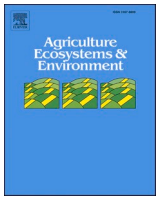
Agriculture, Ecosystems and Environment 410 (2026) 110553

Contents lists available at ScienceDirect

Agriculture, Ecosystems and Environment

journal homepage: www.elsevier.com/locate/agee



Cropland-to-planted forest conversion reconfigures soil microbial communities and shifts soil multifunctionality

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ARTICLE INFO

Keywords:
Cropland-to-planted forest conversion
Soil microbial communities
Network complexity
Soil multifunctionality
Croplands
Planted forests

ABSTRACT

Cropland-to-forest conversion is a widespread strategy for enhancing aboveground carbon sequestration and achieving carbon neutrality. However, the associated changes in soil multi-domain (bacteria, fungi, archaea) and multi-tiered (whole community, core abundant taxa, keystone taxa) microbial communities and their functions following the establishment of planted forests remain unclear. Leveraging a paired-site sampling, we collected 39 pairs of cropland and its adjacent planted forest soil samples across a major grain-producing region in Eastern China. By integrating high-throughput sequencing with network analysis, hierarchical partitioning, and piecewise structural equation modeling, we systematically compared differences in soil microbial community properties and assembly processes between croplands and adjacent planted forests converted from croplands, and elucidated the major factors influencing soil multifunctionality (SMF). Compared to planted forests, croplands showed higher bacterial and archaeal diversity and network complexity, but lower fungal network complexity. A positive correlation between microbial network complexity and diversity observed in croplands was absent in planted forests. The conversion also reconfigured keystone taxa and shifted the archaeal assembly process from a stochastic-deterministic balance to deterministic dominance. Soil pH was the primary factor influencing differences in soil microbial whole community between croplands and adjacent planted forests, whereas soil metallic elements predominantly explained the variations in keystone taxa. Significantly higher SMF was observed in croplands than in planted forests. In croplands, the diversity of archaeal keystone taxa, bacterial network complexity, and fungal community structure were the primary influencing factors of SMF. In contrast, fungal community structure and archaeal network complexity played a major role in planted forests. Our findings demonstrate that cropland-to-planted forest conversion significantly reduces SMF and decouples the relationship between microbial diversity and network complexity, underscoring the importance of comprehensively assessing soil multi-domain and multi-tiered microbial communities for evaluating ecosystem multifunctionality and informing carbon sequestration strategies.

1. Introduction

The global imperative for carbon neutrality has spurred large-scale afforestation initiatives, among which the conversion of croplands to planted forests represents a widely implemented ecological strategy (Cheng et al., 2024; Ma et al., 2024; Yao et al., 2024). One notable example is the Grain for Green Program, an ecological restoration initiative that began in China in 1999, incentivizing the conversion of sloping or marginal croplands to forests or grasslands to mitigate soil erosion and land degradation (Chen et al., 2015). While such land-use transitions are known to enhance aboveground carbon sequestration, its impact on belowground ecosystems remains inadequately

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https://doi.org/10.1016/j.agee.2026.110553
Received 11 December 2025; Received in revised form 28 March 2026; Accepted 26 May 2026
Available online 2 June 2026

understood (Cheng et al., 2024; Ren et al., 2025). This is particularly true for the intricate relationships between soil microbial communities and soil multifunctionality (SMF). Such knowledge is critical, as soil biota play a fundamental role in sustaining multiple ecosystem functions and long-term carbon stability (Delgado-Baquerizo et al., 2016; Crowther et al., 2019; Philippot et al., 2024; Dang et al., 2025). Thus, a central question arises of whether the gain in aboveground carbon storage comes at the expense of belowground ecological processes. Particularly, how does the conversion of croplands to planted forests reconfigure soil microbial communities and alter SMF? Addressing this

