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Nutrient availability explains distinct soil fungal colonization of angiosperm vs. gymnosperm wood

Zhuqi Zhao[a,b,c], Zhenhong Hu[a,b,d,e*], Teng Yang[c,f], Zhiyuan Xu[g], Zhenyin Bai[a,b,c], Emma J. Sayer[h,i,j]

[a] *The Research Center of Soil and Water Conservation and Ecological Environment. Chinese Academy of Sciences and Ministry of Education, Yangling, Shaanxi 712100, China.*

[b] *State Key Laboratory of Soil Erosion and Dryland Farming on the Loess Plateau, Institute of Soil and Water Conservation, Chinese Academy of Sciences and Ministry of Water Resources, Yangling, Shaanxi 712100, China.*

[c] *University of Chinese Academy of Sciences, Beijing 100049, China.*

[d] *College of Soil and Water Conservation Science and Engineering, Northwest A&F University, Yangling, Shaanxi 712100, China*

[e] *CREAF, Campus de Bellaterra (UAB), Cerdanyola del Vallès, Spain*

[f] *State Key Laboratory of Soil and Sustainable Agriculture, Institute of Soil Science, Chinese Academy of Sciences, East Beijing Road 71, Nanjing, 210008, China*

[g] *Key Laboratory of Low-carbon Green Agriculture in Northwestern China, Ministry of Agriculture and Rural Affairs of China, College of Natural Resources and Environment, Northwest A&F University, Yangling, Shaanxi 712100, China*

[h] *Institute of Botany, Ulm University, Albert-Einstein-Allee 11, 89081 Ulm, Germany.*

[i] *Lancaster Environment Centre, Lancaster University, Lancaster, LA1 4YQ, United Kingdom*

[j] *Smithsonian Tropical Research Institute, P.O. Box 0843-03092, Balboa, Ancon, Panama, Republic of Panama*

***CORRESPONDING AUTHOR**

Zhenhong Hu, E-mail: zhhu2020@nwafu.edu.cn

AUTHOR CONTRIBUTIONS

Zhuqi Zhao performed measurements and data analysis, and wrote the manuscript. Zhenhong Hu obtained funding, supervised the study and experiments, and contributed significantly to analysis and manuscript preparation. Teng Yang was involved in writing—review and editing. Zhiyuan Xu and Zhenyin Bai edited the manuscript. Emma J. Sayer advised on data analysis and contributed significantly to manuscript preparation and interpretation of results. All authors contributed critically to the drafts and gave final approval for publication.

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CONFLICT OF INTEREST STATEMENT

All authors declare no conflicts of interest.

Abstract:

1. Soil fungi play an essential role in the fungal colonization of deadwood, with consequences for multiple ecosystem functions such as wood decomposition. Nutrient deposition can substantially affect fungal activity but it is unclear how external nutrient inputs and host plant nutrient content interact to influence soil fungal colonization of deadwood.
2. To advance understanding of fungal dynamics during deadwood decomposition, we conducted a field experiment with eight tree species (four angiosperms and four gymnosperms) under four nutrient additions (no nutrient addition, nitrogen (N) -addition, phosphorus (P) -addition, and combined N- and P-addition), to investigate fungal colonization and communities in different host plant clades (angiosperms and gymnosperms) over three years.
3. The study revealed that host plant clade and nutrient availability interact significantly, which strongly influenced soil fungal colonization of deadwood. The percentage of shared fungi (present in both soil and deadwood) was higher in angiosperms (38.1% - 47.3%) than in gymnosperms (26.5% - 36.5%). Saprotrophs were the dominant functional group in the shared fungal community, with symbiotrophs as the next most abundant group, and the dominant fungal taxa were mainly *K*-strategists, which were more abundant in gymnosperms than in angiosperms. Notably, there was a stronger connection between soil fungi and deadwood fungi in gymnosperms compared to angiosperms, which was likely related to the importance of *K*-strategist fungi for decomposing wood with low nutrient content.
4. Overall, the shared fungal community in angiosperms was more sensitive to nutrient addition than in gymnosperms, resulting in greater changes to fungal taxa and functional groups. In angiosperm wood, N-addition significantly increased α-diversity but decreased β-diversity of the shared fungal community, indicating N-limitation. In gymnosperm wood, P-addition significantly reduced both α-diversity and β-diversity of the shared fungal community, indicating P-limitation.
4. *Synthesis.* Our study demonstrates the divergent effect of nutrient addition on fungal colonization in angiosperms vs. gymnosperms. Considering interactions between inherent plant traits and exogenous nutrient availabilities thus provides a more comprehensive understanding of the association between soil fungi and deadwood fungi during wood decomposition.

Keywords：community assembly; deadwood; ecological omics; ecological strategy; fungi; nutrient addition

1 INTRODUCTION

Deadwood is a crucial carbon (C) reservoir in forest ecosystems that represents about 8% of global forest C stocks (Pan et al. 2011; Russell et al. 2015). During decomposition, a substantial 80% to 90% of deadwood C is released into the atmosphere (Russell et al. 2015). However, we know surprisingly little about the decomposition of wood, compared to the decay of other plant parts, such as litter and fine roots, as it can take many years to decades for large woody structures, such as tree stems, to decay (Harmon et al. 1986; Cornwell et al. 2009). Fungi are the primary decomposers of deadwood, as many of them secrete oxidative and hydrolytic enzymes that enable them to effectively degrade lignin (Boddy and Watkinson 1995). Thus, fungal colonization of deadwood is considered as the predominant control of decomposition rate (Bradford et al. 2014). Determining colonization processes is important because different fungal functional groups have distinct capabilities to degrade different compounds in wood (Chen et al. 2022; Lu et al. 2023; Valmaseda et al. 1990). Indeed, despite being regarded as specialist decomposers, saprotrophic fungi span a wide spectrum of life-history strategies (Lustenhouwer et al 2020), which may be more important in determining decay rates than taxonomic diversity (Vengopal et al. 2017). For example, wood decays faster when the decomposer community is dominated by *r*-strategist fungi, as they can capture and consume resources more rapidly and efficiently. (Lustenhouwer et al. 2020; Lustenhouwer et al. 2020; Bebber et al 2011). Thus, elucidating the colonization of deadwood by fungal functional groups with distinct ecological strategies is key to understanding the decomposition of deadwood.

Soil fungi play a key role in the fungal colonization of deadwood due to close contact, prolonged interaction, and exchange of resources between the fungal communities in soil and deadwood (Makipaa et al. 2017; Purahong et al. 2019). Soil fungal colonization of deadwood depends on both deterministic and stochastic factors (Hanson et al. 2012) because fungi will randomly disperse to wood, and fungi with qualities unsuitable for survival in a given environment will subsequently be eliminated (Boddy and Hiscox 2016). Thus, the local pool of potential colonizing species, substrate physicochemical properties (i.e. wood traits), and environmental conditions are the main factors influencing colonization (Boddy 2001; Boddy and Heilmann-Clausen 2008; Boddy and Hiscox 2016). As soil fungi represent a large potential pool of initial deadwood colonizers, the diversity of the soil fungal pool could play a critical

role in determining the outcome of initial deadwood colonization (Purahong et al. 2019; Peng et al. 2023). However, as deadwood breaks down over time, the importance of deterministic processes such as strong environmental filtering and ecological selection better explain colonization outcomes and fungal community composition (Cline et al. 2018). Nevertheless, we still know very little about the colonization of deadwood by soil fungi (Makipaa et al. 2017; Purahong et al. 2018a; Purahong et al. 2019), as most studies on the mechanisms of colonization to date have been indoor culture experiments (Fukami et al. 2010; Hiscox et al. 2015).

Wood nutrient status plays a major role in environmental filtering of fungal colonizers (Harpole et al. 2016) because fungal activity in deadwood is often limited by both N and P availability (Hoppe et al. 2016). For example, decomposition by fast-growing (*r*-strategist) fungi is strongly influenced by wood nutrient content (Venugopal et al. 2016), and ectomycorrhizal fungi preferentially colonize high-N substrate (Rajala et al 2012). Differences in the wood nutrient content of host plant phyla are therefore likely to influence soil fungal colonization of deadwood. For example, gymnosperm wood contains less N and P than angiosperm wood, and the differences in nutrient status between the two clades strongly influence microbial community composition and functioning (Weedon et al. 2010; Peršoh and Borken 2017; Hu et al. 2018). High wood nutrient content can weaken the environmental filters for microbial colonization and increase the importance of initial colonizers (Zhou and Ning 2017; Liu et al. 2021). Thus, we would expect the diversity of the soil fungal colonizer pool to play a more important role in the colonization of angiosperm wood with high nutrient content. By contrast, low nutrient availability represents a strong environmental filter for colonizers, so the diversity of the colonizer pool should play a much lesser role in the decomposition of gymnosperm wood.

