (e.g. Chisholm *et al.*, 2013).

Materials and Methods

Study site

The study site was located in the Changbai Nature Reserve in Northeast China. As one of the largest biosphere reserves in China, the Changbai Nature Reserve covers an area of *c.* 200 000 ha, with elevations ranging from 740 m to 2691 m above sea level (asl) within Changbai Mountain. Changbai Mountain has long, cold winters and warm summers, belonging to a temperate continental climate (Wang *et al.*, 2012).

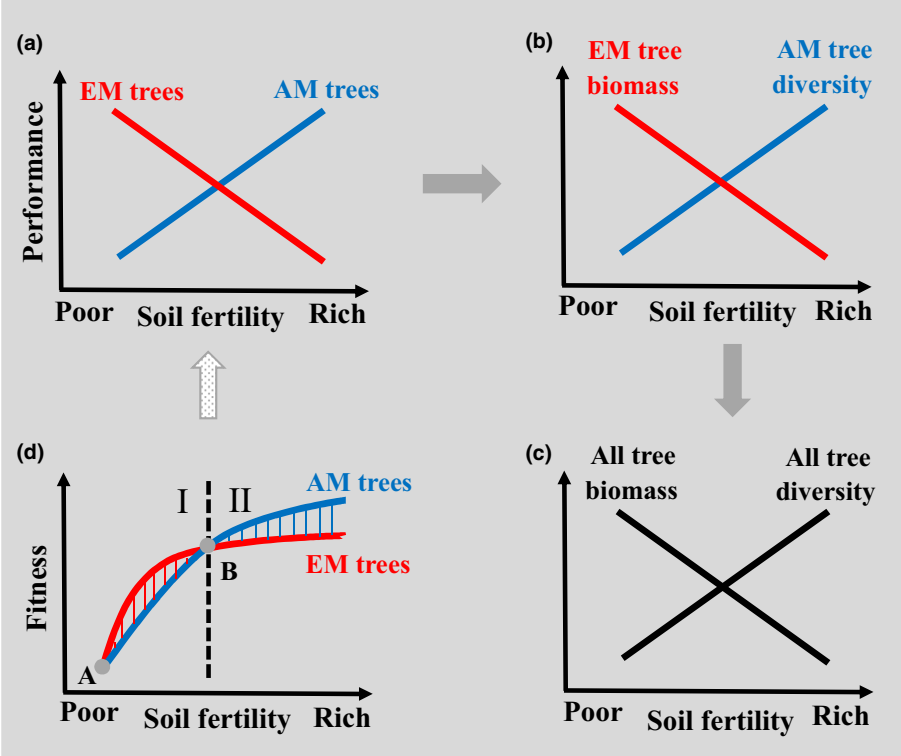

Fig. 1 The expected relationships between ectomycorrhizal (EM) trees, arbuscular mycorrhizal (AM) trees, biomass, diversity and soil fertility. (a) Hypothesis I (HI) concerns the performance of AM and EM trees along the soil fertility gradient. The EM trees should perform better in relatively infertile soil, and the AM trees show a competitive advantage in fertile soil; thus, they should show opposite trends along a local soil fertility gradient. (b, c) Hypothesis II (HII), which concerns the intrinsic relation between 'EM tree biomass' and 'all tree biomass' or 'AM tree diversity' and 'all tree diversity'; the patterns of 'AM tree diversity' potentially dominate the 'all tree diversity' because the AM tree community includes a disproportionately higher diversity of species, whereas the patterns of 'EM tree biomass' potentially dominate the 'all tree biomass' because EM trees contain a much greater biomass. (d) A theoretical expectation of the fitness of the AM and EM trees along the wider soil fertility gradient (fitness here means number of trees or biomass per unit area of AM or EM trees without the competition between the AM and EM trees). The fitness of the AM trees and EM trees both increase along the soil fertility gradient, but when the AM and EM trees contend for soil resources in a local community, AM trees are suppressed by the stronger resource competition of EM trees in part I, and then EM trees are suppressed by the stronger resource competition of AM trees in part II. This scenario starts at a theoretical point when the AM and EM trees initially have the same fitness (point A) and includes one switching point (point B), where AM and EM trees again have the same fitness but their advantages are switched. (Note: the arrows show the logical relationship of these hypotheses. Solid grey arrows show the framework of our research, whereas the open grey arrow from (d) is the theoretical expectation extended from our research (see the Discussion section) but not the verified result of this study.)

Our study was based in the 25 ha Changbaishan forest dynamics plot (hereafter CBS; 42.38°N, 128.08°E) in Changbai Nature Reserve. The CBS forest is a late-successional deciduous broadleaved *Pinus koraiensis* mixed forest that has been undisturbed for at least 300 yr (Wang *et al.*, 2015). This 500 × 500 m plot was established in 2004, with elevations ranging from 791.8 m to 809.5 m asl and a mean elevation of 801.5 m asl. The mean annual temperature in this area is *c.* 3.6°C, and the mean annual precipitation is ~700 mm. All of the living trees with dbh ≥ 1 cm were identified, tagged, measured and mapped in an initial census in 2004 following CTFS-ForestGEO protocols (Anderson-Teixeira *et al.*, 2015), including a total of 38 902 individuals belonging to 52 species, 32 genera and 18 families (Wang *et al.*, 2015). The second and third censuses were completed in 2009 and 2014. Because adult trees in this late-successional forest showed very similar spatial patterns in the three censuses, we used data only from the latest census (2014) in our analyses.

