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RESEARCH ARTICLE

# Soil legacy effects on a temperate tree species depend on the mycorrhizal types and phylogenetic distance of the conditioning trees

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## Abstract

1. Associations of trees with arbuscular mycorrhizal (AM) and ectomycorrhizal (EcM) fungi often shape distinct microbial communities in soils. Whether this distinction can create different soil legacies and to what extent such legacies are correlated to phylogenetic relatedness between the trees remains largely unresolved.
2. In this study, we examine the soil legacy effects of five AM and three EcM conditioning tree species on a dual-mycorrhizal poplar species *Populus tomentosa* and estimate dependence of the legacy on the phylogenetic distance between these species and poplar.
3. EcM tree species overall had a weaker soil legacy effect on biomass and foliar C/N ratio of the poplar than AM trees, and this correlated with lower relative abundances of the bacterial genus *Rubrobacter* and the fungal genus *Mortierella* in soils of EcM trees compared to AM soils.
4. Soil legacy effects on biomass of test poplar correlated negatively with its phylogenetic distance from the conditioning trees. A negative correlation also occurred for concentration of total phenolics in the foliage of poplar with phylogenetic distance, but only when the conditioning trees were EcM species.
5. The negative dependence of soil legacies on phylogenetic distance was mediated by a decreased abundance of the bacterial genera *Agromyces*, *Blastococcus* and the fungal genera *Pseudogymnoascus* and *Metarhizium*, as well as an increased abundance of the fungal genera *Aspergillus* and *Clonostachys* in the soil.

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6. Our results indicate that the effects of soil microbial legacies on a given dual-mycorrhizal species may depend not only on the mycorrhizal type of the conditioning trees but also on its phylogenetic distance from these trees.

**KEYWORDS**
mycorrhizal type, phylogenetic relatedness, soil legacy, soil microbiome

## 1 | INTRODUCTION

Plants can steer (a)biotic characteristics of soils, which may subsequently affect the performance of other plants that later grow in this soil (Heinen et al., 2020; van der Putten et al., 2013). These so-called soil legacy effects occur partly because plants alter the structure and functions of the soil microbial community which, in turn, influences the fitness of the later growing plants (Nannipieri et al., 2023; Pickett et al., 2019). A positive soil legacy effect is generated when later coming plants perform better in the altered soil than in unplanted background soil, due to, for example, enrichment of available nutrients or beneficial microbes in the soil that was altered by the previous plant (Bennett & Klironomos, 2018). In contrast, a negative legacy effect may arise when soil nutrients are depleted by the earlier growing plants or because the earlier plants have increased the abundance of soil-borne pathogens (Heinen et al., 2020; Smith-Ramesh & Reynolds, 2017). Plant species often possess specific traits (e.g. root physiochemical dynamics) that may result in species-specific soil legacies (Bennett & Klironomos, 2019) and hence the direction and magnitude of these soil legacy effects are highly dependent on the plant species that alters the soil (van de Voorde et al., 2011). However, comparing and generalizing soil legacy effects of different plant species according to their ecological or evolutionary relatedness remains challenging (Cortois et al., 2016; Schmid et al., 2021; Teste et al., 2017).

Plant species with similar traits often have similar ecological functions, including the way they interact with soils (Augusto & Boča, 2022). Several studies have found that plant species within the same functional group generate similar soil legacies, and species from different groups, for example, forbs versus grasses or slow- versus fast-growing species, distinguish in their legacies (Huang et al., 2024). In forest systems, the type of mycorrhizae of a tree species is typically associated with its multiple above- and below-ground ecological traits (Kennedy et al., 2018; Tedersoo & Bahram, 2019). Arbuscular mycorrhiza (AM) and Ectomycorrhiza (EcM) root symbionts are the most dominant mycorrhizal types of temperate tree species and greatly differ in the way how they construct the three-way relationships among the host plant, mycorrhizae and the soil (Spitzer et al., 2022). Tree species with EcM are often more efficient in inducing plant resistance against antagonists while trees associated with AMs may be more vulnerable to antagonists as pathogens have been shown to accumulate faster in the soils of AM trees (Bahram et al., 2020; Eagar et al., 2022). Moreover, EcM trees are generally characterized as 'nutrient conservative species' with a better ability to utilize organically bound nutrients via decomposition processes and thus leaving higher nutrient content in the soil, whereas AM trees are considered to be nutritional scavengers (Bennett & Klironomos, 2018; Liang et al., 2020). Hence, tree species that associate with AM exhibit generally more negative legacy effects compared to EcM tree species, the latter often create positive or neutral legacies in soils (Bennett et al., 2017; Bennett & Klironomos, 2018). However, the majority of current studies addressing the differences in legacy effects between AM and EcM species have only compared the effects of singular mycorrhizal species within or between mycorrhizal types (Kadowaki et al., 2018; Segnitz et al., 2020). The existence of dual mycorrhizal species that establish both AM and EcM symbioses, for example, *Populus* spp., allows the use of a single species to test soil legacies of both mycorrhizal types, but this remains relatively unexplored to our knowledge.

Plant phylogeny provides another explanation why plants vary in what kind of soil legacy effects they produce and how they respond to legacy effects created by other plants (Yang et al., 2014), as plant species that are phylogenetically closely related often possess similar traits and show a close similarity in their plant–soil interactions (Anacker et al., 2014). Previous studies have shown that plants perform worse in soils conditioned by closely related species than in soil conditioned by distantly related species (Sweet & Burns, 2017) and that the performance of a plant tends to increase together with further phylogenetic distance from the species that conditioned the soil (Liu et al., 2012). Other studies, however, have argued that phylogenetic distance between plant species pairs is a poor predictor for soil legacy effects (Mehrabi & Tuck, 2015) or that the positive connection between increased phylogenetic distance with the plant that conditioned the soil and the permance of the follow-up plant may be limited to closely related species (Wandrag et al., 2020). Therefore, there currently is no consensus whether and to which extent soil legacy effects depend on the phylogenetic distances between the new plant inhabiting the soil and the species that conditioned it (Wandrag et al., 2020). In particular, whether such potential phylogenetic dependencies differ between trees with EcM and AM symbionts is unknown.

Dual mycorrhizal tree species are capable of forming a symbiosis with both AM and EcM fungi, which is considered an insurance strategy in the face of environmental challenges, particularly in ecosystems where either or both mycorrhizal species are present in low densities (Rog et al., 2025; Teste et al., 2020). One such

benefit may originate from the different soil microbial communities that are stimulated by dual-mycorrhizal tree species compared to those shaped by exclusively AM or EcM trees (Singavarapu et al., 2022; Tedersoo et al., 2020). In this study, we used a dual mycorrhizal tree species, Chinese poplar (*Populus tomentosa*), as a focal plant to examine the role of phylogenetic relatedness and mycorrhizal type on soil legacy effects in a greenhouse experiment (Vozzo & Hacskaylo, 1974). This poplar species is often used as a model species for woody plants due to its small genome (about 480 million bases), rich genetic resources, fast early growth and easy asexual reproduction, as well as its wide global distribution (Podila et al., 2009). To condition the soil, we used three EcM tree species and 5 AM tree species that all co-occur in temperate forests together with *P. tomentosa*. We hypothesized that (1) conditioning tree species with EcM symbionts have an overall positive soil legacy effect on *P. tomentosa*, whereas soil conditioning tree species with AM symbionts have a negative effect on poplar performance; (2) the magnitude of the legacy effects depends on the phylogenetic distance between the conditioning tree species and poplar, with more closely related species showing stronger soil legacy effects; and (3) that phylogenetic dependency of soil legacy effects on poplar differs between conditioning species of AM and EcM types.

## 2 | MATERIALS AND METHODS

### 2.1 | Plant species and soil origins

We used *P. tomentosa* seedlings originating from tissue cultures (grown in sterilized commercial soil for 1 week before planting) to standardize the root mycorrhizal microbiome of the focal plants before the experiment. The seedlings were provided by a nursery at Weixian in Hebei Province, China.