In addition to differences in substrate nutrient availability, anthropogenic inputs of N and P to the biosphere could affect wood decomposition by altering fungal diversity (Liu et al. 2021b) and the predominance of different fungal functional groups (Ma et al. 2022). Indeed, there are three pathways by which nutrient deposition could affect wood decay fungi: First, increasing N deposition relative to P can raise plant N ratios, potentially exacerbating P-limitation during wood decomposition, especially in P-deficient tropical and subtropical forests

(Vitousek et al. 2010; Cui et al. 2022; Peñuelas and Sardans 2022). Second, nutrient deposition may enhance fungal α-diversity by alleviating metabolic constraints (Bebber et al. 2011; Purahong et al. 2018b), but reduce β-diversity by diminishing spatial environmental variability (Chalcraft et al. 2008; Donohue et al. 2009). At the same time, it may also promote could promote growth of r-strategist fungi because their rapid cell division creates particularly high demands for N and P (Elser et al. 2000; Ma et al. 2022). Finally, nutrient inputs can alter the colonization of deadwood by soil fungi through changes in soil physicochemical properties, thereby affecting the overall dynamics of fungal communities (Wallenstein et al. 2006; Makipaa et al. 2017; Zhou et al. 2017; Wang et al. 2021; Ma et al. 2022). Nonetheless, most studies have concentrated on leaf litter or soil fungi, which may respond differently to nutrient inputs compared to wood-decaying fungi (Purahong et al 2018a). Importantly, the impacts of nutrient inputs on wood-colonizing fungi, and therefore on decay rates, are likely to depend at least in part on the initial nutrient content of the decaying wood (Hu et al. 2024). However, we do not know how anthropogenic nutrient inputs might interact with the wood quality of different host plants to affect fungal colonization dynamics. Filling this knowledge gap is important to determine how atmospheric nutrient deposition might affect wood decomposition in different forest types.

We conducted a three-year experiment in a subtropical forest, in which deadwood of four gymnosperms and four angiosperms were placed in unfertilized plots (control), N-addition plots (+N), P-addition plots (+P), and combined N- and P-addition plots (+NP). We aimed to investigate the mechanisms by which substrate nutrient content and nutrient addition interact to shape soil fungi colonization of deadwood in the field using wood from different host plant clades. Based on differences in nutrient availability between host plants (substrate) and environment (soil), we hypothesized that: (H1) By increasing resource availability, nutrient addition will alter the ecological strategies of deadwood-colonizing soil fungi, with a greater effect on fungal diversity and community composition in low-quality substrate (gymnosperms) than high-quality substrate (angiosperms). (H2) By reducing environmental filtering and resource heterogeneity, nutrient addition will promote stochastic processes of community assembly, resulting in higher α-diversity but lower β-diversity of deadwood-colonizing soil

fungi. (H3） As angiosperm wood has higher nutrient concentrations than gymnosperm wood, soil fungal taxonomic richness will be more important than wood nutrient content for shaping deadwood fungal communities in angiosperms than in gymnosperms.

2 METHODS

2.1 Study site and experimental design

The study was conducted at the Tiantong Forest Ecological Observation and Research Station (29°48'N, 121°47'E, 160 m.a.s.l.), in Zhejiang Province, China. The study sites have an average annual temperature of 16.2 ℃, with monthly mean air temperatures varying from 4.2 ℃ in January to 28.1 ℃ in July. The area receives an average annual precipitation of 1374 mm, with 35-40% of the total annual rainfall concentrated between May and August. The terrain in the area is primarily composed of low mountains and hills. The soils in this region are mainly classified as silty clay loam, with a pH range between 4.4 and 5.1 and fall under Ferric Acrisols according to the FAO classification, with a humus layer of approximately 5 cm deprh (Hu et al., 2024; Gao et al. 2014).

The experimental site is predominantly subtropical evergreen broadleaf forest, with some areas of mixed deciduous broad-leaved and evergreen forest. The experimental design of the study is consistent with a previous study by Hu et al. (2024) in the local area. Twelve 20 m × 20 m experimental plots were randomly established in a randomized block design within a representative area of forest at the Tiantong Station. Each plot was separated by a buffer strip > 5 m wide. Four treatments were randomly assigned to the plots within each block: control (CK, no addition), N-addition (N, 100 kg N ha^{-1} yr^{-1}), P-addition (P, 15 kg P ha^{-1} yr^{-1}), and combined N- and P-addition (+NP, 100 kg N + 15 kg P ha^{-1} yr^{-1}). There were three replicate plots for each treatment. Starting in November 2017, nutrients were applied at the start of each month. Nitrogen and P were applied by dissolving 0.952 kg NH_4NO_3 and 0.156 kg H_3PO_4 in 20 L of distilled water, which were uniformly sprayed on each experimental plot at ground level using a manual sprayer. The control plots were sprayed with an equal amount of distilled water. The rates of nutrient addition were based on empirical data for N and P deposition in the region (Du et al., 2016). A greater amount of P, relative to N, was added to overcome sorption of P to soil

minerals and enhance P availability to plants and microbes (Wright et al. 2011; Zheng et al. 2017). The treatments increased the local N deposition by 2.5 times (from 40 kg ha^{-1} yr^{-1} to 100 kg ha^{-1} yr^{-1}) and the P deposition by 6 times (from 2.5 kg ha^{-1} yr^{-1} to 15 kg ha^{-1} yr^{-1})(Zhu et al. 2016). To prevent subsurface and overland flow of water into the plots, the four sides of each plot were enclosed by PVC boards inserted into the soil to a depth of 1.0 m and height of 0.5 m above the ground.

Eight tree species that are abundant in subtropical China were selected for the study, comprising four angiosperms: *Schima superba*, *Castanopsis fargesii, Michelia maudiae*, and *Liquidambar formosana*; and four gymnosperms: *Pinus massoniana*, *Cunninghamia lanceolate*, *Pseudolarix amabilis*, and *Cryptomeria fortune*. All wood samples were obtained from a common even-aged plantation, except for *Castanopsis fargesii*, which was from a non-plantation forest. In November 2017, 1-m long stem sections were cut from 12 individuals per species, choosing stem sections with uniform diameter across the 1-m length, and with similar diameters among species. The mean diameters of the stem sections were 13.52±0.29 cm for angiosperms and 13.80±0.17 cm for gymnosperms. One freshly cut stem section per species was promptly placed at a random location within each of the experimental plots (Figure S1). Thus, the study comprised 96 stem sections from eight tree species, subjected to four nutrient treatments, with three replicates for each species × nutrient combination.

We collected deadwood and soil samples from each plot in October 2020, three years after placing the stem sections in the plots. To determine wood properties and microbial communities in the decaying stem sections, discs (3-cm thick) were cut from one end of a stem section per species and plot, placed in self-sealing bags, and transported to the laboratory in a cooler. An electric drill with a disinfected 8-mm diameter drill bit was used to collect samples from the sapwood and heartwood, and the drill was sterilized with ethanol between samples (van der Wal et al. 2014). At least 20 drill holes were made in each disc and if bark was present, it was also ground and sampled. Woodchip samples used for chemical property analysis were further ground, passed through a 60-mesh sieve, and stored at 4°C until analysis, while samples for microbial analysis were stored at -80°C until analysis. A wedge comprising c. 1/8 of the total disc was taken from each disc for density and moisture content analysis. To determine soil microbial community composition, three soil samples were taken from the topsoil layer (0-5

cm depth) adjacent to each stem section and pooled to one composite sample for a total of 96 samples. Before sampling, living vegetation was removed from the soil surface, and stones and roots were removed from the soil samples. The samples were sieved through a 25-mm mesh sieve and stored at -80℃ until analysis.

2.3 Measurement of physical and chemical properties of deadwood

To calculate the moisture content of the wood samples, we measured the wet weight of the wedges cut from each stem disk, oven-dried the wedges at 60℃ until constant weight, and then determined their dry weight. We determined the volume of the wedges by water displacement. Wood density was then calculated as the unit weight divided by the unit volume ($g \cdot cm^{-3}$). After crushing the samples, the C and N content of all samples was measured by combustion (CHN-2000, LECO Co. Ltd, USA). Phosphorus content was determined by the molybdenum-antimony colorimetric method after digestion with H_2SO_4.