Information on the adult trees in the Changbaishan plot

Only adult trees with dbh ≥ 10 cm were included in the analyses, for a total of 9994 stems belonging to 30 species, 18 genera and 12 families (see Supporting Information Table S1). We selected only adult trees because they are the main contributors to community structure (Chisholm *et al.*, 2013; Lutz *et al.*, 2018). Furthermore, the inclusion of sapling data could easily lead to the misinterpretation of results given that adult trees can significantly dominate the spatial patterns of saplings (e.g. Johnson *et al.*, 2018). The tree species were classified into three mycorrhizal types: AM trees, EM trees and AEM trees based on available literature (Wang & Qiu, 2006; Guo *et al.*, 2008; Brundrett, 2009; Phillips *et al.*, 2013; and see http://mycorrhizas.info/index.html), with AEM referring to species that could associate with both AM and EM fungi (Table S1). The dataset contained eight EM and 15 AM species. The two main dominant species (*Pinus koraiensis* and *Tilia amurensis*) were both EM-associated. The EM and AM trees

accounted for 62% and 29% of the total AGB, respectively (most of the largest trees were EM; Fig. S1). The AM species accounted for 50% of all the species (and 56% of all the species containing >50 individuals), whereas the EM species accounted for only 27% of all the species (and 31% of all the species containing >50 individuals). In general, we found that the AM tree community contributed to a higher species richness, whereas the EM tree community included more AGB in the CBS plot. The AEM species (9% of the AGB; 23% of all the species) were a special group in our analysis, and because they did not belong to the AM or EM species, they were excluded from the individual AM and EM analyses and were only included for the analysis using all trees.

Data collection for the soil map

In 2007, soil samples were collected with a regular point grid every 30 m, and to determine the soil property variation at a fine scale, two additional sample points were selected at 2, 5 or 15 m from each grid point in a random compass direction. In total, 967 samples of topsoil (0–10 cm depth) were analysed chemically (Wang *et al.*, 2012), and ordinary kriging was used to obtain a soil map for 20 × 20 m and 50 × 50 m quadrats. There were eight soil variables in our soil dataset: pH, organic matter, total nitrogen (N), available N, total phosphorus (P), available P, total potassium (K) and available K. These soil properties were used to outline the soil fertility gradient in the CBS plot. Because these soil variables might be correlated with each other, we performed a principal component analysis that included the eight variables; only the first principal component (PC1), which described 54.9% of the total soil variation at the 20-m scale and 63.3% of the total soil variation at the 50-m scale, was used to represent the soil fertility of each quadrat (see Fig. 2 for the results at the 20-m scale and Fig. S2 for the results at the 50-m scale). We found an east–west soil fertility gradient, where the more fertile soil contained more organic matter, more total and available N and P, and was pH-neutral (the soil at CBS is slightly acid: 4.48–6.89) but had less K (Fig. 2a).

Overall trends in the AM/EM/all trees along the soil fertility gradient

Several indexes were used to check for overall trends in AM or EM tree dominance along the soil fertility gradient and to link these trends with community diversity and biomass. For this purpose, we computed the AGB, number of trees, species richness, and Shannon–Wiener diversity Index (SWI) in each 20 × 20 m quadrat and 50 × 50 m quadrat for all trees and for the AM and EM trees, respectively. Dominance was represented by the AGB (in terms of biomass, Mg ha^{-1}) and the number of trees (in terms of abundance), whereas the species richness and SWI together represented the community diversity. The AGB was calculated using available species-specific allometric regression equations (Table S1; Yuan *et al.*, 2016). The SWI value was computed using the VEGAN package in R v.3.5.0 statistical software (R Core Team, 2018). A total of 625 20 × 20 m quadrats and 100 50 × 50 m quadrats were available for the analysis.

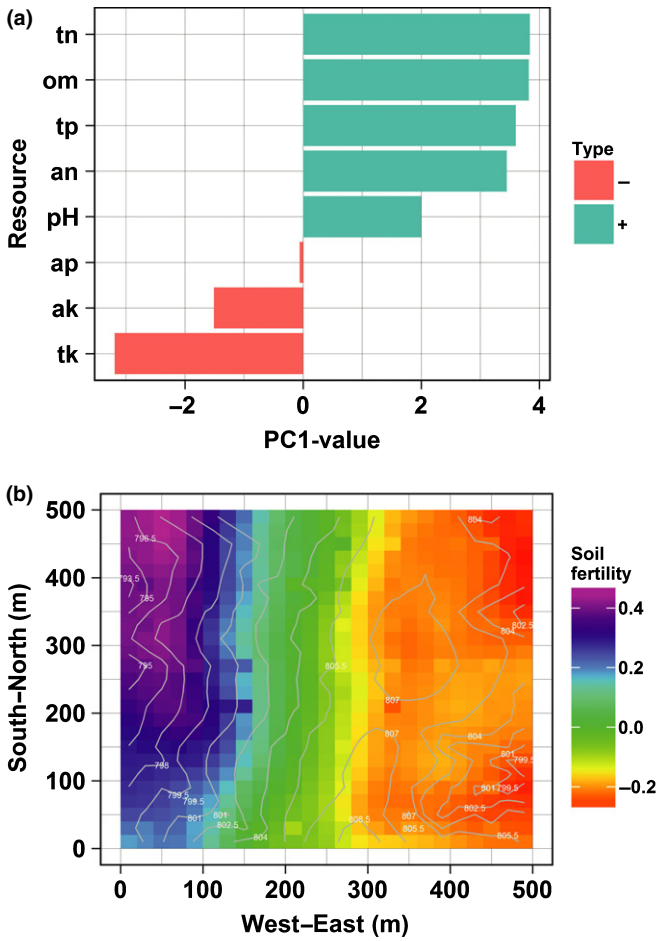

Fig. 2 The soil fertility gradient of the Changbaishan (CBS) plot at the 20-m scale. (a) The scores of every soil variable in PC1 (tn, total nitrogen; om, organic matter; tp, total phosphorus; an, available nitrogen; ap, available phosphorus; ak, available potassium; tk, total potassium). (b) The soil fertility gradient of the CBS plot at the 20-m scale with the PC1 scores, and the topography (grey contour lines; elevation in m above sea level) of the CBS plot is also shown. See Supporting Information Fig. S2 for the soil fertility gradient at the 50-m scale.