Soils used to test soil legacy effects were collected at Lucheng Forest Farm (39°51′18″ N, 116°48′29″ E) in Tongzhou district, Beijing, China. The soil was a loamy soil with pH = 7.96, containing 14.02 g/kg SOC, 12.97 mg/kg N-$NO_3^-$, 4.79 mg/kg N-$NH_4^+$ and 20.07 mg/kg available P. This forest farm is one of the first collective forest farms in North China, established in Beijing in 2009 to accomplish sustainable uses of farmland, protect the ecological environment and promote biodiversity. In this forest farm, more than 20 tree and shrub species have been planted in patches of variable sizes (varying from 100 to 1800 $m^2$ due to the availability of seedlings and the growth rates of the planted species). All the planted species originate from North China and are well adapted to the local environment. Based on the patch area (>900 $m^2$) and plantation age (>10 years) of the available tree species at the farm, we selected three ectomycorrhizal species and five AM species. For EcM species, we used corkscrew willow (*Salix matsudana*), Mongolian oak (*Quercus mongolica*) and Machurian red pine (*Pinus tabuliformis*), and for AM species, we used the golden rain tree (*Koelreuteria paniculata*), Chinese bean tree (*Catalpa fargesii*), ginko (*Ginkgo biloba*), hardy rubber tree (*Eucommia ulmoides*) and Chinese juniper (*Juniperus chinensis*). The unequal numbers of EcM and AM tree species in the design resulted from the overall limited number of tree species, particularly for EcM trees, to be selected in the forestry farm. In this study, *S. matsudana* was considered EcM species, even though it can form associations with both EcM and AM mycorrhizae. However, the colonization rates by AMF are extremely low in the natural situation (Parádi & Baar, 2006). The focal tree species *P. tomentosa* was also included as a control species in the conditioning phase and used to calculate soil legacy effect sizes in the testing phase (see below). Therefore, in total, we selected nine tree species that were available in the forest farm from which soil was collected as inoculum.

### 2.2 | Experimental set-up

For collection of soil samples that were used later to prepare soil inocula to be added to the focal species *P. tomentosa*, we randomly tagged eight similarly sized healthy individuals from each tree species, with at least 10 m distance between the sampled trees. To achieve this, the height and diameter at breast height of each sampled tree were recorded, and the health of the tree was estimated based on observing the leaves and trunk for the presence of pest damage and symptoms of plant diseases. For each tagged tree, the leaf litter at the soil surface as well as the shrub and grass vegetation under the canopy were removed using a shovel before soil collection. Topsoil at 0–15 cm depth from soil surface was collected at least from nine spots around the tree at a distance of 50 cm from the trunk using a soil sampler (ø 5.5 cm). Each individual soil core was sampled to collect at least 500 g soil sample, and then, the cores were mixed to form a composite soil sample which was put into a plastic bag, resulting in total of 4500 g soil for each individual tree. The soil samples were sealed, labelled and stored in an icebox and immediately transported to the laboratory. Additionally, roughly 500 kg of soil was collected from an open area next to the patches of sampled trees and used as growing substrates for the focal trees in the greenhouse (hereafter referred to as background soil), to standardize soil characteristics between the conditioning and test trees.

In the laboratory, each composite soil sample was separately sieved through a 5-mm mesh to remove roots or stones and stored at 4°C for later use. For each composite soil sample, a subsample soil was further sieved through 2-mm mesh and 5 g of this soil was stored at −80°C for microbial analysis. The meshes were thoroughly cleaned and sterilized using 70% alcohol between the sieving events. The remaining material from each composite soil sample was used as soil inoculant for *P. tomentosa* seedlings.

The background soil was sieved through a 5-mm mesh and fully mixed, and six samples were randomly collected to measure the physiochemical characteristics of the soil following the regular protocols. The remaining soil was sterilized using γ-radiation (>50 kg) at China Institute of Atomic Energy, Beijing, China. To

ensure sufficient nutrient provision and water drainage, sterilized background soil was mixed with sterilized peat moss substrate (Pindstrup Plus, Pindstrup Mosebrug A/S, Denmark). Soil inoculants were then mixed with the soil mixture following a ratio of 8:1:1 (sterilized soil: sterilized substrate: inoculant) by volume. Then, eight replicates for each of the nine soil conditioning treatments (1 poplar species + 3 EcM species + 5 AM species), together with eight replicates of a control treatment consisting of an inoculum of non-sterilized background soil (soil collected from the open area), were generated by filling each plastic pot (30 cm in diameter × 20 cm in height) with 3-L mixed soil. A total of 80 pots were obtained and then planted with similar sized seedlings of *P. tomentosa*. One seedling (grown in a tray containing sterilized soil-rite at 25°C with a 16:8 h day:night light regime) was planted at the centre of each pot. The seedlings were immediately watered after planting and were maintained in a greenhouse (with temperature ranging from 20°C to 35°C due to natural day–night temperature fluctuation). Natural daylight was supplemented by 400 W metal halide bulbs to keep light intensity ≥300 PAR (photosynthetic active radiation) during the day throughout the experiment. All pots were placed on a table in the greenhouse according to a split-block design with one replicate of all treatments composing a block. The seedlings were regularly irrigated by adding water to the dishes where the pots were placed on.

The height, stem diameter and the size of the largest leaf were measured weekly starting from the seventh week after transplantation to monitor plant growth. The diameter of the basal stem of each sapling was measured using a Vernier calliper and the height as well as the length and width of the largest leaf (or all the leaves in case the number of leaves was low) were measured using a steel ruler. At the 13th week after the establishment of the transplantation, all saplings were harvested for biomass measurements. Leaves, stems and roots were harvested into separate paper envelopes, after which they were dried in an oven at 70°C for 48 h and their dry mass was weighed. The dried leaf samples were ground with a ball mill for chemical analyses for measuring C and N content with an elemental analyser (Vario EL III, Elementar, Germany). The total P content was analysed using ICP-OES after microwave ablation pretreatment (Sichler et al., 2022). We also measured concentration of total phenolics using the Folin–Ciocalteu assay (Noreen et al., 2017), as well as concentration of the total flavonoids in the leaves using Spectrophotometric Methods (Matić et al., 2017) as a proxy of plant defence.

## 2.3 | DNA extraction, PCR amplification and sequencing

Soil samples packed in dry ice were transferred and stored at −80°C in laboratory until DNA extraction. The extraction of microbial genomic DNA was conducted from 0.5 g soil in each sample using the E.Z.N.A.® soil DNA Kit (Omega Bio-tek, Norcross, GA, US) according to manufacturer's instructions. The quality and concentration of DNA were determined by 1.0% agarose gel electrophoresis and a NanoDrop2000 spectrophotometer (Thermo Scientific Inc., USA). The primer pairs 338F (5′-ACTCCTACGGGGAGGCAGCAG-3′) and 806R (5′-GGACTACHVGGGGTWTCTAAT-3′) were used to amplify the bacterial V3-V4 region of the 16S rRNA gene (Huse et al., 2008), and the primer pairs ITS3F (5′-GCATCGATGAAGAACGCAGC-3′) and ITS4R (5′-TCCTCCGCTTATTGATATATGC-3′) were used to amplify the internal transcribed spacer 2 (ITS2) region of the fungal ITS gene (Toju et al., 2012).

The PCR amplification of 16S rRNA gene was performed as follows: initial denaturation at 95°C for 3 min, followed by 27 cycles of denaturing at 95°C for 30 s, annealing at 55°C for 30 s and extension at 72°C for 45 s, single extension at 72°C for 10 min and end at 10°C. The PCR mixtures contain 5 × TransStart FastPfu buffer 4 μL, 2.5 mM dNTPs 2 μL, forward primer (5 μM) 0.8 μL, reverse primer (5 μM) 0.8 μL, TransStart FastPfu DNA Polymerase 0.4 μL, template DNA 10 ng and finally $ddH^2O$ up to 20 μL. The PCR reactions were performed in triplicate. PCR product was extracted from 2% agarose gel and purified using the PCR Clean-Up Kit (YuHua, Shanghai, China) according to manufacturer's instructions and quantified using Qubit 4.0 (Thermo Fisher Scientific, USA). The qualified PCR products were mixed and paired-end sequenced on an Illumina PE300 platform (Illumina, San Diego, USA) according to the standard protocols by Majorbio Bio-Pharm Technology Co. Ltd. (Shanghai, China).