2.4 Fungal sequencing and bioinformatic analysis

Total DNA in deadwood was extracted from 0.5-g subsamples using PowerSoil DNA Kits (Qiagen) and genomic DNA from soil was extracted from c. 0.5-g subsamples using FastDNA Spin Kits (MP Biomedicals, Solon, OH, USA). To target fungi, we amplified the ITS1 region using the primer set ITS5-1737F (5'-GGAAGTAAAGTCGTAACAAGG-3') and ITS2-2043R (5'-GCTGGTTCTTCATCGATGC-3') for both soil and wood samples (Innis et al. 2012; Wang et al. 2022). All PCR reactions were carried out using 15 μl of Phusion® High-Fidelity PCR Master Mix (New England Biolabs), 0.2 μM of forward and reverse primers, and *c.* 10 ng template DNA. Amplification was performed under the following conditions: initial denaturation at 98°C for 1 min, followed by 30 cycles of denaturation at 98°C for 10 s, annealing at 50 °C for 30 s, extension at 72°C for 30 s, and a final extension at 72°C for 5 min.

Amplicons from triplicate reactions were pooled together for each sample and subjected to electrophoresis detection in a 2% (w/v) agarose gels. PCR products were mixed thoroughly and using the Qiagen Gel Extraction Kit (Qiagen) for purification. The purified PCR amplicon products were sequenced on the Illumina NovaSeq (250-bp paired-end reads) platform (Illumina Inc., San Diego, USA) at Novogene Bioinformatics Technology Co., Ltd. (Beijing,

China). We used FLASH（V1.2.7, http://ccb.jhu.edu/software/FLASH/）to join reads in each sample (Magoč and Salzberg 2011), and strict filtering and quality control procedures were performed in QIIME (V1.9.1, http://qiime.org/scripts/split_libraries_fastq.html) (Bokulich et al. 2013). The Uparse software (Uparse v7.0.1001, http://www.drive5.com/uparse/) was then used to cluster the quality-filtered reads from each sample into Operational Taxonomic Units (OTUs), using a 97% sequence identity cut-off (Edgar 2013), following the recommendations of Tedersoo et al. (2022). To eliminate the influence of uneven sample sequencing depth on diversity statistics, the OTU table was rarefied to the minimum sequence number of each sample. After rarefaction, the sequencing depth was standardized to 28,973.

The OTUs were classified against the UNITE databases for fungi (Kõljalg et al. 2013) and we calculated deadwood colonization by soil fungi following Mäkipää et al. (2017) and Purahong et al. (2019) by identifying 'shared' OTUs that were detected in both the deadwood and the adjacent soil samples. The ecological strategies and functional guilds of shared OTUs was determined using FungalTraits annotation (Põlme et al. 2020). In order to avoid over-interpretion, we only retained taxa for which the classification into fungal functional guilds was 'highly probable' or 'probable'. We considered *Basidiomycota* as *K*-strategists (oligotrophs), while *Ascomycota* and *Mortierellomycota* were considered *r*-strategists (copiotrophs; Chen et al. 2022). Throughout, we refer to fungal groups and taxa that occurred in both deadwood samples and adjacent soil samples as 'shared'.

2.5 Calculations and Statistical analyses

All calculations and data analyses were conducted in R version 4.2.2 (R Core Team 2022). First, phylogenetic distributions and relative abundances of fungal taxa were constructed using the ggtree package (Yu et al. 2017). We then examined the differences in relative abundance between treatments within the same host plant clade using Kruskal-Wallis tests followed by Dunn's test for multiple comparisons (*Kruskal.test* function in the rstatix package; Kassambara 2021). To assess the diversity and taxonomic richness of the shared fungal taxa, α-diversity was calculated using OTU richness (henceforth 'richness') and phylogenetic diversity. Fungal β-diversity was estimated based on Bray-Curtis distances between deadwood samples. To

evaluate the effects of nutrient treatment, host plant clade (angiosperm or gymnosperm) and their interaction on the α-diversity of shared taxa, we used non-parametric two-way analysis of variance (ANOVA) using the *scheirerRayHare* function in the companion package (Mangiafico 2016). We then examined the differences in α-diversity between treatments within the same host plant clade using Kruskal-Wallis tests followed by Dunn's test for multiple comparisons (*Kruskal.test* function in the rstatix package). To assess whether fungal communities differed among treatments and host plant clades, we performed principal coordinate analysis (PCoA; *pcoa* function in the vegan package; Oksanen 2019) to visualize the shared fungal community, and then tested differences among species and nutrient addition treatments using permutational multivariate analysis of variance (PERMANOVA; *adonis* function in the vegan package; Oksanen 2019). The Bray–Curtis dissimilarities of shared fungal communities between angiosperms and gymnosperms or among the treatments were examined using Wilcoxon rank-sum tests, performed using the *wilcox.test* function in the stats package in R (Bolar 2019). We determined indicator species for N and P using a correlation-based analysis in the indicspecies package (De Cáceres et al. 2010). OTUs with significant differences in abundance between nutrient addition treatments and controls (at a false discovery rate corrected p-value < 0.05) were considered to be responsive to nutrient addition and therefore an indicator species for the added nutrient.

To predict the influence of deadwood physical and chemical properties (deadwood C, N and P content, wood density and moisture content) and soil fungal diversity on the α-diversity of the shared fungal community for different tree clades, we used Random Forest (RF) analysis for all nutrient addition treatments under each tree clade. The importance of explanatory variables was estimated based on their percentage mean squared error (MSE%), where higher MSE% indicates greater explanatory power (Breiman 2001). The significance of the model and the cross-validated R^2 were evaluated using 1,000 permutations of the response variable with the A3 package (Fortmann-Roe 2013). Additionally, the rfPermute package (Archer 2018) was used to assess the importance of each predictive variable for the corresponding response variable based on 800 trees. To test the relationships between environmental variables and shared fungal community structure of different tree clades, we then used Mantel tests (*mantel* function in the vegan package) for all nutrient addition treatments under each tree clade. To

determine whether fungal ecological strategy affected deadwood colonization, we used linear models (*lm* function) to assess the relationships between shared fungal richness to the richness of soil *r*- or *K*-strategists.

3 RESULTS

The chemical and physical properties of deadwood differed significantly between gymnosperms and angiosperms, whereby angiosperm wood had lower C content, higher N and P content and thus a lower C:N, C:P and N:P ratios than gymnosperm wood (Figure 1). Wood density did not differ significantly between the two clades, but angiosperm wood had higher water content than gymnosperm wood (Figure 1).