In order to examine the overall trends in the trees along the soil fertility gradient while accounting for autocorrelation among the quadrats, we used these indexes and the soil fertility values of each quadrat to fit linear models with and without a spherical autocorrelation structure (i.e. generalized least squares methods; Beale *et al.*, 2010; Chisholm *et al.*, 2013) and compared the separate models with the Akaike Information Criterion (AIC). Finally, the model with the lowest AIC score was selected as the optimal model, and its parameters were extracted to show the relationships between these indexes and the soil fertility values.

Spatial information of the observed patterns under the null model test

Codispersion analysis has been used in previous studies to quantify the spatial patterns of species–environment relationships by measuring the spatial covariation of two or more spatially explicit datasets (Buckley *et al.*, 2016). We used the paired datasets

(AGB ~ soil fertility, number of trees ~ soil fertility, species richness ~ soil fertility, SWI ~ soil fertility; here, '~' links two spatially explicit datasets to measure the spatial covariation) in the 20 × 20 m (50 × 50 m) grids to run a codispersion analysis with a 20 m (50 m) kernel bandwidth up to 200 m for the X spatial lag (east–west distances between points) and Y spatial lag (north–south distances between points). The magnitude of the codispersion values and the context of the final codispersion maps could provide information about the strength and the directionality of covariation for each of the paired variables at increasing distances (see Buckley *et al.*, 2016 for details). The R code for the codispersion analysis was acquired from the supporting information of Buckley *et al.* (2016).

Two null models, the toroidal shift model (TSM) and the complete spatial randomness model (CSRM) (Wiegand & Moloney, 2014), were selected to further test our hypotheses. The toroidal shift model was used here to assess the stationarity and significance of the observed patterns (i.e. Hypothesis I (HI) and all other relationships; Fig. 1a,b,c). In this model, we permutated the entire community of trees in a random distance and direction while holding the spatial pattern of soil fertility fixed in space (Wiegand & Moloney, 2014; Buckley *et al.*, 2016). One great advantage of the TSM is that it could break the spatial association between trees and soil fertility while retaining the autocorrelation structure of the trees by conserving the relative spatial positions and properties (i.e. dbh and species identity) of the trees. Thus, the reassembled spatial patterns after toroidal shift also could retain most of the structures that are driven by some underlying processes (e.g. dispersal limitation). In short, the codispersion analysis with the TSM tested whether the covariation between the above tree indexes and the soil fertility was equal in different directions and lags. Specifically, the TSM was used to generate 199 new datasets and codispersion maps. Then, we used our observed values minus the expected values (i.e. mean values) of 199 simulated patterns at each spatial lag to check the factuality of observed patterns. Finally, we compared the observed values with the range limited by 195th and fifth null values at each spatial lag, and if the observed value fell outside of the range, we concluded that it was significantly different from the expected value at $P < 0.05$ (i.e. a two-tailed test).

The complete spatial randomness model was used to test Hypothesis II (HII) (Fig. 1b,c). In general, CSRM can relocate trees with new and random spatial locations, and therefore, this model easily breaks any nonrandom covariation in observed patterns (Wiegand & Moloney, 2014; Buckley *et al.*, 2016). To make CSRM suitable for testing our hypothesis, we produced two submodels in our analysis: CSRMam and CSRMem. In CSRMam, we only relocated the AM trees with random spatial locations while holding the pattern of the other trees fixed within the CBS plot. To conserve the dbh distributions of the different species, we held the other information of the AM trees (i.e. species identity and dbh) fixed in this null model. Theoretically, the relocation for the AM trees in CSRMam should completely mix the AM species richness pattern and remove the spatial patterns of number and dbh of the AM trees in the whole plot. Thus, this model removed the spatial patterns of the AM trees (diversity + biomass + abundance) from the observed community patterns while retaining the spatial patterns of the other trees. Similar to the CSRMam model, we randomly relocated the EM trees but held the other trees unchanged in CSRMem. Then, we tested the departure of the observed patterns from the expected patterns of these null models with a similar procedure as was used in the TSM to check the contribution of the AM trees to the diversity and the EM trees to the biomass (i.e. HII). Under the HII scenario, for all of the trees, there should be a significant departure of the observed patterns from the null patterns for the AGB in CSRMem and for the species richness and SWI in CSRMam.

Diversity–biomass relationship and the scale problem

We used two paired datasets (AGB ~ species richness, AGB ~ SWI) to fit linear models with and without a spherical autocorrelation structure for all of the trees. Note that the species richness and the SWI both indicated diversity, and we expected similar results for these two datasets. To account for the scale problem of the diversity–biomass relationship, we conducted this analysis at both the 20-m and 50-m scales. To compare our results with the results of Chisholm *et al.* (2013), we used the same approach by treating the species richness or SWI as the independent variable.

Results

Overall trends in the AM/EM/all trees along the soil fertility gradient

The AGB, number of trees, species richness and SWI of the AM tree species all showed a positive relationship with the soil fertility, whereas for the EM tree species, these same variables showed an overall negative relationship with the soil fertility (Fig. 3; Table S2). For all of the trees, only the AGB showed a significant negative relationship with the soil fertility, which was consistent with the EM trees being dominant in the community, whereas all the other indexes showed a significant positive relationship with the soil fertility (Fig. 3; Table S2). Furthermore, the results showed very similar patterns at the 20-m and 50-m scales, even though some of the relationships were weaker at the 50-m scale. These results mainly support HI and HII (Fig. 1).