## 2.4 | Bioinformatics processing

Raw FASTQ files were de-multiplexed and quality-filtered using the fastp tool (v.0.20.0) (Chen et al., 2018). Briefly, reads were truncated at any site receiving an average quality score of <20 over a 50-bp sliding window. Paired-end reads with at least 10 bp overlap and <0.2 mismatch ratio were merged using FLASH software (Version 1.2.7) (Magoč & Salzberg, 2011). Chimeric sequences were checked and removed using the UCHIME algorithm from the USEARCH package (V.11) (Edgar & Flyvbjerg, 2015). Subsequently, the DADA2 plugin in QIIME2 (Version 2020.2) was employed for filtering, denoising and quality control, resulting in the generation of the Amplicon Sequence Variants (ASV) table (Bolyen et al., 2019; Callahan et al., 2017). The taxonomic identities of the gene sequences for each 16S and ITS were assigned by Naive Bayes against the bacterial database SILVA (Version 138.1) and the fungal database UNITE (Version 8.2), respectively. ASVs associated with chloroplasts and mitochondria as well as taxa belonging to unassigned category of lower resolution, for example, genera within an unassigned family, were excluded from the procedure. Considering that the sequencing depth varied across samples, we further conducted a subsampling procedure to standardize the number of reads to the minimum observed across all the samples (37,118 and 36,855 for fungal and bacterial ASVs, respectively, Figure S1) by subSeq (Robinson & Storey, 2014).

## 2.5 | Estimation of phylogenetic relatedness between *P. tomentosa* and soil conditioning tree species

Gene regions (rbcL) of tree species used in our study, including *S. matsudana*, *Q. mongolica*, *P. tabulaeformis*, *K. paniculata*, *C. fargesii*, *G. biloba*, *E. ulmoides*, *J. chinensis* and *P. tomentosa*, were searched in Genebank databases (Chase et al., 1993), and the sequences of each plant species were aligned using MAFFT software and L-ins-i algorithm (Katoh & Standley, 2013). The aligned sequences were used for phylogenetic tree construction using RaxML (Stamatakis, 2006). Fossil records were used to calibrate the time of species divergence (Nitta et al., 2022), which in turn yielded phylogenetic distance between poplar and the other tree species (Mehrabi & Tuck, 2015). The constructed phylogenetic tree indicating the phylogenetic relatedness between *P. tomentosa* and other conditioning tree species is shown in Figure S2.

## 2.6 | Replication statement

| Scale of inference | Scale at which the factor of interest is applied | Number of replicates at the appropriate scale |
|---|---|---|
| Plant | Species | 1 species, 8 replicates |
| Soil | Field | 9 origins of species |

## 2.7 | Data analysis

We assessed soil legacy effects by comparing performances of *P. tomentosa* poplar in soils created by other tree species with performance (growth and chemical characteristics) in soils of its own (Crawford & Hawkes, 2020):

$$\text{Effect size} = \ln \frac{\text{Heterospecific performance}}{\text{Conspecific performance}}$$

In the equation, heterospecific performance indicates poplar performance in soils created by other tree species. Conspecific performance indicates poplar performance in its own soil. The effect size was first calculated on poplar individuals within blocks, upon which the mean was obtained on average. Poplar performance is represented by above-ground (AG) biomass, below-ground (BG) biomass, AG:BG ratio, C/N ratio and C/P ratio as well as concentrations of total phenolics and flavonoids in poplar foliage.

To compare soil legacy effects of AM and EcM tree species on poplar, we used a nested ANOVA to analyse the data of above-ground (AG) biomass, below-ground (BG) biomass, AG:BG ratio, C/N ratio and C/P ratio in poplar foliage and concentrations of total phenolics and flavonoids in poplar foliage. In the models, these variables were used as a response variable and the 'mycorrhizal type' (EcM vs. AM) of the conditioning tree species as a fixed factor, with the identity of conditioning tree species nested within the 'mycorrhizal type' factor. A one-sample *t*-test was employed to compare legacy values of each AM or EcM tree species with zero, aiming to examine the heterospecific soil legacy effects of each tree species within mycorrhizal types (Brinkman et al., 2010).

For the analysis of the soil microbiome data, α-diversity including Shannon index (*H*) and Pielou's evenness (*J'*) of bacterial and fungal communities in soils conditioned by tree species were calculated using the 'vegan' package (Oksanen et al., 2013), and the data were analysed using the nested ANOVA under the 'car' package in R (Fox et al., 2012). One-way ANOVA was followed by a Dunnett's post hoc test to compare α-diversity of each tree species within mycorrhizal types with α-diversity of *P. tomentosa* poplar its own. In this model, the α-diversity in soils of AM or EcM tree species was contrasted with the diversity of poplar soil. The effects of mycorrhizal type of conditioning tree species on soil bacterial and fungal community compositions were examined by Permutational Analyses of Variances (PERMANOVAs) with Bray–Curtis dissimilarity (999 permutations) using the 'vegan' package in R. Separations between treatment 'mycorrhizal type' (EcM vs. AM) of tree species were visualized using principal coordinate analysis (PCoA) under the GGPLOT 2 package in R (Villanueva & Chen, 2019). To examine responses of the obtained α-diversity, β-diversity (Bray–Curtis dissimilarity matrix) and soil legacies on poplar performances (AG biomass, BG biomass, AG/BG biomass ratio, C/N ratio, C/P ratio, total phenolics, total flavonoids) to increasing phylogenetic distance between poplar and conditioning tree species, these microbial diversity indices and effect sizes of soil legacies were further regressed against the phylogenetic distance using linear regressions in 'car' package in R.

Significant differences in the relative abundance of top 10 abundant bacterial and fungal genera between EcM and AM soils were analysed using a Kruskal–Wallis non-parametric test with a nested structure. Correlations between soil legacy and relative abundances of the bacterial and fungal genera significantly differing between EcM and AM soils were examined by Spearman's correlation analyses with a Bonferroni correction for multiple comparisons, using the 'corr.test' function in the 'psych' package (Revelle & Revelle, 2015). The correlation coefficients and p-values were visualized in a heat map in the 'ggplot2' package (Nguyen et al., 2021). Multivariate regression models were performed using the 'anova' function in the 'mvabund' package, to screen the bacterial and fungal taxa from the top 20 abundant genera within or across mycorrhizal types that had relative abundances significantly changing with the phylogenetic distance. In the models, all the top 20 abundant bacterial or fungal genera were included simultaneously as response variables, and the phylogenetic distance as the independent predictor under a negative binomial distribution (Hidalgo & Goodman, 2013). Random forest (RF) models were used to further identify the screened taxa that significantly affected soil legacy effects using the 'rfPermute' function in the 'rfPermute' package (Wang et al., 2025). In the RF models, we selected above-ground biomass, below-ground biomass, C/N ratio and total phenolics in foliage of test poplar as measurements of soil legacy effects according to the significances in results from the linear regressions of these measurements against the phylogenetic distance. The RF models were chosen because we aimed to identify microbial indicators out of the screened

microbial genera, separately for each of the soil legacy measurements (Wang et al., 2023). To achieve this, the candidate genera were simultaneously used to predict only one measurement of soil legacy, creating an univariate dataset that better fits RF models than multivariate analyses such as species indicator analyses or redundancy analyses (Meng et al., 2013).

All the analyses and visualization were performed in R version 4.4.0 (R Core Team, 2020).

## 3 | RESULTS

### 3.1 | Soil legacy effects of tree species differing in mycorrhizal type and phylogenetic distance

The legacy effects for both above-ground (AG) and below-ground (BG) biomass of *P. tomentosa* were neutral to slightly positive in pots inoculated with soils collected from EcM tree species but were negative in pots with soils from AM tree species (Table 1; Figure 1a,b). The negative soil legacies of AM tree species were significant for *E. ulmoides* (Eu), *J. chinensis* (Jc) and *G. biloba* (Gb), indicating that, in these soils, plant AG or BG biomass was lower than in soil of *P. tomentosa* (*t*-tests: all $p<0.05$, Figure 1a,b). In contrast, the legacy effects on AG/BG biomass ratio were overall positive, but effect sizes were higher when *P. tomentosa* was growing in soils inoculated with AM than with EcM soils (Table 1; Figure 1c). The negative legacy effect for both above-ground ($R^2=0.13$, $p=0.014$; Figure 1d) and below-ground ($R^2=0.12$, $p=0.018$; Figure 1e) biomass increased with increasing phylogenetic distance of *P. tomentosa* from the conditioning species, but this was only true when data from EcM and AM trees were combined. There was no significant relation between legacy effect and phylogenetic distance for the shoot/root ratio and for both above- and below-ground biomass when EcM or AM tree species were analysed separately (Figure 1d–f).