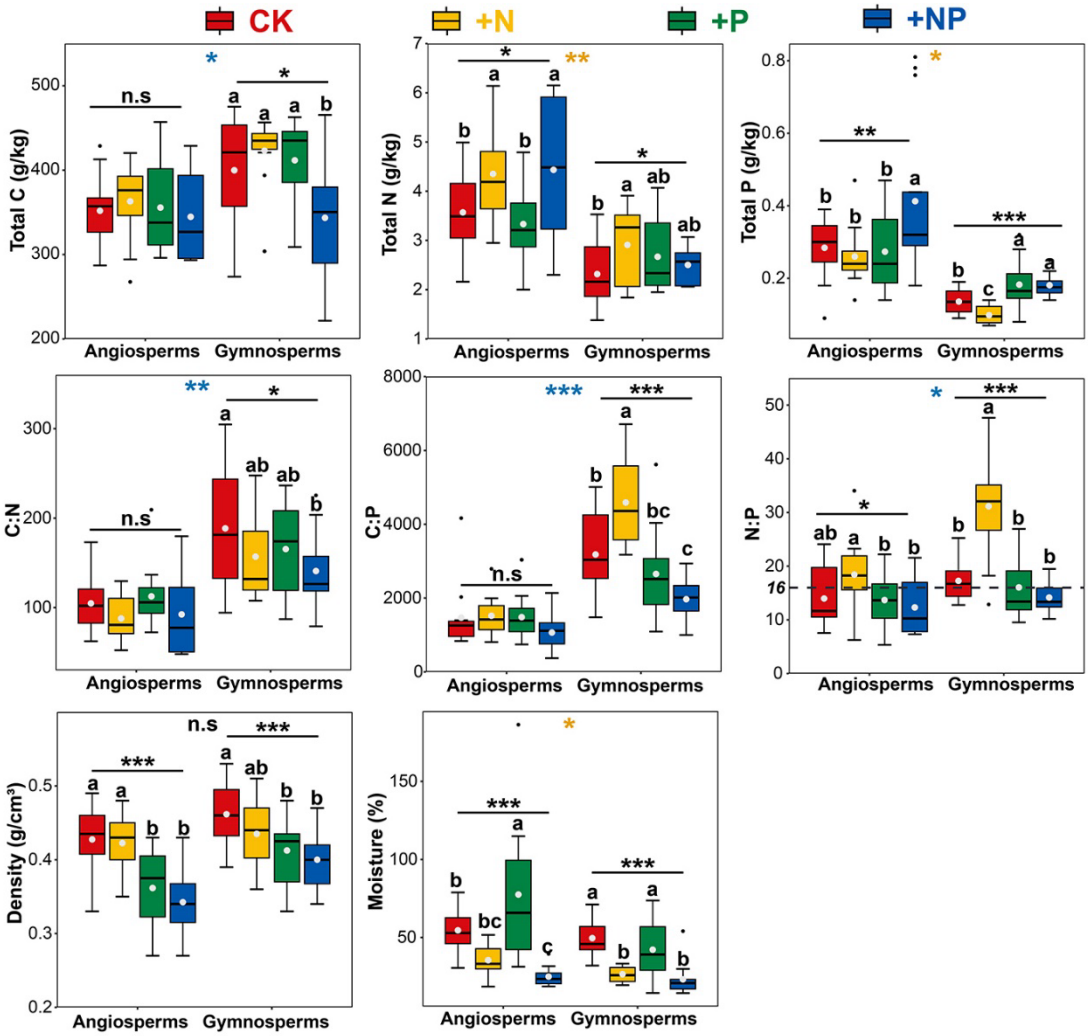

Figure 1 Properties of angiosperm and gymnosperm deadwood after three years of decomposition in nutrient addition plots, where CK, +N, +P, and +NP represent control, nitrogen addition, phosphorus addition, and combined nitrogen and phosphorus addition, respectively. Yellow asterisks indicate the significantly high values in、angiosperms, blue asterisks indicate the significantly

high values in gymnosperms. Asterisks indicate the significance of differences between host tree clades, where n.s is $p > 0.05$, * is $p < 0.05$, ** is $p < 0.01$, and *** is $p < 0.001$); different lower-case letters indicate significant differences between nutrient treatments at $p < 0.05$.

Nutrient addition had variable effects on wood nutrient and carbon content, depending on the added nutrient and the tree clade (Figure 1; Supplementary Results). Interestingly, P-addition influenced wood density in both tree clades, as wood density was lower in +NP and +P plots compared to controls (Figure 1). By contrast, N-addition appeared to reduce wood water content, as angiosperm and gymnosperm wood water content was lower in +N and +NP compared to controls (Figure 1).

3.1 The composition of shared fungal communities

Soil was the main source of fungal colonizers in deadwood across all nutrient treatments (Figure 2A). Across all 192 samples (96 soil and 96 wood), a total of 8,306 OTUs were obtained. Of the 3370 OTUs identified in deadwood, 1302 (38.6%) were shared taxa that occurred in both deadwood and adjacent soil samples. The percentage of shared fungi was higher in angiosperms (38.1% ~ 47.3%) than in gymnosperms (26.5% ~ 36.5%) and nutrient addition reduced the importance of soil as a source of fungi in both angiosperm and gymnosperm deadwood (Figure 2A). However, whereas the proportion of shared fungi in angiosperms was lowest in +P plots (9.2% lower than in the controls), the proportion of shared fungi in gymnosperms was lowest in +NP plots (10.0% lower than the controls; Figure 1A).

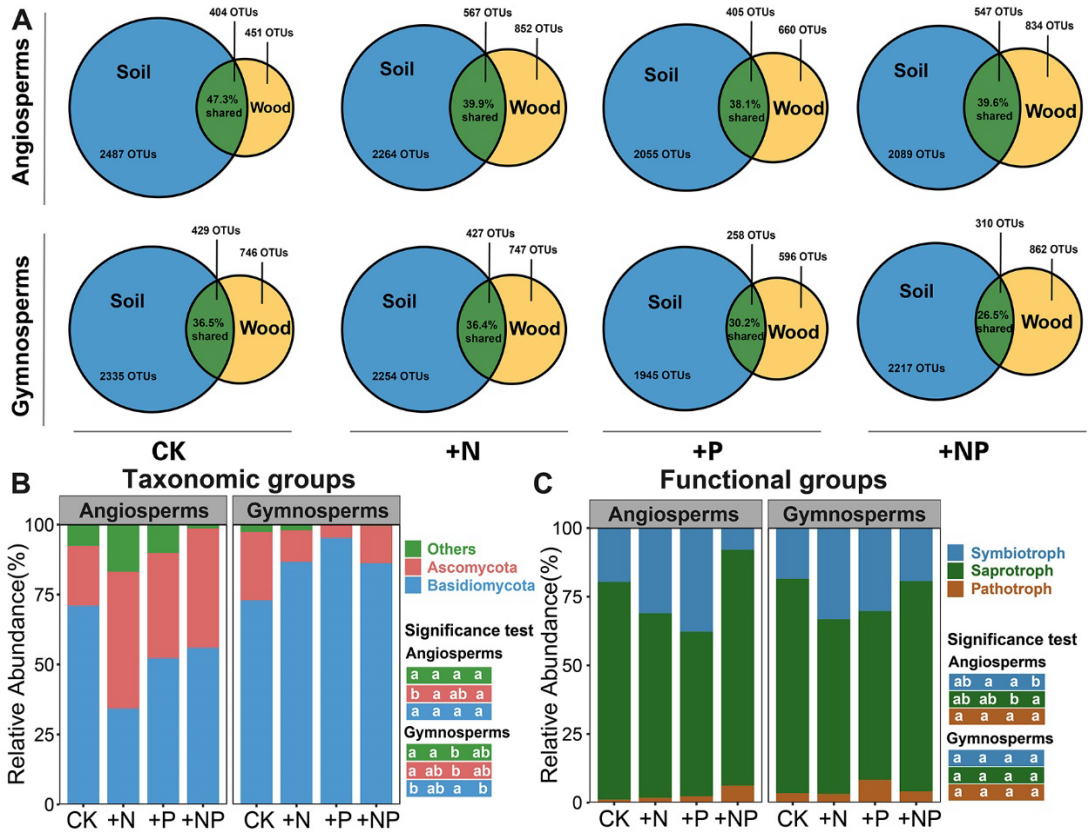

Figure 2 Fungal communities in soil and angiosperm or gymnosperm deadwood in nutrient addition plots in a subtropical forest, showing **(A)** Unique and shared operational taxonomic units (OTUs) in soil and deadwood fungal communities; **(B)** The relative abundance of taxonomic groups and (C) The functional guilds of shared fungi. CK, +N, +P, and +NP represent control, nitrogen addition, phosphorus addition, and combined nitrogen and phosphorus addition treatments, respectively. In (B), different lower-case letters indicate significant differences at $p < 0.05$ among nutrient addition treatments and host tree clades for each taxonomic group. In (C), the text colour for each guild corresponds to the trophic mode.

Ascomycota and Basidiomycota dominated the shared fungal community in both gymnosperms and angiosperms (Figure 2B), but their relative contribution was influenced by nutrient addition. In angiosperms, the proportion of Ascomycota in deadwood was significantly higher in N-addition (+N and +NP plots; 48.9% and 42.6%) compared to controls (21.4%; $p < 0.05$), whereas in gymnosperms, the proportion of Basidiomycota was significantly higher in +P plots (95.2%) compared to controls (72.9%; $p < 0.05$). Functional analysis of the shared fungal communities revealed that they were dominated by saprotrophs in both angiosperms (70.75%) and gymnosperms (68.95%; Figure 2C, Table S1), including wood and dung

saprotrophs but not litter saprotrophs (Table S1). Besides saprotrophs, the most common fungal functional groups were ectomycorrhizal fungi and plant pathogens (Figure 2C; Table S1).

3.2 Ecological strategies of deadwood fungal communities

Overall, the soil fungal community was dominated by *r*-strategists (copiotrophic taxa) but the deadwood fungal community and shared fungal community were dominated by *K*-strategists (oligotrophic taxa; Figure 3A; Figure S2). In the shared fungal community, the relative abundance of *K*-strategists was greater in gymnosperms than in angiosperms (Figure 3A). However, the relative abundance of shared *K*-strategist fungi was also influenced by nutrient addition. In angiosperms, the relative abundance of *K*-strategists was lower in +N plots (41.2%) compared to the controls (76.8%; Figure 3A). By contrast, in gymnosperms, the relative abundance of *K*-strategists was higher in +P plots (95.3%) compared to the controls (74.9%; Figure 3A). These shifts in the abundance of shared *K*-strategist fungi were reflected in the proportions of fungal colonizers from the soil. In angiosperms, the colonization of deadwood by *K*-strategist soil fungi was lower in +N plots, where the relative abundance of shared *K*-strategists was 54.8% compared to 76.7% in the controls. In gymnosperms, the colonization of deadwood by *K*-strategists from the soil was higher in P-addition plots, with 93% shared taxa, compared to the controls with 83.2% shared taxa (Figure 3B).