Spatial information of the observed patterns under the null model test

Overall, the results of the codispersion analysis for the observed patterns ('Observed' column in Fig. 4 for the 20-m scale and Fig. S3 for the 50-m scale) were consistent with the results of the linear models. Specifically, the AM trees showed a positive covariation, whereas the EM trees showed a negative covariation with the soil fertility. For all of the trees, the AGB was negatively correlated, whereas all of the other indexes were positively correlated with the soil fertility. The observed patterns also suggested that each relationship was similar in different distances and directions, despite some evident direction-dependence for the EM tree

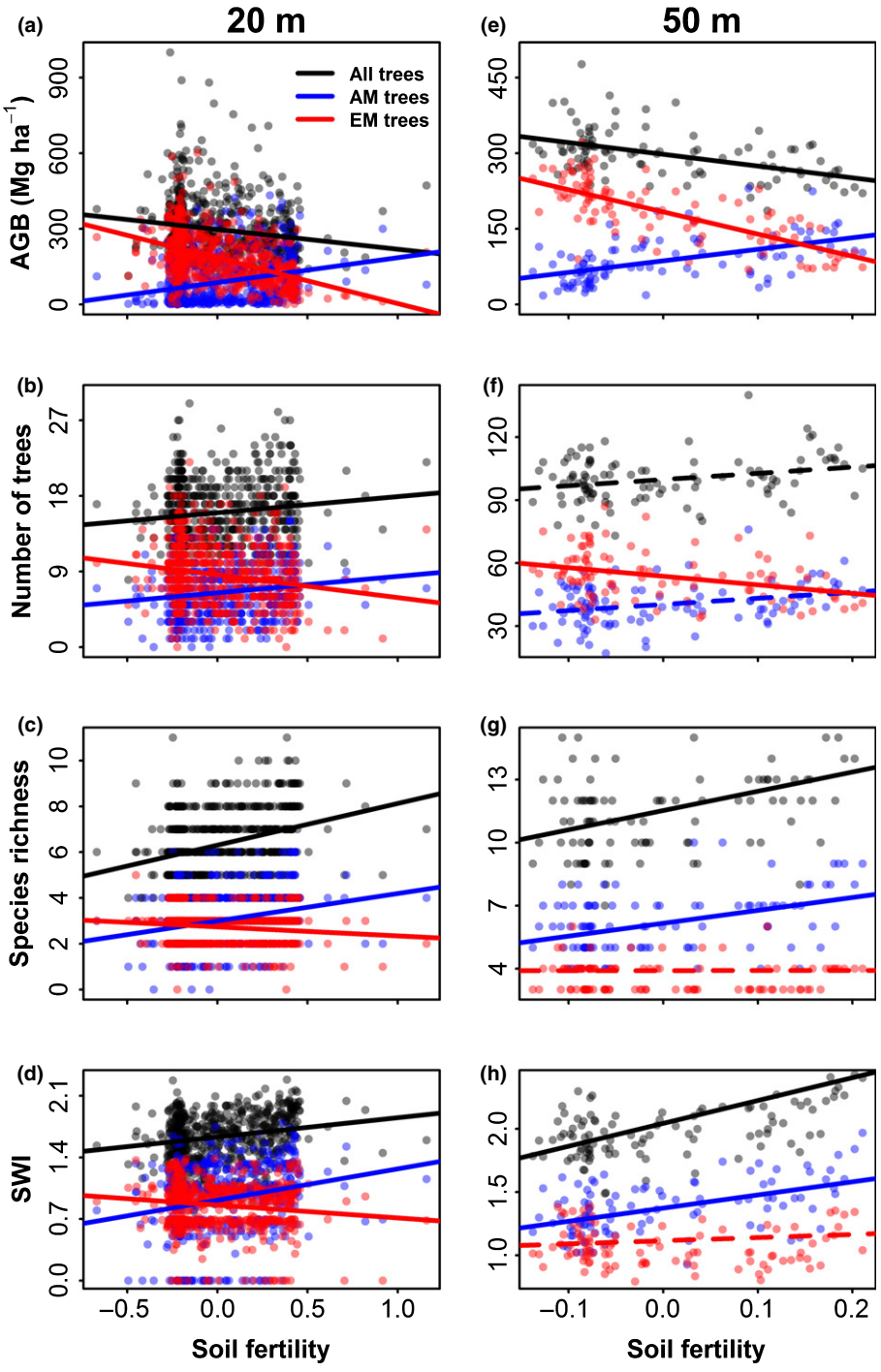

Fig. 3 The overall trends of the arbuscular mycorrhizal (AM)/ectomycorrhizal (EM)/all trees along the soil fertility gradient at (a–d) 20-m and (e–h) 50-m scales (AGB, aboveground biomass; SWI, Shannon–Wiener diversity index). Each point represents one quadrat (20 × 20 m or 50 × 50 m), and the lines show the fitted linear models with the lowest AIC scores (see Supporting Information Table S2 for details). Solid lines show statistically significant slopes ($P < 0.01$), whereas dashed lines represent statistically insignificant slopes ($P \geq 0.01$). Black, all trees; blue, AM trees; red, EM trees.

diversity at the 50-m scale (panel 'EM trees' in Fig. S3). Moreover, all of the observed patterns suggested a large distance trend; namely, larger lags showed more significant relationships (darker colours), which may be due to the gentle soil fertility gradient of the CBS plot (Fig. 2b), and these prevalent large distance trends also potentially contributed to the large variations in the overall relationships (Fig. 3).