The legacy effect on C/N ratio in the foliage of poplar was positive for one species (*Salix matsudana*, abbreviated as 'Sm') and negative for all the others. Overall, it was more negative in saplings grown in pots inoculated with soils of AM tree species than in pots with soil inocula originating from EcM trees (Table 1; Figure 2a). This was mainly due to a significantly lower C/N ratio in poplar foliage in *G. biloba* (Gb) soil than in its own soil (*t*-test: $p=0.033$). Neither the legacy effect on the C/P ratio nor the legacy effect on the concentration of total phenolics and flavonoids in the foliage of poplar were significantly affected by mycorrhizal type or identity of the conditioning trees (Table 1; Figure 2b–d). The legacy effect on the C/N ratio in poplar foliage significantly increased with an increase in phylogenetic distance between poplar and the conditioning trees, but only when the conditioning trees of AM and EcM species were combined ($R^2=0.13$, $p=0.012$; Figure 2e). The legacy effect on the concentration of total phenolics in poplar foliage also significantly changed with an increase in phylogenetic distance, when the conditioning trees were EcM species ($R^2=0.32$, $p=0.008$; Figure 2g).

**TABLE 1** Results of nested ANOVAs for effects of mycorrhizal type (AM vs. EcM) of conditioning tree species on soil legacies for performance of testing poplar species *Populus tomentosa* and on Shannon and Pielou's diversity indices of bacterial and fungal community in soil.

| | Myc | | Tree species (Myc) | |
|---|---|---|---|---|
| **Soil legacy effects** | ***F*** | ***p*** | ***F*** | ***p*** |
| AG biomass | 11.37 | **0.001** | 2.29 | **0.048** |
| BG biomass | 12.69 | **<0.001** | 1.56 | 0.183 |
| AG/BG | 7.02 | **0.012** | 2.25 | 0.058 |
| C/N ratio | 7.75 | **0.008** | 0.77 | 0.596 |
| C/P ratio | 0.02 | 0.884 | 1.38 | 0.246 |
| Total phenolics | 0.58 | 0.453 | 1.85 | 0.114 |
| Total flavonoids | 0.04 | 0.839 | 0.64 | 0.696 |
| Shannon-B | 15.72 | **<0.001** | 3.98 | **0.003** |
| Pielou-B | 1.01 | 0.321 | 5.32 | **<0.001** |
| Shannon-F | 0.01 | 0.913 | 1.10 | 0.379 |
| Pielou-F | 0.04 | 0.849 | 0.98 | 0.452 |

*Note*: Plant performance was represented by above-ground (AG) biomass, below-ground (BG) biomass and AG/BG ratio as well as C/N ratio, C/P ratio and concentration of total phenolics and total flavonoids in the foliage of poplar. Shannon and Pielou's diversity of bacterial community were referred as Shannon-B and Pielou-B, respectively, and the diversity indices of fungal community were Shannon-F and Pielou-F. In the models, species identity of the conditioning trees (Tree species) was used as a factor nested within mycorrhizal type (Myc). Bold *p* values indicate significant results at $p<0.05$ level.

### 3.2 | Soil microbial communities of tree species differing in mycorrhizal type and phylogenetic distance

Shannon diversity but not Pielou's evenness of bacterial communities was significantly higher in soils conditioned by AM tree species than in soils conditioned by EcM tree species (Table 1; Figure 3a). However, both Shannon and Pielou's indices were lower in soil conditioned by *P. tabulaeformis* (Pt) than in conditioned soil of *P. tomentosa* (Dunnett test: $p<0.05$; Figure 3a). The Shannon index of bacterial communities decreased when the phylogenetic distance between the conditioning EcM trees and poplar increased, while the Pielou index increased with an increase in the phylogenetic distance between the AM trees and poplar (Figure 3c). The diversity indices of fungal communities did not differ between soils conditioned by AM and by EcM species (Table 1; Figure 3b) and were not related to the phylogenetic distance between conditioning trees and poplar (Figure 3d).

Multivariate analyses showed that the composition of the soil bacterial communities significantly differed between AM and EcM species (PERMANOVA: $R^2=0.08$, $p<0.001$; Figure 4a). Similarly, the composition of fungal communities differed between the two mycorrhizal types of tree species (PERMANOVA: $R^2=0.16$, $p<0.001$; Figure 4b). The results also indicated that the composition of the soil bacterial (PERMANOVA: $R^2=0.22$, $p<0.001$) and fungal (PERMANOVA: $R^2=0.40$, $p<0.001$) communities significantly differed between

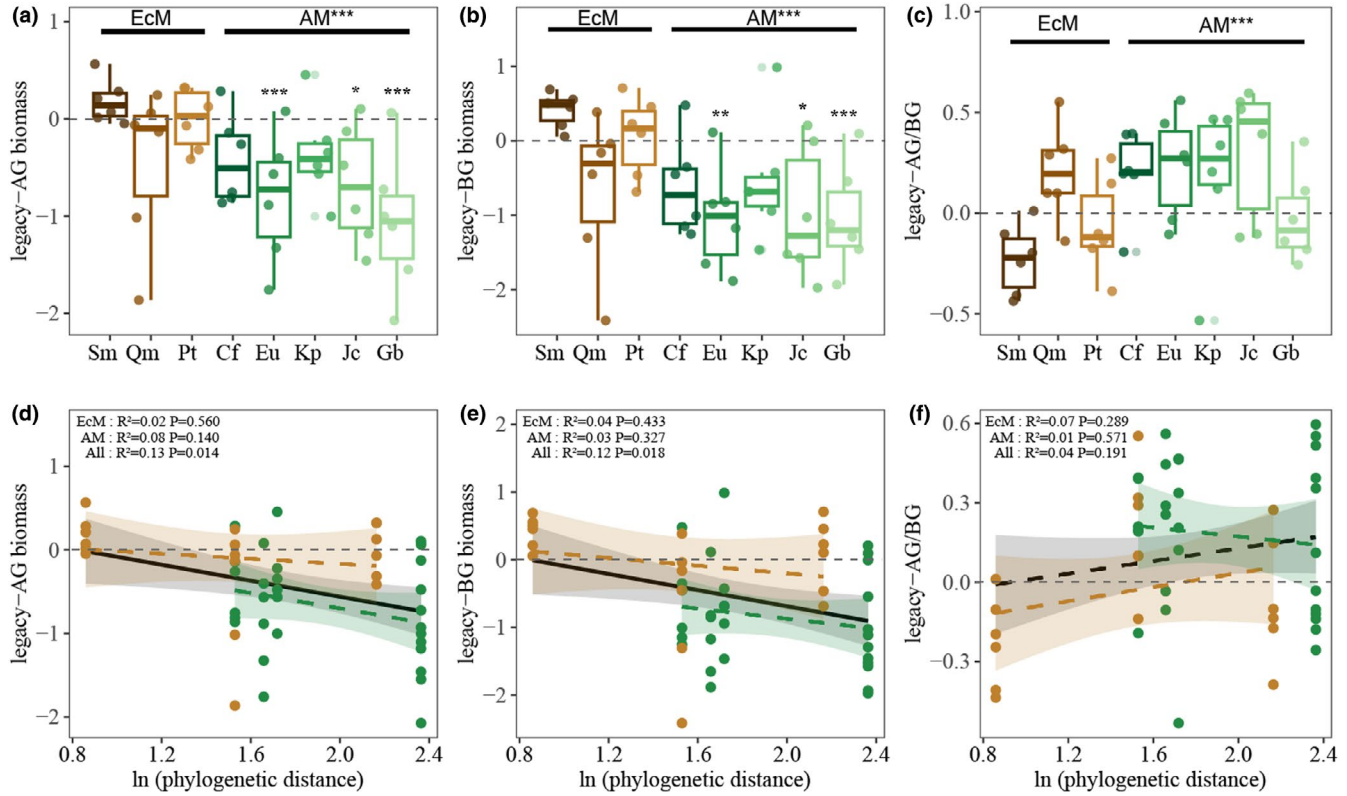



**FIGURE 1** Boxplots showing effect size of soil legacy using (a) above-ground (AG) biomass, (b) below-ground (BG) biomass and (c) AG:BG ratio of poplar as proxies, created by tree species of AM and EcM mycorrhizal guilds. The boxplots in brown and green colour represent EcM and AM tree species with the median, lower quartiles and upper quartiles shown. Regression plots showed changes in (d) AG biomass, (e) BG biomass and (f) AG:BG ratio of poplar in response to phylogenetic distance of all conditioning species, and species within EcM or AM type. Brown and green represented EcM and AM species, respectively, and their corresponding shaded areas indicated 95% confidence intervals of the data. Solid and dashed lines indicated significant and insignificant results at $p < 0.05$, respectively. The asterisks above horizontal lines showed significant differences between AM and EcM guilds, and asterisks above boxplots show that the legacy value for each EcM or AM tree species is significantly greater than or less than 0 ($^{*}p < 0.05$, $^{**}p < 0.01$, $^{***}p < 0.001$).

the conditioning tree species within AM or EcM mycorrhizal types (Figure 4a,b). Bacterial community composition (dissimilarity) in soils of conditioning trees did not change with increasing phylogenetic distance between the conditioning tree species and poplar (all $p > 0.05$; Figure 4c), but the compositional differences in fungal communities in soils conditioned by AM trees significantly increased with an increase in phylogenetic distance ($R^2 = 0.46$, $p < 0.001$; Figure 4d).