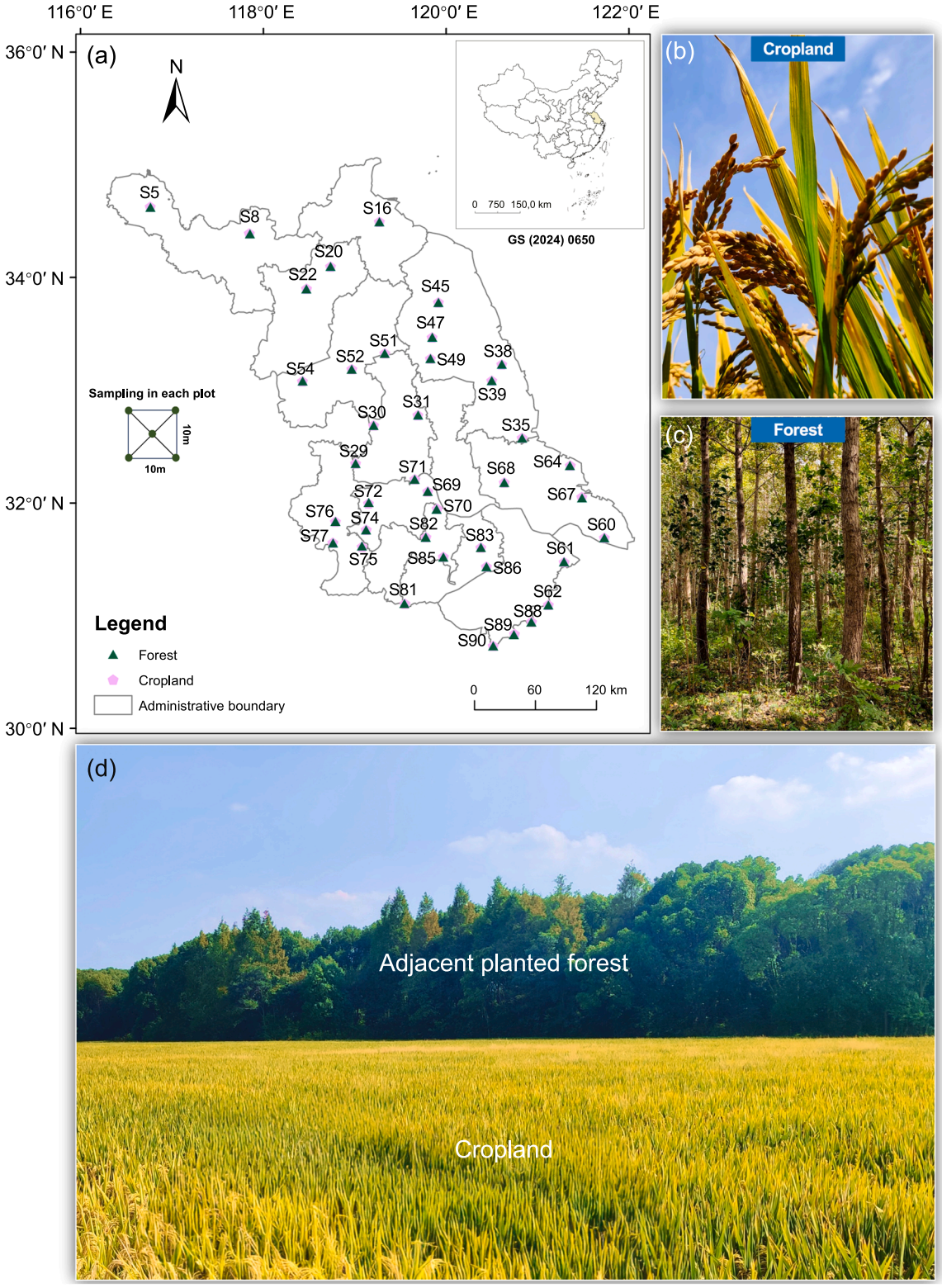

Fig. 1. Study area and site characteristics. (a) Geographical context and distribution of sampling points in the study area; (b) Close-up photograph of the cropland site; (c) Close-up photograph of the adjacent planted forest site; (d) Photograph illustrating the spatial proximity and boundary between the cropland and adjacent planted forest.

question is essential for elucidating the potential trade-offs between aboveground carbon sequestration goals and the maintenance of belowground ecosystem functioning.