The differences between the observed patterns and the complete spatial randomness models mainly supported HII (columns 'CSRMam' and 'CSRMem' in Figs 4, S3). The observed patterns showed significant positive (negative) trends for all of the indexes of the AM (EM) trees at most lags compared with the null expectations in the CSRMam (CSRMem) null model. As predicted by HII, for all of the trees, there was a significant positive departure of the observed patterns from the null patterns for diversity in the CSRMam model and a significant negative departure for the AGB in the CSRMem model. Unexpectedly, a positive departure of the observed patterns from the null patterns for the AGB also was detected in the CSRMam model (column 'CSRMam' in Figs 4, S3).

The codispersion values of the differences between the observed patterns and the toroidal shifting patterns (column 'TSM' in Figs 4, S3) roughly mirrored the observed values. However, the significance test in the TSM suggested largely directionality, with east-to-west codispersions being more significant than west-to-east codispersions in most cases. For the AM and EM trees, the observed codispersion values were significantly different from those of the null expectation at more than half of lags, except the species richness and SWI of the EM trees (HI; Fig. 4). For all of the trees, the tree diversity showed a significant positive relationship with the soil fertility, but the negative relationship between the AGB and soil fertility was significant at the 50-m but not the 20-m scale (column 'TSM' in Figs 4, S3).

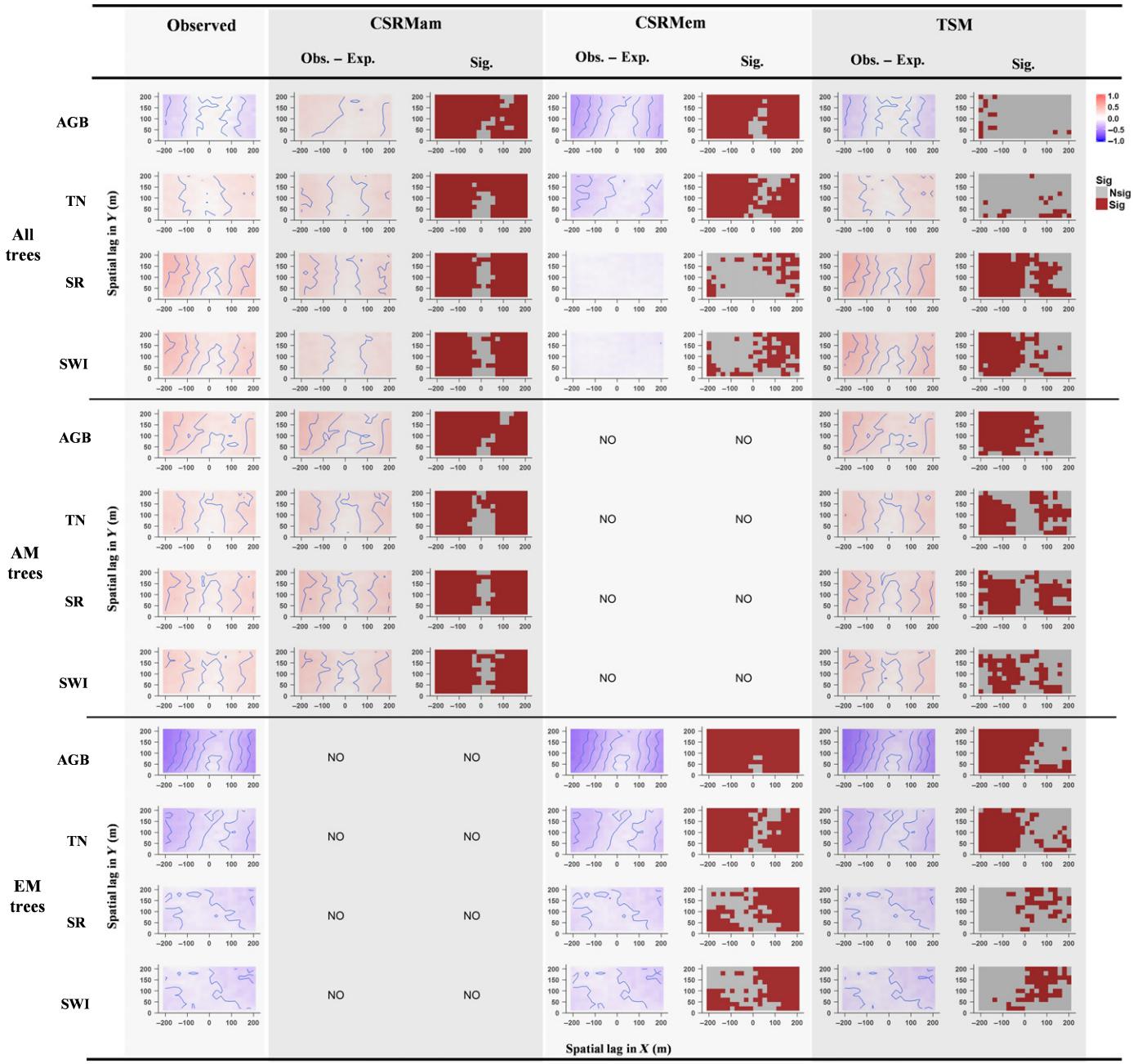

Fig. 4 Observed codispersion values, observed minus expected values (Obs. – Exp.) and significance test (Sig.) for the combinations between the different indexes (AGB, aboveground biomass; TN, number of trees; SR, species richness; SWI, Shannon–Wiener diversity index) and soil fertility at the 20-m scale. The colour of each cell represents the value of the codispersion coefficient of the corresponding index and soil fertility: red, positive covariation; blue, negative covariation. For the significance test, brown represents significant covariation, whereas grey represents statistically insignificant covariation at the $P < 0.05$ level relative to the null expectation of the null models. Because the information about the ectomycorrhizal (EM) trees in the CSRMam model and the information about the arbuscular mycorrhizal (AM) trees in the CSRMem model remain fixed, there is *NO* result for the EM trees in the CSRMam model and for the AM trees in the CSRMem model. Please see Supporting Information Fig. S3 for the results at the 50-m scale.