3.3 Effect of nutrient addition on shared fungal diversity

The presence of deadwood did not significantly alter the soil microbial community (Figures S3 - 4). However, the diversity of shared fungal communities differed among host tree clades and nutrient treatments (Figure 4A, B; Figure S5), indicated by a significant interaction between nutrient addition and host plant clade on shared fungal α-diversity (OTU richness: $p = 0.007$, $df = 3$, H = 12.02, and phylogenetic diversity: $p = 0.004$ $df = 3$, H = 13.15; Figure 4A, B). Specifically, the α-diversity of shared fungal communities was higher in +N plots relative to controls in angiosperms, but lower in +P and +NP plots in gymnosperms (Figure 4A, B). However, host plant identity had a stronger influence on shared fungal communities than nutrient addition (PERMANOVA: Treatment: R^2=0.067, $p < 0.001$; Plant phyla: R^2= 0.094, $p < 0.001$, Figure 4C). Across all samples, the β-diversity of shared fungal communities was greater in all nutrient addition plots compared to controls, but the increase was greater with N-

addition (+N and +NP; Figure 4D). Within host plant clades, β-diversity in angiosperms was significantly lower in +N and +NP plots compared to the controls, whereas β-diversity in gymnosperms was lower than the controls in +N and +P plots, but higher in +NP plots (Figure 4E, F).

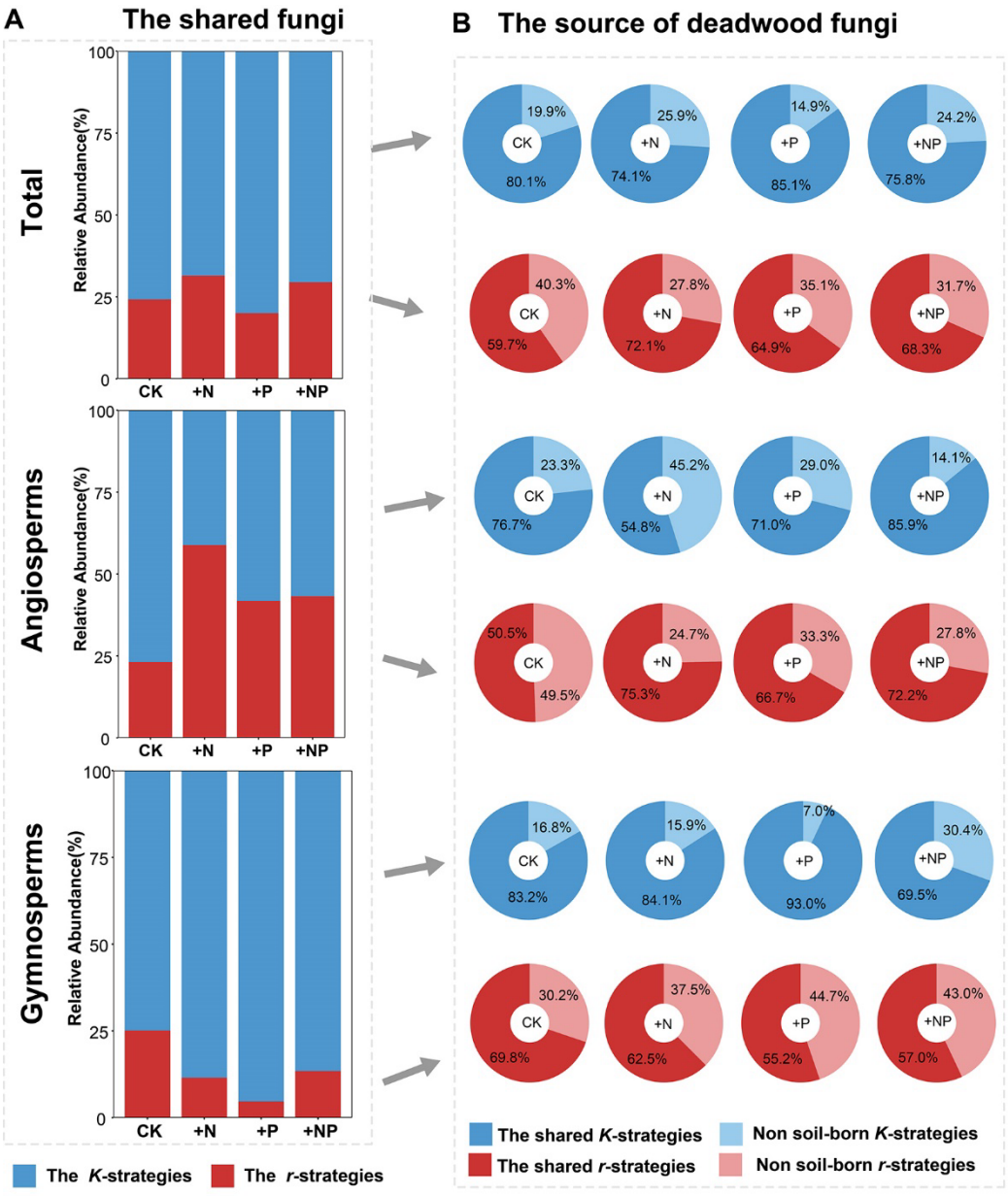

Figure 3 Ecological strategies and source of fungal communities in angiosperm or gymnosperm deadwood in nutrient addition plots in a subtropical forest, showing **(A)** the relative abundances of r- vs. K-strategist fungi and **(B)** the proportions of r- vs. K-strategist fungi shared between deadwood and soil, or found only in deadwood. CK, +N, +P, and +NP represent control, nitrogen addition, phosphorus addition, and combined nitrogen and phosphorus addition treatments, respectively.