For bacterial communities, the relative abundance of the genera *Rubrobacter*, *Mcirovirga* and *Nitrospira* was higher in the soils of AM tree species than in the soils of EcM tree species (Mycorrhizal type: all $p < 0.05$; Figure 5a). For fungal communities, the relative abundance of the genera *Fusarium*, *Mortierella* and *Alternaria* was also higher, but the abundance of the genus *Inocybe* was lower in soils conditioned by AM species than in the soils of trees of the EcM type (Mycorrhizal type: all $p < 0.01$; Figure 5b). The relative abundance of the bacterial genus *Rubrobacter* and fungal genus *Mortierella* were negatively correlated with the soil legacy effect for the biomass and foliar C/N ratio of poplar, but positively correlated with the soil legacy effect for AG/BG biomass ratio. The bacterial genus *Rubrobacter* showed a negative correlation, and the fungal genus *Inocybe* showed a positive correlation between relative abundance and the soil legacy for the concentration of total flavonoids in the poplar foliage. The relative abundance of bacterial genus *Microvirga* negatively correlated with the concentration of total phenolics in the foliage (Figure 5c).

### 3.3 | Linkages between plant phylogenetic relatedness and mycorrhizal types to poplar performance

The multivariate regression models identified six bacterial genera and eight fungal genera in soils conditioned by all tree species for which the relative abundances significantly varied with plant phylogenetic distance. In soils conditioned by AM and by EcM species, the numbers were 4 and 4 for bacterial genera and 10 and 8 for fungal genera, respectively (Table S1; Figure 6a). Among these microbial taxa, the relative abundances of the bacterial genera *Agromyces* and *Blastococcus* as well as fungal genera *Aspergillus*, *Clonostachys* and *Pseudogymnoascus* positively correlated with the soil legacy for above-ground, below-ground biomass and foliar C/N ratio of test poplar (Figure 6b). The relative abundances of the fungal genera *Metarhizium* and *Exophiala* positively correlated with the soil

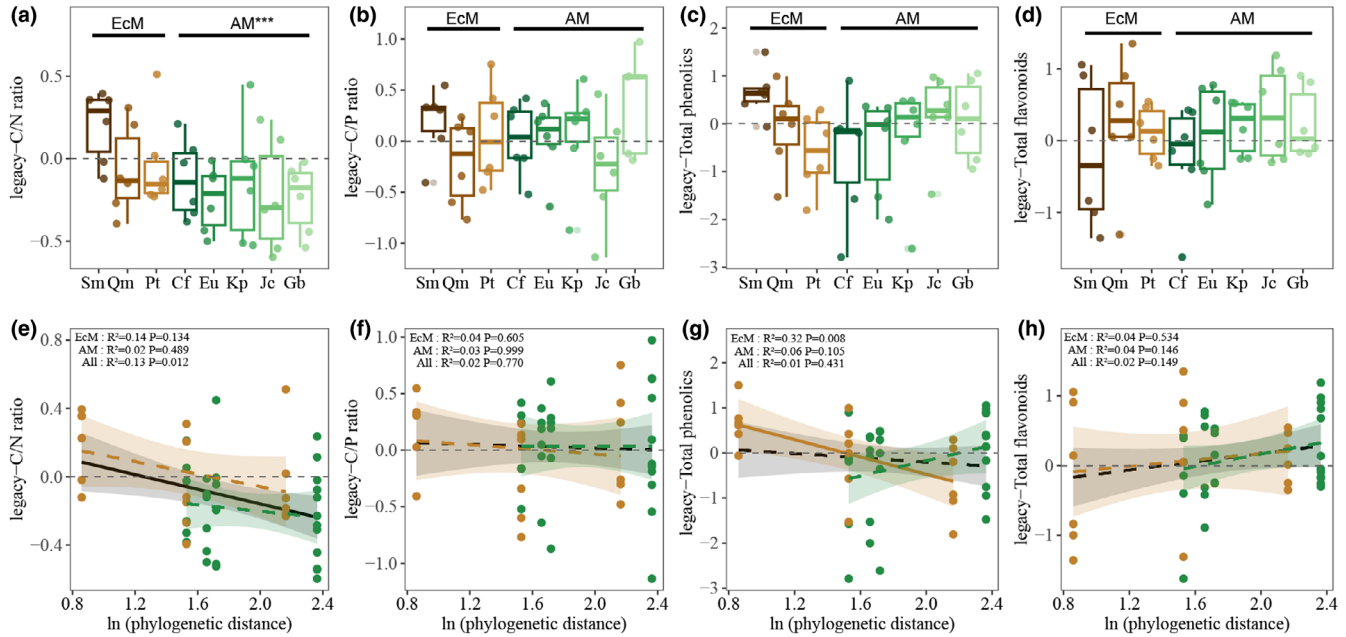



**FIGURE 2** Boxplots showing the effect size of soil legacy using (a) C/N ratio, (b) C/P ratio, (c) total phenolics and (d) total flavonoids in the foliage of poplar as proxies created by tree species of AM and EcM mycorrhizal guilds. The boxplots in brown and green represent EcM and AM tree species with the median, lower quartiles and upper quartiles shown. Regression plots showed changes in (e) C/N ratio, (f) C/P ratio, (g) total phenolics and (h) total flavonoids in the foliage of poplar in response to phylogenetic distance of all conditioning species, and species within EcM or AM type. Brown and green represented EcM and AM species, respectively, and their corresponding shaded areas indicated 95% confidence intervals of the data. Solid and dashed lines indicated significant and insignificant results at $p < 0.05$, respectively. The asterisks above horizontal lines showed significant differences between AM and EcM guilds, and asterisks above boxplots show that the legacy value for each EcM or AM tree species is significantly greater than or less than 0 (***$p < 0.001$).