Diversity–biomass relationship and the scale problem

There was no significant relationship between the diversity and biomass at the 20-m scale ($slope_{species\ richness} = 5.32$ with $P = 0.124$; $slope_{SWI} = 6.98$ with $P = 0.722$), whereas a negative diversity–biomass relationship was detected at the 50-m scale ($slope_{species\ richness} = -5.47$ with $P = 0.022$; $slope_{SWI} = -81.88$ with $P < 0.001$; Table S3), even though the negative relationship between the species richness and AGB was statistically insignificant under the criterion $P < 0.01$ (Fig. 5). This result was consistent with results of Chisholm *et al.* (2013), where the diversity and biomass tended to be more negatively associated at larger scales. Thus, the opposite AGB and tree species diversity trends along the soil fertility gradient potentially led to a negative diversity–biomass relationship at the 50-m but not at the 20-m scale (Fig. S4).

Discussion

In this study, we examined the tree community patterns (i.e. diversity and aboveground biomass (AGB)) along a local soil fertility gradient, and evaluated how the tree mycorrhizal associations contributed to these patterns in a temperate forest community. Generally, we found that the positive diversity trend along the soil fertility gradient was mostly driven by a positive relationship between the arbuscular mycorrhizal (AM) tree abundance and the soil fertility, whereas the negative biomass trend along the soil fertility gradient was mostly driven by the negative relationship between the ectomycorrhizal (EM) tree biomass and the soil fertility. Furthermore, the opposite biomass and tree species diversity trends along the soil fertility gradient potentially led to a negative diversity–biomass relationship at the 50-m scale but not at the 20-m scale. To our knowledge, this work is the first to demonstrate that the interactions between tree mycorrhizal associations and soil fertility play a critical role in driving community structure within local forest communities.

Differences in soil preferences between the AM and EM trees

Recent studies have explicitly shown that EM fungi can directly decompose soil organic matter (Lindahl & Tunlid, 2015; Shah *et al.*, 2016) and that EM trees can adapt well to soil environments with a low inorganic nitrogen (N) or phosphorus (P) availability (e.g. Corrales *et al.*, 2016; Rosling *et al.*, 2016). By contrast, it has been found that AM fungi appear to be insensitive to the soil organic matter content (Peay, 2016; Liu *et al.*, 2018) and that AM trees forage mainly for soil nutrients with their roots rather than mycorrhizal hyphae (Chen *et al.*, 2016; Cheng *et al.*, 2016). Thus, AM trees should have an advantage in more fertile

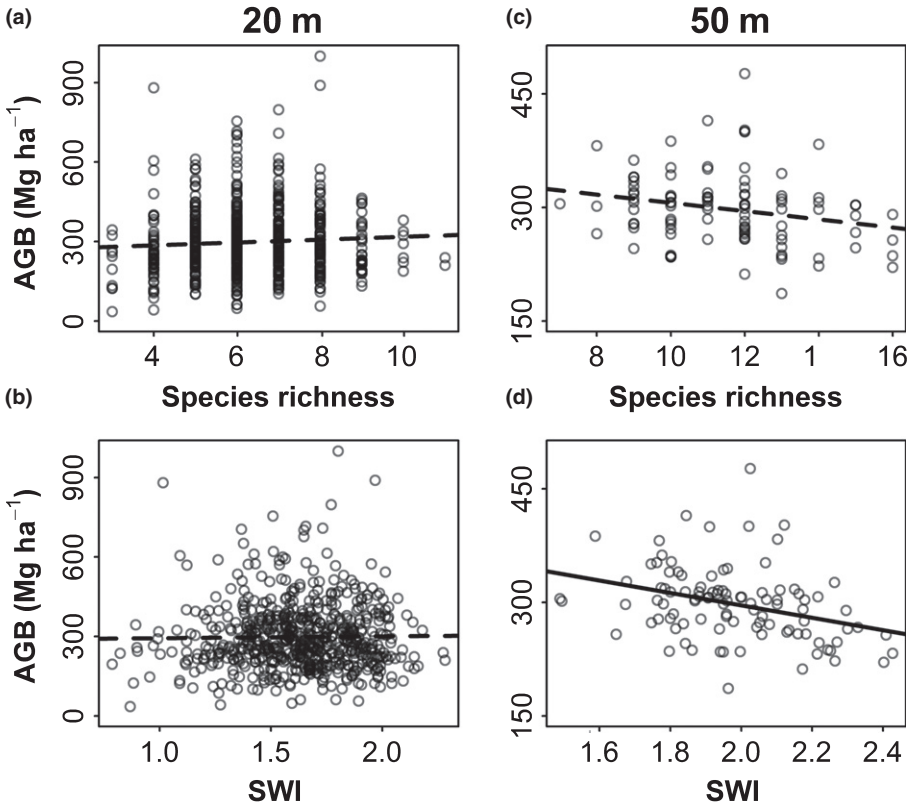

Fig. 5 The relationships between diversity and (aboveground) biomass (AGB) for all trees at the (a, b) 20-m scale and (c, d) 50-m scale. Species richness and Shannon–Wiener diversity index (SWI) together indicate diversity. Each point represents one quadrat (20 × 20 m or 50 × 50 m), and the lines show the linear models with the lowest AIC scores (see Supporting Information Table S3 for details). Solid lines show statistically significant slopes ($P < 0.01$), whereas dashed lines represent statistically insignificant slopes ($P \geq 0.01$).