Most previous studies on soil microbial communities have focused on the conversion of natural ecosystems to human-managed systems, particularly the transformation of native forests or grasslands to croplands or planted forests (Wang et al., 2021; Pan et al., 2024; Tong et al., 2025). These studies generally indicate that such conversion often reduces soil microbial diversity and alters community composition and structure (Vitali et al., 2016; Ding et al., 2024; Zhou et al., 2025). Notably, unlike the conversion of rice paddies or rice-wheat rotations to planted forests examined in this study, previous studies on cropland afforestation have mainly focused on uplands (Jiao et al., 2018; Zhong et al., 2020; Kong et al., 2022; Zhang et al., 2023). Furthermore, existing research has predominantly focused on bacteria or fungi (Zhong et al., 2020; Guo et al., 2021; Kong et al., 2022). This has resulted in the frequent omission of archaea, and even when multiple domains are considered, the analyses are often restricted to microbial diversity and composition (Jiao et al., 2018; Guo et al., 2021; Qi et al., 2025), neglecting other functionally critical properties such as microbial network topology and community assembly mechanisms (Wang et al., 2023b; Zhang et al., 2024a; Riddley et al., 2025). More importantly, few studies on cropland afforestation have analyzed microbial responses across soil multi-tiered microbial communities, including whole community, core abundant taxa (the top 10 most abundant taxa by relative abundance), and keystone taxa (critical nodes whose removal destabilizes network modules). This limited perspective hinders a comprehensive understanding of belowground ecological processes and fails to elucidate how these changes ultimately influence SMF.

Microbial networks can reveal potential interactions among microorganisms, and their topological properties, such as network complexity and modularity, serve as key indicators of microbial community functioning (Barberán et al., 2012; He et al., 2025b; Xiao et al., 2025). Furthermore, keystone taxa play a central role in maintaining network structure and ecosystem processes through their disproportionately large ecological influence (Banerjee et al., 2018; Qiao et al., 2024; Lu et al., 2026). Existing studies have revealed that forest-to-cropland conversion reduces key soil microbial clusters (Ding et al., 2024), whereas the conversion of grasslands to croplands enhances the network complexity of both soil fungal and bacterial communities (Xiao et al., 2025). The assembly of microbial communities is governed by both deterministic (e.g., homogeneous and heterogeneous selection) and stochastic processes (e.g., homogenizing dispersal, dispersal limitation, and drift) (Hubbell, 2011; Ning et al., 2019). For instance, previous research in the semi-arid region of China's Loess Plateau demonstrated that changes in topsoil nutrients after cropland-to-planted forest conversion can shift bacterial community assembly from deterministic to stochastic dominance (Kong et al., 2022). Despite these insights, direct comparisons of soil microbial network topology and keystone taxa between croplands and planted forests established on former croplands remain scarce. The extent to which the conversion of croplands to planted forests alters the balance between deterministic and stochastic processes remains unclear.

SMF is not determined by microorganisms alone, but rather emerges from complex interactions between soil properties and microbial community properties (Chen et al., 2022; Wang et al., 2023b; Hu et al., 2024). Soil properties establish an environmental matrix for survival and metabolism, directly filtering microbial taxa and supplying metabolic substrates, while microorganisms in turn modify and reshape the soil environment through their metabolic activities. Previous studies have confirmed that soil pH, total phosphorus (TP), soil organic matter, and soil water content (SWC) are key factors driving microbial community structure (Zhou et al., 2020; Lin et al., 2025). Soil microbial community composition, diversity, and network complexity significantly influence SMF (Wagg et al., 2014, 2019; Chen et al., 2023). Some studies have found that microbial network complexity can be a better predictor of SMF than diversity (Chen et al., 2022; Xiao et al., 2025), suggesting that network complexity serves as a key microbial trait mediating the relationship between primary productivity and multifunctionality during land-use change. However, contrasting evidence reports that microbial diversity outperforms network complexity in predicting multifunctionality in planted forests (He et al., 2025b). However, it remains unclear whether different tiers of microbial communities are driven by distinct environmental factors during the conversion of croplands to planted forests. Most critically, how changes in soil and microbial properties cascade to influence SMF remain poorly understood. Elucidating these underlying mechanisms is essential for accurately assessing the ecological outcomes of the Grain for Green Program and for understanding and predicting the impacts of management practices on ecosystem functions.