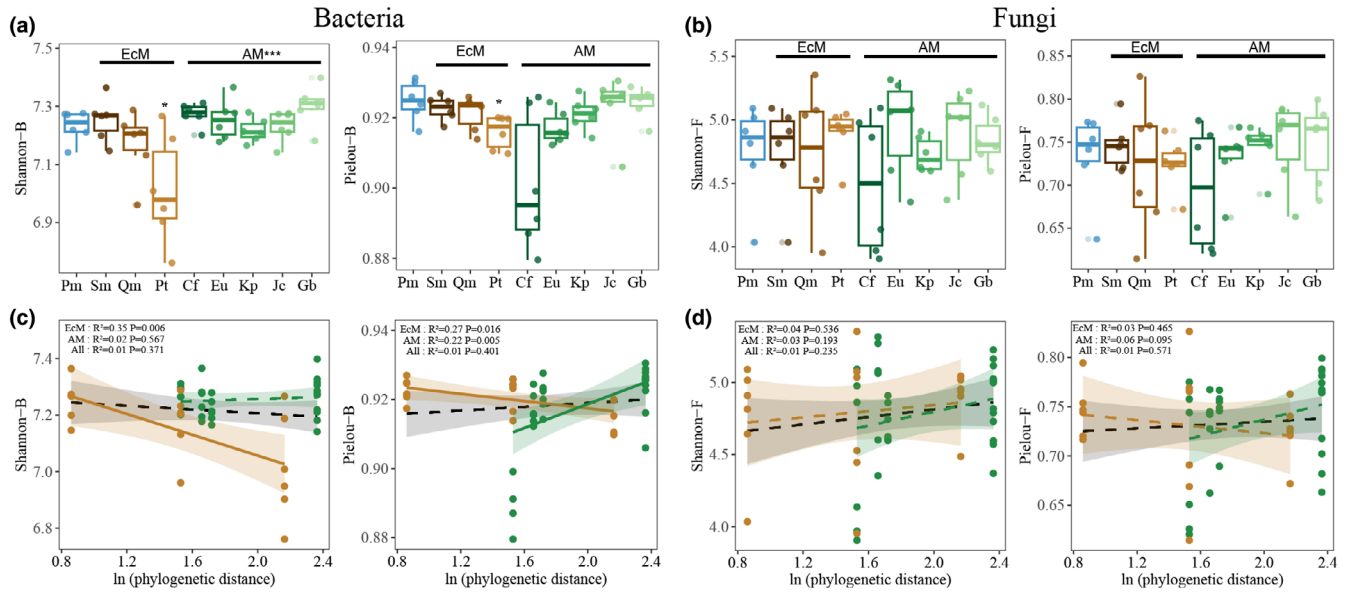



**FIGURE 3** Boxplots showing Shannon and Pielou's indices of (a) bacterial and (b) fungal community in soils conditioned by poplar, as well as tree species belonging to EcM or AM mycorrhizal guilds. The boxplots in blue, brown and green represent poplar, EcM and AM tree species, respectively. The median, lower quartiles and upper quartiles were shown. Regression plots showed changes in Shannon and Pielou's indices of (c) bacterial and (d) fungal community in soil conditioned by AM or EcM trees in response to phylogenetic distance of these conditioning species from poplar. Brown and green represented EcM and AM species, respectively, and their corresponding shaded areas indicated 95% confidence intervals of the data. Solid and dashed lines indicated significant and insignificant results at $p < 0.05$, respectively. The asterisks above horizontal lines showed significant differences between AM and EcM guilds, and asterisks above boxplots show that the legacy value for each EcM or AM tree species is significantly greater than or less than 0 (*$p < 0.05$, ***$p < 0.001$).

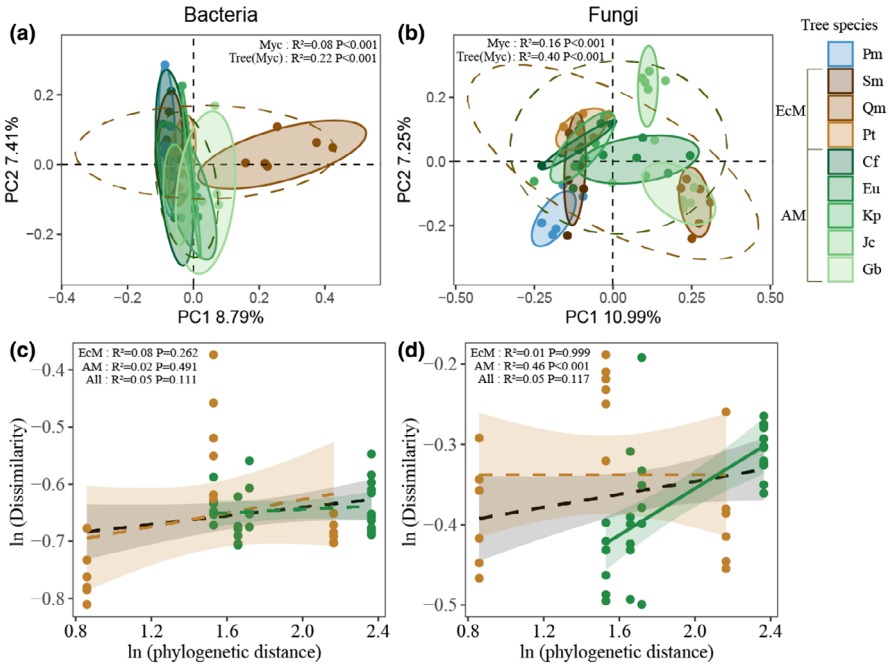



**FIGURE 4** Ordination diagram of principal coordinate analyses (PCoA) of (a) bacterial and (b) fungal community compositions in soils conditioned by tree species of AM and EcM mycorrhizal guilds and poplar itself. Effects of mycorrhizal type and tree species within the mycorrhizal type on the community compositions were assessed using PERMANOVAs. Regression plots showed relative values in dissimilarity index of soil (c) bacterial and (d) fungal communities in response to phylogenetic distance of all conditioning species, and species within EcM or AM type. Brown and green represented EcM and AM species, respectively, and their corresponding shaded areas indicated 95% confidence intervals of the data. Solid and dashed lines indicated significant and insignificant results at $p < 0.05$, respectively.

legacy of EcM trees for total phenolics in the foliage of test poplars (Figure 6b).

## 4 | DISCUSSION

EcM and AM tree species typically have different soil microbial communities related to their differences in nutrient cycling and rhizodeposition, which may result in differential plant–soil feedbacks (Bahram et al., 2020; Eagar et al., 2022; Kadowaki et al., 2018). One of the main aims of our study was to compare soil legacy effects of EcM and AM temperate tree species on the performance of a dual-mycorrhizal species *Populus tomentosa*. The results show an overall stronger negative soil legacy effect of AMF trees than EcM trees on growth and nutrient status of *P. tomentosa* measured as biomass and foliar C/N ratio, respectively, which is in line with the findings of other studies (e.g. Eagar et al., 2022; Kadowaki et al., 2018). Additionally, we also observed that the effect size of the negative soil legacy became larger with an increase in phylogenetic distance between these conditioning tree species and the testing poplar regardless of their mycorrhizal types. This was opposite, however, for the legacy for poplar resistance to stresses measured by total phenolic content in the poplar foliage which decreased with phylogenetic distance but only when the conditioning trees were EcM species. Altogether, these results suggest that dual mycorrhizal species such as *Populus* spp. may benefit more (or suffer less) from soil legacies of EcM species than AM species and that the magnitude of such legacies may depend on the phylogenetic distance between these conditioning tree species and the test species used to measure the legacy effects (Wandrag et al., 2020).

EcM and AM fungi substantially differ in genome-encoded capacity, such as in favouring the host plant in nutrient uptake or induction of resistance to stresses (Tedersoo & Bahram, 2019). In our study, we observed a smaller soil legacy effect for the AG/BG biomass ratio of poplar trees in EcM soil, which indicates that test poplars in EcM soil are more similar to those in their own soil with respect to biomass allocation strategies, when compared to poplars in AM soil (Eziz et al., 2017). This suggests that poplars may experience similar soil environments in EcM and conspecific soils that yet differ from the environment in AM soil (Poorter et al., 2012). The differences may include the amount of readily available nutrients or the relative density of symbiotic and pathogenic microbes that underlie the observed higher biomass of poplars or weaker soil legacies in EcM soil than in AM soil (Bennett & Klironomos, 2019). Given that EcM plants typically accumulate less pathogenic fungi in their mycorrhizosphere than AM plants, less soil-borne pathogens in EcM soil may also explain the better performance of poplars (Johnson et al., 2023; Tedersoo et al., 2020). Alternatively, the worse performance of poplar in AM soil than in EcM soil might have been due to inadequate mycorrhizal fungal colonization in roots (Kadowaki et al., 2018). However, since we did not compare the available soil nutrient content at the end of the experiment, or species-specific plant pathogens and overall mycorrhization in soils of EcM and AM plants, these possible explanations unfortunately cannot be verified