soils due to their higher root foraging precision but lower carbon investment to maintain mycorrhizal symbiosis. Our results suggest that the AM trees performed better in fertile soils in both biomass (AGB) and abundance (number of trees), whereas the EM trees performed better in infertile soils (Fig. 3a,b,e,f). Given the large variation observed in these results, we further corroborated the significance and spatial information of these patterns with a codispersion analysis (Buckley *et al.*, 2016). The codispersion analysis showed results similar to those above (panels 'AM trees' and 'EM trees' in Figs 4, S3). The covariation between the AM trees and soil fertility was mainly positive, whereas the covariation between the EM trees and soil fertility was negative. Moreover, the toroidal shift model (TSM) detected significant patterns at the 20-m scale but not at the 50-m scale, which implies that these relationships are diluted at a larger scale (column 'TSM' in Figs 4, S3). This scale-dependence may derive from the clumping of trees for two reasons. First, Wang *et al.* (2015) suggested that dispersal limitation, which could influence the clumping of trees (Buckley *et al.*, 2016), accounted for the observed community structure at scales below 150 m in the Changbaishan (CBS) forest dynamics plot; however, the TSM null model could not detect these clumping patterns. Second, after removing any spatial patterns, including clumping, using complete spatial randomness (CSRM) null models, we found that the observed codispersion values were significantly different from the expected values for the AM and EM trees at both the 20-m and 50-m scales (columns 'CSRMam' and 'CSRMem' in Figs 4, S3).

Our results suggest differences in the soil preferences between the AM and EM trees in the CBS plot. However, the lower performance of the EM trees in the more fertile soils should be critically rethought because fertile soils usually tend to facilitate the survival and growth of plants due to having more resources to support them. Although both AM and EM fungi can facilitate their host plants, AM and EM trees usually colonize the same habitat and contend with each other for soil resources in natural communities (Steidinger *et al.*, 2015; Peay, 2016). Therefore, the emphasis is on 'who is a better competitor' rather than 'who is a good adapter'; that is, the competitive advantage of AM trees potentially contributes to the lower abundance of EM trees in more fertile soils. In this scenario, the fitness of both the AM and EM trees should increase along the soil fertility gradient (Fig. 1d; the fitness here means the number of trees or biomass per unit area of AM or EM trees without the competition between the AM and EM trees), but differences in the modes of nutrient acquisition between AM and EM fungi (Phillips *et al.*, 2013; Sulman *et al.*, 2017) likely switch the competitive advantages of AM and EM trees along the soil fertility gradient. Thus, a wider soil fertility gradient could be divided into two parts by a switching point (Fig. 1d, and see fig. 2 in Averill *et al.*, 2018), with EM trees being more competitive in infertile soils (part I) and AM trees being more competitive in fertile soils (part II). Then, given the soil-resource competition between AM and EM trees in this scenario, two opposite effects explained the performance of the EM trees along the soil fertility gradient, namely, stronger simulation from the richer soil and stronger inhibition from the AM trees. However, we only focused on the aboveground community structure and not on the belowground processes in this analysis, thus, this potential mechanism still needs to be further verified.

Tree mycorrhizal association and forest community structure

With increasing knowledge about the potential effects of tree mycorrhizal associations on community structure from controlled experiments and large-scale field studies (e.g. Moora & Zobel, 2010; Bennett *et al.*, 2017), forest ecologists urgently need to corroborate their findings within local communities. Previous studies have observed the potential relationship between tree mycorrhizal association type and community structure (e.g. Connell & Lowman, 1989; Hart *et al.*, 2003; van der Heijden *et al.*, 2008; Corrales *et al.*, 2016), but most of them have focused only on community diversity or biomass. Our results suggest that the spatial distribution patterns of AM and EM trees could account, to some extent, for the spatial patterns of both community diversity and biomass in the CBS plot, with AM trees mainly affecting diversity and EM trees mainly affecting biomass (Fig. 3; columns 'CSRMam' and 'CSRMem' in Fig. 4). Given the same positive trends in the number of all trees and the number of AM trees along the soil fertility gradient, the same negative trends in the AGB of all trees and the AGB of the EM trees (Fig. 3) suggest that the EM trees account for the biomass by their larger tree size (Fig. S1) rather than by having more stems. Moreover, the CSRMam and CSRMem null models suggest that the AM trees mainly affect the plant diversity and the EM trees mainly affect the biomass (Figs 4, S3), but the CSRMam null model also indicates that the AM trees could significantly affect the biomass. These results imply that the observed patterns of all of the trees were actually the result of a combination of the AM and EM trees, which also could explain why the TSM null model could not detect significant trends in the AGB and the number of trees when all of the trees were included at the 20-m scale (column 'TSM' in Fig. 4). For the AGB and the number of trees, we found opposite significant trends for the AM and EM trees in the TSM model, and these opposite trends most likely cancelled each other out when all of the trees were included in the model.