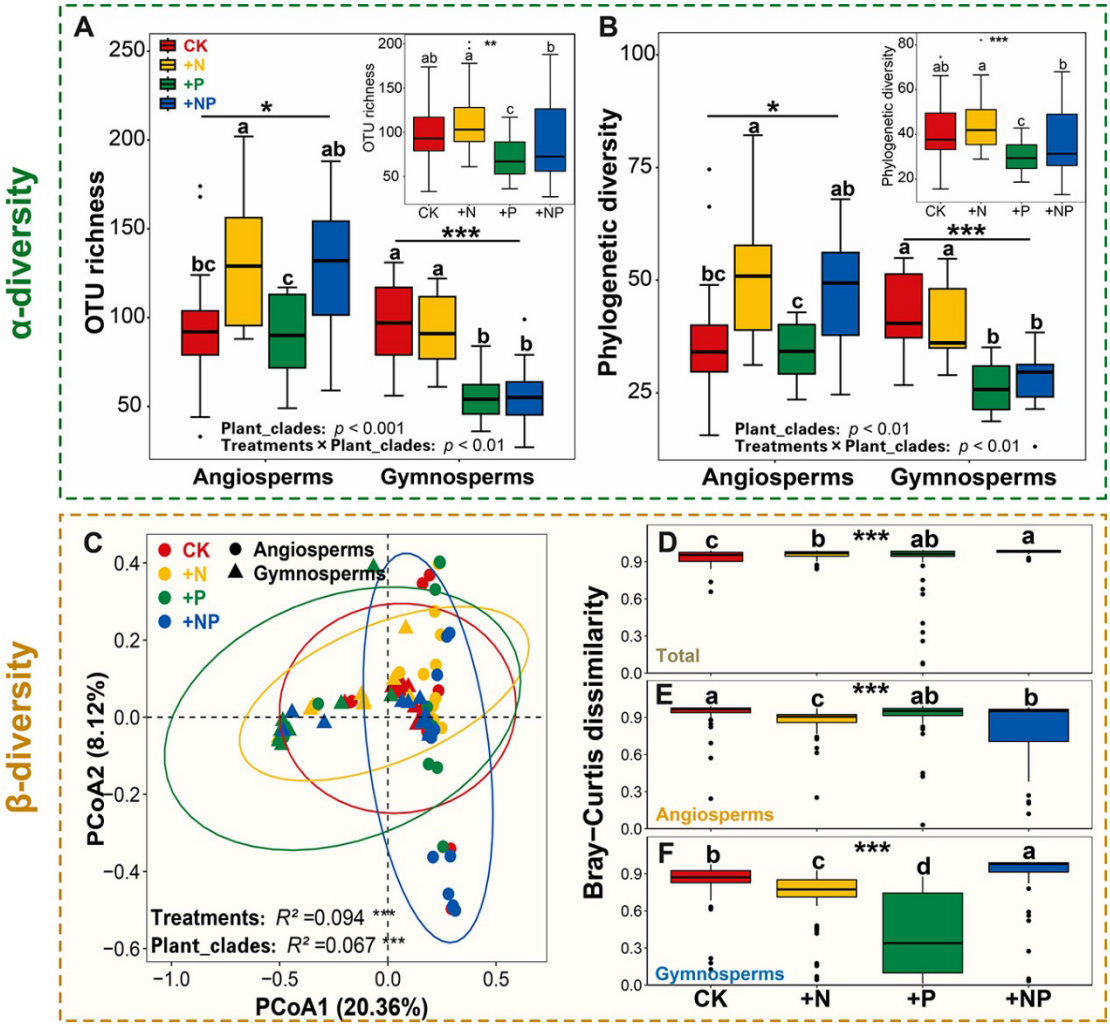

Figure 4 The *α*-diversity (A, B) and *β*-diversity (C-F) of shared fungi in deadwood across tree clades, and in angiosperms or gymnosperms in different nutrient treatments. (A) OTU richness and (B) phylogenetic diversity of the shared fungal community with the results of Kruskal-Wallis tests; (C) Principal Coordinate Analysis plot of the community structure with the results of multivariate analysis of variance; (D-F) Compositional variation among nutrient treatments based on Bray–Curtis distance with the results of Kruskal-Wallis tests for (D) both tree clades, (E) angiosperms and (F) gymnosperms. CK, +N, +P, and +NP represent control, nitrogen addition, phosphorus addition, and combined nitrogen and phosphorus addition, respectively. Asterisks indicate significant differences between tree clades, where * is at $p < 0.05$, ** is at $p<0.01$, and *** is at $p < 0.001$; different lowercase letters indicate significant differences among nutrient treatments.

3.4 Fungal indicator species of nutrient additions

Shared fungi were more sensitive to nutrient addition in angiosperm deadwood compared to gymnosperm deadwood. In angiosperms 84 OTUs (8.2% of shared fungal OTUs; Figure 5A)

were considered indicator species for nutrient addition compared to 56 OTUs in gymnosperms (7.4% of shared fungal OTUs; Figure 5A). Accordingly, overall community stability of shared fungi was lower in angiosperms than in gymnosperms (Figure S6). Indicator species were mostly composed of Ascomycota in angiosperms (49 OTUs; 58.23% of indicator OTUs;) and gymnosperms (30 OTUs; 53.6% of indicator OTUs;). Additionally, in both clades, nutrient-sensitive indicator species were mainly pathotrophs, saprotrophs and symbiotrophs (Figure 5B).

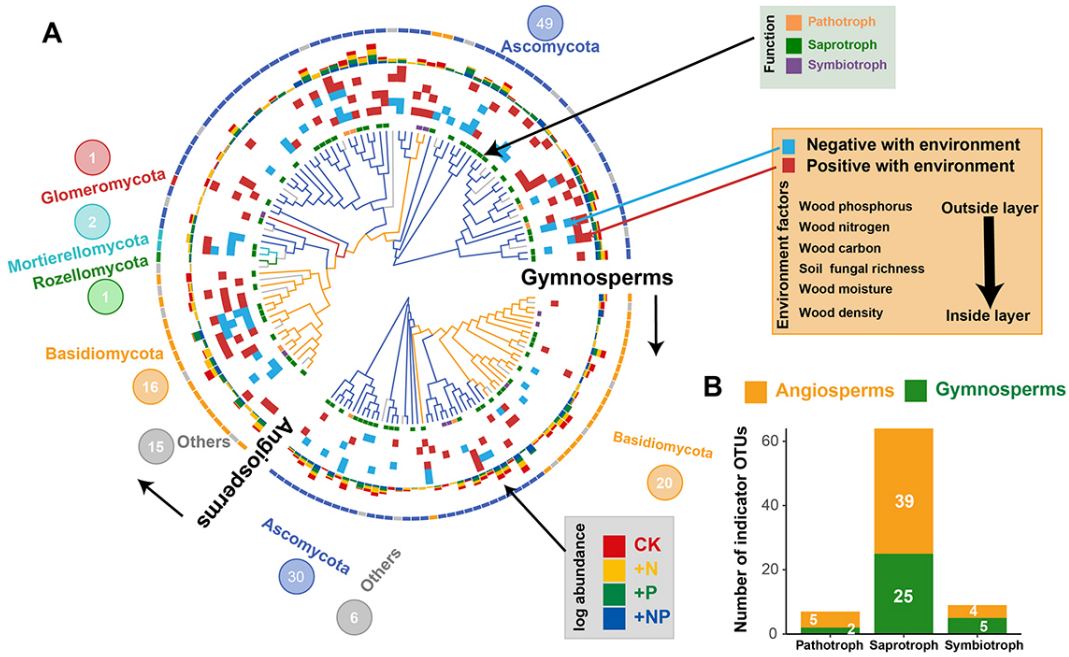

Figure 5 Response of indicator fungal species to nutrient addition in angiosperm and gymnosperm deadwood, showing (A) Soil fungal phylogenetic diversity, where colors of the outermost ring (first ring) correspond to individual phyla of the phylogenetic tree. The bars of the second ring represent the change in OTUs in response to nutrient addition as log abundance of each OTU; the bars of the third ring represent the relationships between OTU abundance and deadwood physicochemical properties or soil fungal diversity (from inner to outer rings: wood density, wood moisture, soil fungal richness, wood carbon, wood nitrogen, wood phosphorus), positive correlations are shown as red and negative correlations are shown in blue; the bars of the innermost ring represent the trophic mode assigned to OTUs. (B) The number of OTUs belonging to specific trophic modes.

3.5 Environmental filtering shape deadwood fungal communities

Environmental filtering played a strong role in shaping fungal colonization of deadwood (Figure S7). Across all samples, the α-diversity of shared fungal communities was best predicted by soil fungal species richness (r = 0.411, p = 0.009) and wood N concentrations (r

= 0.435, p = 0.009; Figure 6A), whereas the β-diversity of shared fungal communities was best predicted by wood N and P concentrations (r = 0.115, p = 0.002 and r = 0.169, p = 0.001, respectively). However, the main predictors of fungal diversity in deadwood differed between tree clades.

In angiosperms, the most important predictors of shared fungal diversity in deadwood were wood N (r = 0.589, p = 0.009) and C concentration (r = -0.440, p = 0.009), and soil fungal OTU richness (r = 0.280, p = 0.029; Figure 6B), whereas the most important predictors for shared fungal community composition were wood P (r = 0.185, p < 0.001) and N concentration (r = 0.117, p < 0.001; Figure 6D, Table S2). In gymnosperms, both shared fungal diversity and community structure were best predicted by soil fungal richness (r = 0.489, p = 0.009 and r = 0.143, p < 0.001, respectively) followed by wood P concentration (r = -0.353, p = 0.029 and r = 0.096, p = 0.002, respectively; Figure 6C, D, Table S2). Finally, regression analysis showed that shared fungal OTU richness in angiosperms increased with the richness of the *r*-strategist fungi in the soil, whereas shared fungal OTU richness in gymnosperms increased with the richness of both the *r*- and K-strategist fungi in the soil (Figure 7).