Eastern China, particularly the Yangtze River Delta region, characterized by intensive agriculture, urban expansion, and widespread afforestation, provides an ideal natural laboratory for investigating soil microbial community shifts (Liu et al., 2026). This landscape allows for paired sampling of croplands and adjacent former-cropland planted forests, offering a direct comparison to elucidate the effects of afforestation on soil microbial communities and their functions. We hypothesized that: (1) soil microbial community properties and assembly processes differed between croplands and adjacent planted forests due to variations in soil moisture and nutrient availability; (2) the positive correlation between microbial community diversity and network complexity observed in croplands was weakened or absent in planted forests; (3) the responses of microbial communities across different domains and tiers to soil properties differed between croplands and planted forests; and (4) the conversion of croplands to planted forests reduced SMF, and the factors influencing SMF differed between croplands and planted forests. To test these hypotheses, we examined paired cropland-planted forest soil systems using high-throughput sequencing of bacterial, fungal, and archaeal communities, combined with network analysis, hierarchical partitioning, and piecewise structural equation modeling. The specific objectives of this study were: (1) to compare the soil multi-domain (bacteria, fungi, archaea) microbial community properties (including diversity, composition, structure, and network topology), community assembly processes, and SMF between croplands and adjacent planted forests; (2) to quantify how soil properties (i.e., physicochemical properties and metallic elements) influence differences in multi-domain and multi-tiered (whole community, core abundant taxa, keystone taxa) microbial communities between croplands and adjacent planted forests; (3) to determine the relative importance of soil properties and microbial community properties for SMF and microbial network complexity between croplands and adjacent planted forests. Our results offer a transformative perspective for designing and managing global afforestation efforts. They provide the scientific basis for developing microbiome-guided soil management strategies that enhance SMF, safeguard soil health, and ultimately support climate change mitigation, adaptation goals, and carbon-neutral futures.

2. Materials and methods

2.1. Study region and field sampling

A paired-site design covering 39 cropland-planted forest sites was conducted in Jiangsu Province, Eastern China (Fig. 1). This region is a low-lying plain region characterized by a subtropical humid monsoon climate. The climate across the sampling area (116°49'–121°39' E, 30°78'–34°65' N) featured a MAT of 14.28–16.65 °C and a MAP of 730.91–1181.66 mm. A total of 78 soil samples (0–20 cm depth) were collected in October 2023 using a Latin Hypercube sampling design (Minasny and McBratney, 2006) and a five-point method (Mao et al., 2020). The 0–20 cm depth was selected because this topsoil layer represents the most active zone for soil biogeochemical processes, where land-use conversion from croplands to planted forests exerts the most

immediate and pronounced effects on soil properties and microbial communities (Zhong et al., 2020; Labouyrie et al., 2023; Zhang et al., 2023; Qi et al., 2025). Paired sampling was conducted for croplands (dominated by rice paddies or rice-wheat rotations) and adjacent planted forests (established 10–20 years ago on former croplands), with pairwise distances under 1 km (Fig. 1). Adjacent planted forests experienced lower anthropogenic disturbance than cropland soils. In the croplands, a mixed application of mineral and organic fertilizers was practiced. In contrast, the adjacent planted forests received mineral fertilization and irrigation only during the initial establishment phase, with minimal subsequent inputs. Additionally, the croplands underwent conventional tillage and fertilization annually during the sowing period.