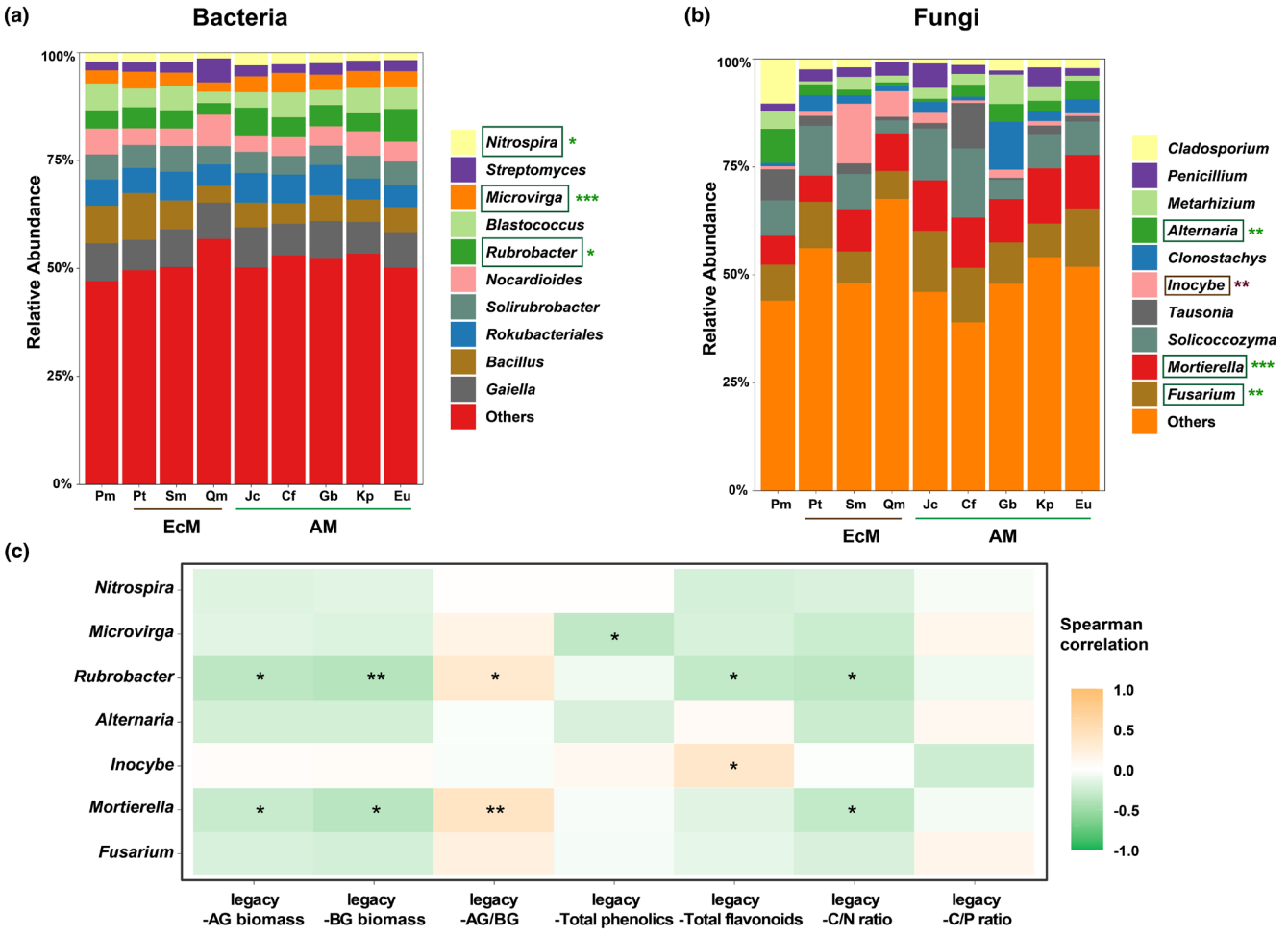



FIGURE 5 Stacked bars showing relative abundances of the 10 most abundant (a) bacterial and (b) fungal taxa at genus level in soils conditioned by EcM and AM tree species. The genus marked in box were those differing in relative abundances between EcM and AM soils, with brown and green boxes indicating significantly higher abundance of the genus in EcM and AM soil, respectively. The significance was analysed using Kruskal–Wallis non-parametric test at $p < 0.05$ level. The heat map of Spearman's correlation showed (c) the relationship between soil legacy for AG biomass, BG biomass, AG:BG ratio, C/N ratio, C/P ratio, total phenolics and total flavonoids in the foliage of the poplar, and the relative abundance of the bacterial and fungal genera that differed between EcM and AM soil. The gradient of orange and green colours indicates the positive and negative effect, respectively, and the asterisks (*) and (**) indicate significant correlations at $p < 0.05$ and $p < 0.01$ levels.

in the present study. It is also important to note that even though we detected significant differences in soil microbial communities conditioned by EcM and AM trees, the heterogeneity among the microbial communities of tree species within mycorrhizal types was substantial, which suggests a strong species-specific control of soil microbes that may have influenced the effects on poplar performances (van de Voorde et al., 2011). Therefore, even though the results suggest that the overall better performance of poplar trees in EcM soil than in AM soil may have resulted from the positive effects of EcM trees in steering soil microbial communities (Singavarapu et al., 2022), further work is required to examine these plant–soil community links in more detail.

Specific shifts in the soil microbial community incurred by a conditioning plant species are often considered a key driver in the outcomes of soil legacies (van der Putten et al., 2013). In the current study, we found lower bacterial diversity and significantly different compositions of both bacterial and fungal communities in EcM soil than in AM soil. EcM trees often produce poorer quality litter with lower nutrient contents compared to AM trees (Jacobs et al., 2018; Keller & Phillips, 2019). Hence, the observed difference in microbial diversity or community composition may be a result of selective shifts in the relative abundance of some key species driven by the nutritionally inferior tissues of EcM trees (Midgley et al., 2015). This possibility is supported by the finding that abundances of taxa in the microbial community in EcM soils from AM soils differ, such as the bacterial genera *Rubrobacter*, *Microvirga* and *Nitrospira* as well as the fungal genera *Fusarium*, *Mortierella*, *Inocybe* and *Alternaria*. These genera are reported to be responsible for carbon or nutrient turnover (Oleńska et al., 2020; Tedersoo et al., 2017). For example, the genus *Rubrobacter* has been reported as an important denitrifier, and its lower relative abundance in microbial communities in EcM than in AM soil may contribute to less nitrogen loss from EcM