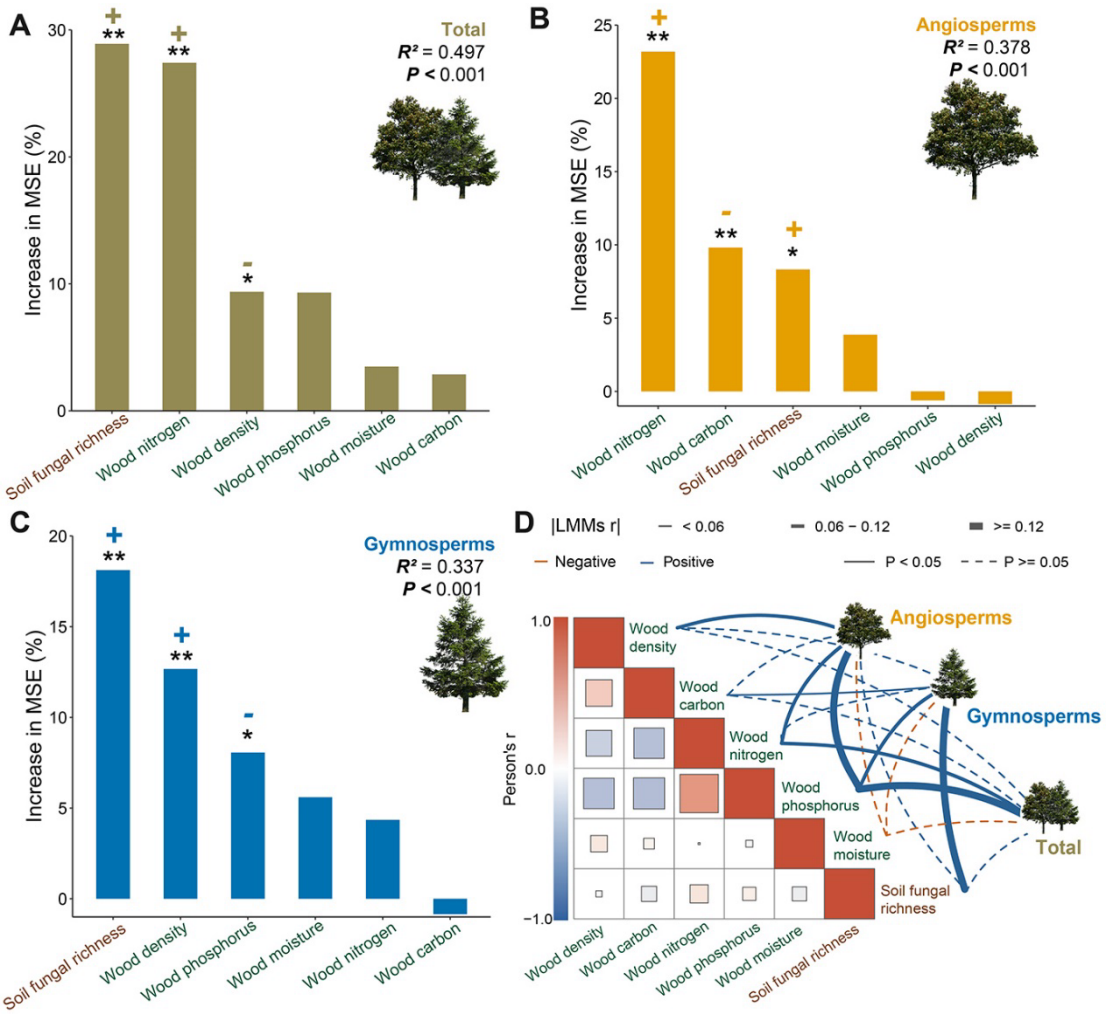

Figure 6 Relationships between shared fungal richness (A-C) or community structure (D) and deadwood physicochemical properties or soil fungal diversity. The bar charts in A-C show the importance of each predictor based on Random Forest analysis, where MSE is mean square error for shared fungal richness of angiosperms (A), gymnosperms (B), and both tree clades (C). The + and – signs refer to positive and negative effects of soil properties or wood physiochemistry on OTU richness based on Pearson correlation coefficients, and significance levels are indicated by * for $p < 0.05$ and ** for $p < 0.01$. In (D) solid lines denote significant correlations between shared fungal community composition and each predictor, assessed using Mantel tests, and the width of the lines correspond to Mantel's r statistic for the corresponding distance correlations. Pairwise comparisons of environmental factors are shown on the left, where the size of squares indicates the strength of relationship between predictors, where red indicates a positive correlation and blue indicates a negative correlation.

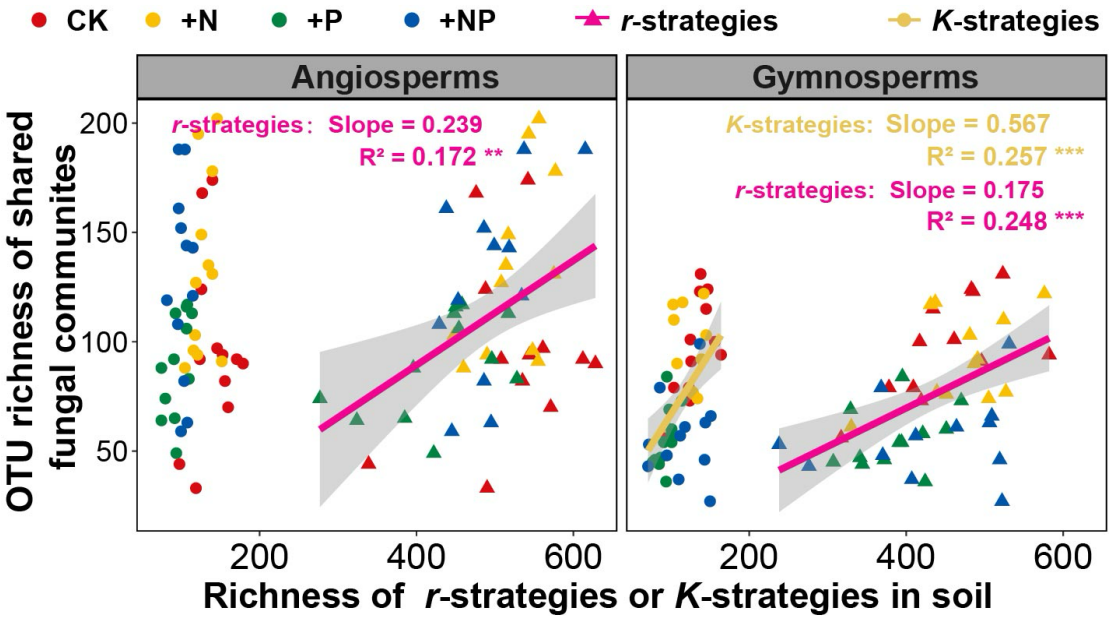

Figure 7 Relationships between the soil fungal functional group diversity and the diversity of the shared fungal community in deadwood, expressed as OTU richness. The significance of a relationship was determined by linear models and is indicated by asterisks, where ** is $p < 0.01$ and *** is $p < 0.001$. Relationships are shown across nutrient addition treatments, where CK, +N, +P, and +NP represent the control, nitrogen addition, phosphorus addition, and combined nitrogen and phosphorus addition, respectively.

4 DISCUSSION

This study demonstrated that soil fungal colonization of deadwood differed between gymnosperms and angiosperms and was influenced by nutrient addition. Our findings partly supported our first hypothesis, as nutrient addition affected the shared fungal community, but the effect depended on both host tree clade and the added nutrient. Our results were also not fully consistent with the second hypothesis, as the changes in α-and β-diversity of fungal colonizers differed between angiosperm and gymnosperm wood, and depended on the added nutrient. Finally, contrary to our third hypothesis, the taxonomic richness of the soil fungal community played a more important role in the colonization of gymnosperms than angiosperms. Here, we discuss the possible mechanisms by which nutrient availability influences the colonization of deadwood by soil fungi, and how these mechanisms differ between ecological strategies of fungi and host plants.

4.1 Host plant clade regulates the effect of nutrient addition on fungal colonization

The greater influence of N-addition on the shared fungal community in angiosperm deadwood but of P-addition in gymnosperms (Figure 4A, B, E, F) suggests that soil fungal colonizers might be N-limited in angiosperms wood and P-limited in gymnosperm wood. Previous research suggests that microbial N:P should be 16:1 under balanced conditions, with deviations indicating nutrient limitations (Isanta-Navarro et al. 2022; Kafri et al. 2016; Lpololadze 2019). In our study, we observed higher N:P ratios in gymnosperm wood (17:1) compared to angiosperm wood (14:1) without nutrient additions (Figure 1), so our findings align with the Growth Rate Hypothesis, emphasizing that microbial requirements for P are prioritized over N (Elser et al. 1996; Elser et al. 2000). Notably, co-addition of N and P neutralized the impacts observed in response to individual additions of these nutrients on colonization. (Figure 2, 3). While N:P ratios to indicate nutrient limitation must be used with caution (Rosinger et al. 2022), our study nonetheless implies that the intrinsic N:P ratio of deadwood may regulate the influence of added nutrients on fungal colonization.