Our work studies the effect of soil fertility on community structure through the lens of mycorrhizae with field data by what appears to be a 'three-step pathway': (1) Checking the different soil preferences of the AM vs EM trees within a natural community; (2) Discussing the relationship of the AM and EM trees with diversity and biomass; and (3) Integrating steps 1 and 2 to predict the diversity and biomass trends along the soil fertility gradient (or patches) in this plant community. Given the increasing attention that forest ecologists are giving to the differences in nutrient cycling (e.g. Phillips *et al.*, 2013; Averill *et al.*, 2014; Sulman *et al.*, 2017; Liu *et al.*, 2018) and nutrient foraging strategies (e.g. Cheng *et al.*, 2016; Chen *et al.*, 2018) between AM and EM trees, this 'three-step pathway' might switch the ecological focus from functional differences between AM and EM trees to the effect of these functional differences on plant community structure. Furthermore, different plant–soil feedback between AM

and EM trees have been suggested by recent studies (e.g. Bennett *et al.*, 2017; Johnson *et al.*, 2018), which potentially contribute to the intrinsic relationship between AM trees and plant diversity or EM trees and biomass. Specifically, the prevalent positive plant–soil feedback of EM trees (Bennett *et al.*, 2017; Johnson *et al.*, 2018) can help them achieve local dominance with a greater biomass (Ehrenfeld *et al.*, 2005; van der Putten *et al.*, 2013; but also see Corrales *et al.*, 2016). For AM trees, their plant–soil feedback is generally negative (Bennett *et al.*, 2017; Johnson *et al.*, 2018), which potentially stabilizes plant diversity patterns in natural communities (Ehrenfeld *et al.*, 2005; Mangan *et al.*, 2010; van der Putten *et al.*, 2013).

Given the empirical nature of our dataset, we were limited to mapping the soil fertility gradient with some coarse indexes (e.g. total N, total P). Although these indexes could map the overall soil fertility gradient (LaManna *et al.*, 2016), it was not possible to specifically determine which belowground processes were driving the observed spatial patterns of the AM trees, EM trees and all trees. Additionally, to avoid misdiagnosing their mycorrhizal status (Brundrett & Tedersoo, 2019), some tree species were classified as capable of associating with both AM and EM fungi (AEM) due to the contradictory reports found in the literature (Table S1). Further experimental studies should be performed to establish a definitive mycorrhizal classification of these species in the CBS plot.

Diversity–biomass relationship and the plant community–soil system

A scale-dependent relationship between species richness and biomass in forests has been found in previous studies (e.g. Chisholm *et al.*, 2013). Environmental variations and stochastic processes (e.g. selection effect) can both contribute to these patterns (Loreau *et al.*, 2001; Fowler *et al.*, 2012), where environmental variations play a major role at larger scales (Fowler *et al.*, 2012; Chisholm *et al.*, 2013). Our results indicated a negative diversity–biomass relationship at a larger scale (50 m) but not a smaller scale (20 m) in the CBS plot (Fig. 5). Then, given the effect of soil fertility, the opposite diversity and biomass trends along the soil fertility gradient potentially resulted in the negative diversity–biomass relationship at the 50-m scale but not at the 20-m scale (Figs 3, 5). In other words, the large variations among the quadrats produced too much 'stochastic noise' (i.e. stochastic processes), which diluted the effect of soil fertility on diversity and biomass when integrating them into a diversity–biomass relationship at the 20-m scale but not at the 50-m scale (Fig. S4).

Based on our entire analysis and the experimental research conducted by Luo *et al.* (2017), we agree that soil factors (e.g. fertility and biomes) could mediate the diversity–biomass relationship at larger but not smaller scales. Furthermore, because both diversity and biomass can independently respond to soil variations within natural communities (e.g. Perroni-Ventura *et al.*, 2006; van der Sande *et al.*, 2018 and our research), direct relationships between plant diversity and biomass might be unstable within heterogeneous soil environments (Fowler *et al.*, 2012; Ammer, 2019). Thus, it is time to integrate soil conditions (e.g. fertility) into the traditional diversity–biomass relationship to build a 3D plant community–soil system (e.g. Fig. S4) in which ecologists can give better consideration to aboveground–belowground linkages (Kardol & Wardle, 2010). Given the effect of tree mycorrhizal associations, the results of our research predict a potential biological pathway by which soil fertility contributes to the community diversity–biomass relationship. Soil fertility dominated the distribution patterns of the AM trees and EM trees, which resulted in the different spatial patterns of plant diversity and biomass along the soil fertility gradient and finally led to the community diversity–biomass relationship in the CBS plot (Figs 3, 5, S4). Future studies exploring the mechanisms driving the diversity–biomass relationship should consider the joint contributions of soil fertility and tree mycorrhizal associations.

Conclusions

Our study uncovered the link between the different soil preferences of the AM vs EM tree species and the plant community structure in the CBS plot. We found that the AM trees contributed disproportionately to the diversity, whereas the EM trees drove the biomass in this forest community (Hypothesis II). Our results support the existence of different soil preferences between AM and EM trees and further suggest that this difference might drive changes in the community structure along the soil fertility gradient in this natural community. Additionally, our results suggest that soil fertility and tree mycorrhizal associations could act as mediators of plant diversity–ecosystem function (e.g. biomass) relationships in temperate forest communities.

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Author contributions

XW, ZM and AC conceived the idea; ZY, FL and JY performed the research and collected the data; ZM, KZ, XW and ZH analysed the data; ZM and AC wrote the first draft of the manuscript, and all of the authors contributed substantially to the revisions.

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Supporting Information

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

Fig. S1 The dbh distributions of adult trees (dbh ≥ 10 cm) in the CBS plot.

Fig. S2 The soil fertility gradient of the CBS plot at the 50-m scale.

Fig. S3 The results about codispersion analysis and null model test at the 50-m scale.

Fig. S4 The relations among AGB, SWI of all trees and soil fertility at the 20-m and 50-m scales.

Table S1 Information about the adult trees (dbh ≥ 10 cm) in the CBS plot.

Table S2 Numerical output from the fits of the generalized least squares methods of tree community indexes on soil fertility.

Table S3 Numerical output for all trees from the fits of the generalized least squares methods of AGB on the community diversity.

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