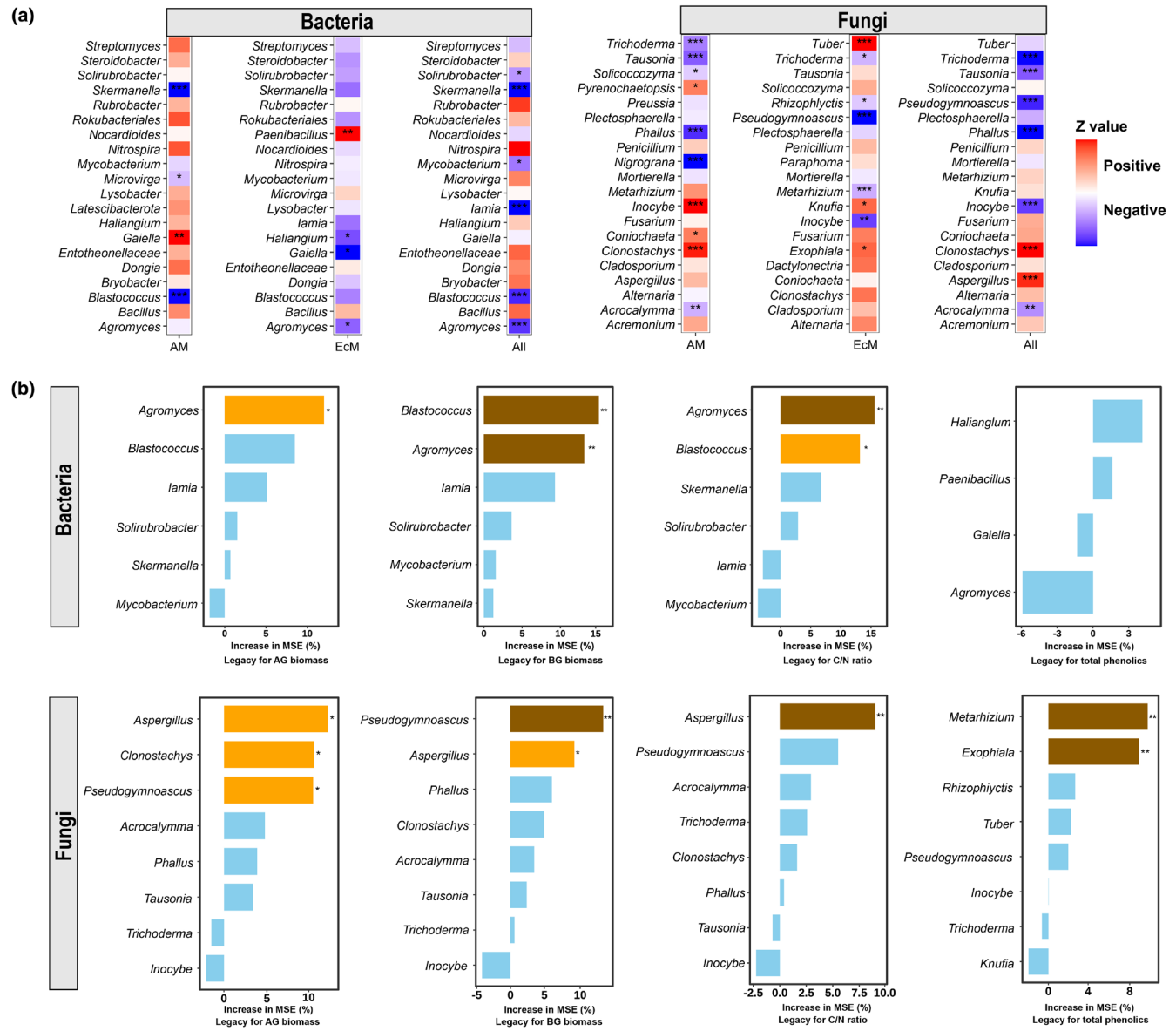



FIGURE 6 The screening of microbial taxa that potentially mediate soil legacy effects of plant species on poplar performance. (a) The heat map showing relationships between the relative abundances of top 20 abundant bacterial and fungal genera in conditioned soil by tree species within and across mycorrhizal types (AM or EcM), and the phylogenetic distance between these conditioning trees and test poplar. The gradient of red and blue colours indicates the positive and negative effect, with the asterisks (*), (**) and (***) indicating statistical significance at $p < 0.05$, $p < 0.01$ and $p < 0.001$ levels, respectively, according to multivariate regression models. (b) Random forest analyses showing the percentage of soil legacy effects for above-ground (AG) biomass, below-ground (BG) biomass, C/N ratio and foliar total phenolics of test poplar, contributed by the relative abundances of selected bacterial and fungal genera by multivariate regression models. The bars coloured brown and orange, respectively, indicate significant contribution of the corresponding taxa at $p < 0.05$ and $p < 0.01$, and the bars of light blue indicate insignificant contribution of the taxa at $p > 0.05$.

soil, subsequently enabling more nitrogen to retain in soil which is then available for the growing poplar seedlings (Ke et al., 2023). This assumption is supported by the negative correlation between the relative abundance of *Rubrobacter* and the soil legacy effects for poplar biomass and concentration of N-based (total) flavonoids in the foliage that both rely on the availability of nitrite in the soil (Figure S3). In contrast, for the genus *Inocybe*, its abundance was positively correlated with the concentration of total flavonoids, suggesting that systemic induction of plant secondary metabolites by some ectomycorrhizal taxa to combat environmental stresses may be another reason for the better performance of poplar grown in EcM soil than in AM soil (Gille et al., 2024; Kebert et al., 2022). Future studies should examine the roles of these genera in plant–soil feedbacks in more detail.

An important aim of this study was to identify the role of phylogenetic relatedness of tree species in driving soil legacy effects (Senior et al., 2018). Our results show an overall negative soil legacy effect of trees on poplar biomass that significantly increased

with the phylogenetic distance between poplar and conditioning tree species. This suggests that phylogenetically distantly related tree species tended to generate stronger negative soil legacy effect on poplar growth (Segnitz et al., 2020). This result may be due to decreases in relative abundances of beneficial microbial taxa, for example, the bacteria *Agromyces* and *Blastococcus* or fungus *Pseudogymnoascus* that promote soil biological N fixation and nitrification in the soil of distantly related plant species to poplar (De Maria et al., 2011; Li et al., 2024; Wang et al., 2017). On the contrary, increases in relative abundance of harmful fungal genus *Aspergillus* in soil of more distantly related trees, which also contributes to the observed increasingly negative soil legacy for poplar biomass (Paulussen et al., 2017). In addition, we also detected a decrease in the relative abundance of the plant beneficial fungus *Metarhizium* in soil microbial communities over the phylogenetic distance between conditioning EcM tree species and poplar, and this may also have contributed to the decrease in concentration of total phenolics in the foliage of the poplar seedlings (Rasool et al., 2023; Zhang et al., 2022). However, the roles of the microbial genera identified in the current study remain speculative given the lack of mechanistic measurements that are needed to verify their functions and interactions with poplar trees. Further investigations are required to quantitatively analysing the dynamics of these microbial taxa across mycorrhizal types and phylogenetic distances as well as experimentally manipulating them to verify their contribution to the observed soil legacies (Luo et al., 2021).

## 5 | CONCLUSIONS

Our study shows that soil legacy effects of temperate tree species on a dual mycorrhizal poplar species not only depend on the mycorrhizal type of these conditioning tree species but also on their phylogenetic distance from poplar. The difference in α-diversity of the bacterial community as well as the composition of both the bacterial and fungal communities appeared to be involved in this differentiation of soil legacies between EcM and AM trees. However, shifts in relative abundances of specific functional microbial taxa in the community may better explain the dependence of these legacy effects on the phylogenetic relatedness between conditioning and response poplar. This work highlights the necessity to include both mycorrhizal guilds and phylogenetic relatedness of tree species when studying soil legacy effects in forest ecosystems, and such findings can support future forest conservation and management decisions.

### AUTHOR CONTRIBUTIONS

Minggang Wang, Laiye Qu and T. Martijn Bezemer conceived the idea and designed the methodology; Minggang Wang and Meilin Wang collected the data; Minggang Wang, Wei Xue and Hongwei Xu analysed the data. Minggang Wang and Meilin Wang led the writing of the manuscript. All authors contributed critically to the drafts and gave final approval for publication.

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### CONFLICT OF INTEREST STATEMENT

The authors declare no competing interests.

### DATA AVAILABILITY STATEMENT

The data used in this study are available from the Dryad Digital Repository: https://doi.org/10.5061/dryad.bg79cnprx (Wang et al., 2026).

### STATEMENT ON INCLUSION

The majority of authors are based in China. Furthermore, all the work related to the study was carried out in China.

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## SUPPORTING INFORMATION

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

**Table S1.** Multivariate regression models showed the bacterial and fungal genera in soil conditioned by tree species with their relative abundances significantly varied with the phylogenetic distance of all conditioning species (All), and species within AM or EcM type from the response poplar (*Populus tomentosa*). The *Z* values calculated by Wald test and the corresponding *p* values for each genus were presented in the table. Significances of the regression models were determined at *p*-value of 0.05.

**Figure S1.** The rarefaction curves of bacterial (a) and fungal (b) community in soils conditioned by tree species of *Salix matsudana* (Sm), *Quercus mongolica* (Qm), *Pinus tabuliformis* (Pt), *Koelreuteria paniculata* (Kp), *Catalpa fargesii* (Cf), *Ginkgo biloba* (Gb), *Eucommia ulmoides* (Eu), *Juniperus chinensis* (Jc) and *Populus tomentosa* (Pt). The rarefaction curves of both the bacterial and fungal communities showed that the sequencing work was comprehensive to cover the bacterial and fungal diversity, respectively, as all the rarefaction curves tended to approach saturation plateau.

**Figure S2.** A phylogenetic tree showing phylogenetic relatedness between the testing species *Populus tomentosa* and the tree species that conditioned the soil in the study. The values on the tree branches indicate phylogenetic distances in mya (million years ago) of each conditioning species from the response poplar species *Populus tomentosa*. The coloured area of the phylogenetic tree indicates mycorrhizal guilds of these conditioning species, with brown and green representing EcM and AM types, respectively. Pm are abbreviations of response poplar species *Populus tomentosa*, and Sm, Qm, Pt, Cf, Eu, Kp, Jc and Gb represent the conditioning tree species of *Salix matsudana*, *Quercus mongolica*, *Pinus tabulaeformis*, *Catalpa fargesii*, *Eucommia ulmoides*, *Koelreuteria paniculata*, *Juniperus chinensis* and *Ginkgo biloba*, respectively.

**Figure S3.** Relative abundances and the corresponding significant differences in (a) main bacterial ecological functions and (b) fungal functional guilds in soils conditioned by EcM and AM tree species. The functions marked in box were those differing in relative abundances between EcM and AM soils, with brown and green boxes indicating significantly higher abundance of the genus in EcM and AM soil, respectively. The significance was analysed using the nested ANOVA at $p = 0.05$ level, in which 'tree species identity' was nested in 'mycorrhizal type'. The asterisk (*) and (**) indicate significant correlations at $p < 0.05$ and $p < 0.01$ levels.

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