In angiosperm deadwood, the strong response of the shared fungal community to N- and combined N- and P-addition (Figure 4A, B) is consistent with the stimulatory effect of N on fungal diversity in leaf litter in a lowland tropical forest (Kerekes et al. 2013) but in stark contrast with the negligible effect of N-addition on wood-decomposer fungi in temperate forest (Purahong et al. 2018a). Nutrient limitations can be more intense in tropical and subtropical regions compared to boreal and temperate areas (Kerekes et al. 2013; Santiago et al. 2012), so alleviating this constraint by adding nutrients may boost fungal diversity. The strong relationship between shared fungal richness and angiosperm wood N concentrations demonstrates the importance of limiting nutrients for wood decomposer fungi (Figure 6B). In deadwood with lower N: P such as angiosperms, fungi may require additional N for protein synthesis (Sinsabaugh et al. 2008). Consequently, an external N supply boosts fungal colonization and taxonomic richness (Purahong et al. 2018b; Rozmoš et al. 2022), which in turn could result in faster decomposition rates (Yang et al. 2021). By contrast, in gymnosperm deadwood, the overriding effect of P-addition upon the shared fungal community can be explained by the high P requirement for fungal growth (Elser et al. 1996; Elser et al. 2000; Isanta-Navarro et al. 2022), and the lower P-concentrations gymnosperm wood compared to

angiosperm wood.

Interestingly, the lower β-diversity of the shared fungal community in gymnosperm wood in the P-addition plots and in both tree clades in the N-addition plots indicates homogenization of the community when nutrient limitation is alleviated (Chalcraft et al. 2008; Liu et al. 2021a). Previous work has suggested that high nutrient availability can reduce bacterial interaction strength and weaken community stability (Ratzke et al. 2020; Figure S8). Thus, the lower co-occurrence and diversity of shared fungi we observed in gymnosperm deadwood in response to P-addition (Figures 4; Figure S8) might be attributed to increased negative interactions, which exclude certain fungal species from the community (Ma et al. 2022). However, in angiosperm wood, co-occurrence and α-diversity of shared fungi was higher in N-addition plots. The distinct effect of nutrient addition on shared fungal diversity and co-occurrence in angiosperms and gymnosperms, respectively, was reflected in the abundance of *K*-strategist fungi (Figure 3). Thus, changes in the functional composition and ecological strategies of the shared fungal community likely determine the overall patterns in diversity and interaction strength in response to the addition of limiting nutrients.

4.2 Fungal ecological strategies mediate soil fungal colonization of deadwood

We expected that environmental filtering would be weaker in nutrient-rich substrates, and that the shared fungal community in angiosperm deadwood would therefore be more strongly associated with the soil fungal species pool (Zhou and Ning 2017). However, in contrast to our third hypothesis, soil fungal richness was a much more important predictor of deadwood fungal communities in gymnosperms than in angiosperms (Figure 6B-D). This result is particularly surprising, as angiosperm deadwood generally had a higher proportion of shared fungi than gymnosperm deadwood (Figure 2).

The stronger relationship between soil fungal richness in gymnosperm deadwood is likely related to the particular importance of *K*-strategist fungi (Figure 3), which play a greater role in decomposing wood with low nutrient content (Iqbal et al. 2024). Gymnosperms contain guaiacyl lignin, which is more difficult to decompose than the syringyl lignin in angiosperms (Cornwell et al. 2009). In our study, gymnosperm wood had a significantly higher proportion of recalcitrant aromatic C and a significantly lower proportion of labile acetal C compared to

angiosperm wood (Table S3-4). The recalcitrant C of gymnosperms thus requires K-strategist fungi with slow growth rates and long-term resource utilization (Ho et al., 2017; Lu et al., 2023). Accordingly, the richness of the shared fungal community was related to the richness of *K*-strategist soil fungi in gymnosperms but not in angiosperms (Figure 7B). It is important to note that decaying wood also shapes the soil fungal community (Mäkipää et al. 2017). Wood, with its recalcitrant C compounds, tends to harbor many K-strategists, while nutrient-rich soils are often dominated by r-strategist fungi (Lustenhouwer et al. 2020; Fontaine et al. 2004). The recalcitrant compounds from gymnosperm wood could therefore have influenced the taxonomic richness of *K*-strategist fungi in the soil (Figure S2). By contrast, *r*-strategists rapidly utilize simple organic substances (Fontaine et al. 2004; Miki et al. 2010; Chen et al. 2016), have a short lifespan and rapid reproduction under favorable conditions and therefore have higher nutrient requirements (Fontaine and Barot 2005; Neill and Gignoux 2006; Fierer et al. 2007). Higher nutrient availability in angiosperm deadwood might therefore facilitate rapid colonization by *r*-strategist fungi (Leff et al. 2015, Fierer et al. 2012), reducing the importance of the soil fungal pool in the intermediate term. Although environmental filtering plays a key role in determining which fungi can survive in specific environments (Kraft et al. 2015), the final composition of fungal communities is also affected by interactions among fungi and their adaptability to specific habitats (Jiao et al. 2020). Our research suggests that the stronger connections between soil and deadwood fungal diversity in gymnosperm wood are explained by the importance of *K*-strategist fungi as decomposers of substrate with low nutrient content.

4.3 Linking fungal taxa to ecological functions

We found a range of functional guilds in the shared fungal community (Table S1), which reflects the importance of soil-deadwood connections for the transport of resources by fungal hyphae (Makipaa et al. 2017; Purahong et al. 2019). As expected, saprophytes dominated the shared fungal community in both angiosperms and gymnosperms (Figure 2C), but many saprophytes responded strongly to nutrient addition (Figure 5C, D). Whereas in angiosperms, nutrient addition resulted in new dominant saprophytic fungal species (Figure S9), in gymnosperms, nutrient addition led to the disappearance of previously dominant saprophytic

fungi (Figure S9). These distinct responses of dominant saprophytes to nutrient addition might differentially affect the decomposition of angiosperm and gymnosperm deadwood (Hoppe et al. 2016; Purahong et al. 2019). This may be related to competition between species. Nutrient addition promoted fungal competition in gymnosperm deadwood (Figure S8), and since aprophytic fungi are typically considered *r*-strategists, they may lose their competitive advantage under such conditions (Li et al. 2021).

It is noteworthy that the second most abundant trophic mode after saprotrophs was symbiotrophs (Figure 3; Table S1) and many symbiotrophs also acted as indicator species for nutrient addition in both angiosperm and gymnosperm wood (Figure 5B). Many mycorrhizas are also important decomposers (Talbot et al. 2008) but their role in decomposing organic matter is frequently overlooked (Talbot et al. 2008; Lindahl and Tunlid 2015). We found that mycorrhizal fungi were more predominant in gymnosperms than angiosperms in control plots, suggesting that mycorrhizas might play a greater role in the decay of gymnosperm wood, e.g. by active transport of nutrients required for decomposing recalcitrant C compounds (Makipaa et al. 2017, Hobbie and Hobbie 2006).

4.4. Implications for forest management

The importance of deadwood amount for forest diversity and C storage is now widely recognized in the management of both natural forests and plantations (e.g. Vitkova et al. 2018). However, our findings also suggest that differences in deadwood characteristics among tree clades or species could affect forest C storage by influencing the diversity of fungal decomposers. For example, although angiosperm wood had greater shared fungal richness, our results show that gymnosperm wood contributes to the functional diversity of decomposer fungi, which in turn affects important forest ecosystem functions such as soil C storage (Anthony et al. 2024). The strong relationship between soil *K*-strategists and shared *K*-strategist fungi we observed in gymnosperm wood could translate to distinct effects of host plant clades on soil carbon stabilization in forest ecosystems. *K*-strategist microbes can store more assimilated C in cells, promoting C stabilization and accumulation rather than conversion to atmospheric CO_2 release, which could play a crucial role in soil C sequestration in forest ecosystems (Lu et al., 2023; Duan et al. 2023). The replacement of some coniferous tree species

in China and Europe by resilient broadleaf species (Naudts et al. 2016; Sheng 2018) might therefore affect the contribution of deadwood to soil C storage. To maintain soil fungal diversity and C sequestration during deadwood decomposition, forest management should therefore consider inclusion of coniferous tree species that are suited to future climates (Naudts et al. 2016).

5 CONCLUSIONS

Our study fills knowledge gaps around wood decomposition by demonstrating that interactions between deadwood nutrient content and external nutrient inputs influence the colonization of deadwood by soil fungi. Importantly, differential effects of N- vs. P-addition on the diversity, stability and dominant species of the shared fungal community between tree clades indicate that nutrient additions through atmospheric deposition or fertilization are likely to have distinct effects on the decay of angiosperm vs. gymnosperm wood. The stronger connection between soil and deadwood fungi in gymnosperms compared to angiosperms, is likely related to the importance of *K*-strategist fungi for decomposing wood with low nutrient content and could influence soil C storage. Given the importance of wood decay for soil C sequestration in forest ecosystems, future studies should investigate how changes in the links between soil and deadwood fungal diversity will affect carbon sequestration or release during deadwood decomposition.

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