The planted forests in our sampling area primarily consisted of *Populus* spp., *Betula* spp., *Cunninghamia lanceolata*, and *Zelkova serrata* (stand age approximately 15 ± 5 years). The dominant tree species in these stands is the *Populus* spp. The soils in our study have a long-term land-use history as paddy fields, dating back to at least the 1980s. The average textural composition of all cropland soils was 36.04% sand, 27.59% silt, and 36.37% clay, and that of all planted forest soils was 37.23% sand, 28.81% silt, and 33.96% clay, classifying both soil types as clay loam. According to the United States Department of Agriculture (USDA) Soil Taxonomy (Soil Survey Staff, 2022), both the cropland and planted forest soils are mainly classified within the order of Inceptisols. In the World Reference Base for Soil Resources (WRB; IUSS Working Group WRB, 2022), these correspond to Hydragric Anthrosols and Cambisols, respectively. All samples were transported to the laboratory within 6 h in insulated boxes with ice packs. Upon arrival, each soil sample was subdivided: one portion (10 g) was stored at –80 °C for molecular analysis, while the remainder was stored at 4 °C for the assessment of soil properties.

2.2. Soil properties analysis and calculation

The detailed methodologies for determining soil properties [e.g., soil organic carbon (SOC), dissolved organic carbon (DOC), particulate organic carbon (POC), mineral-associated organic carbon (MAOC), microbial biomass carbon (MBC), microbial necromass carbon (MNC), SWC, pH, total nitrogen (TN), ammonium nitrogen (NH_4^+-N), nitrate nitrogen (NO_3^--N), TP, available phosphorus (AP), total potassium (TK), available potassium (AK), electrical conductivity (EC), metallic elements (Ca, Mg, Mn, Cr, Cu), and soil texture (sand, silt, clay)], are described in the Supplementary Material.

2.3. DNA extraction, Illumina sequencing, and sequence processing

Genomic DNA was extracted from soil samples using the E.Z.N.A.® Soil DNA Kit (Omega Bio-tek, Norcross, GA, USA). DNA integrity was assessed by 1% agarose gel electrophoresis, while purity and concentration were determined using a NanoDrop 2000 spectrophotometer. Extracted DNA was stored at –20 °C until further use. The bacterial V3-V4 hypervariable region of the 16S rRNA gene (using primers 341 F and 806 R, sequences 5′−CCTAYGGGRBGCASCAG−3′ and 5′−GGACTACNNGGGTATCTAAT−3′), the archaeal V4-V5 hypervariable region of the 16S rRNA gene (using primers Arch519F and Arch915R, sequences 5′−CAGCCGCCGCGGTAA−3′ and 5′−GTGCTCCCCCGCCAATTCCT−3′), and the fungal ITS1 region (using primers ITS1F and ITS2, sequences 5′−CTTGGTCATTTAGAGGAAGTAA−3′ and 5′−GCTGCGTTCTTCATCGATGC−3′) were amplified in 20-μL reaction volumes, each in triplicate. The PCR system consisted of 4 μL of 5 × FastPfu Buffer, 2 μL of 2.5 mM dNTPs, 0.8 μL of each primer (5 μM), 0.4 μL of FastPfu Polymerase, and 10 ng of template DNA. After purification, amplicons were paired-end sequenced (2 × 250 bp) on an Illumina NovaSeq PE250 platform (Shanghai BIOZERON Co., Ltd).

Raw reads were processed using a multi-step pipeline. First, demultiplexing was performed based on barcode sequences, allowing zero mismatches for barcodes and up to two mismatches for primers. Reads containing ambiguous bases were discarded. Reads were then quality-filtered by trimming low-quality bases at the 3′ end using a 10 bp sliding window: when the average quality score within a window fell below 20, all subsequent bases were truncated. Reads shorter than 50 bp after quality trimming were discarded. Paired-end reads were assembled based on their overlap sequence, requiring a minimum overlap length of 10 bp and a maximum mismatch ratio of 0.2 in the overlapping region. Reads that could not be assembled were discarded (Liu et al., 2026).

Noise reduction and amplicon sequence variant (ASV) inference were performed using the DADA2 algorithm (Callahan et al., 2016). Briefly, quality filtering and trimming were performed with a maximum of two expected errors per read (maxEE = 2). Reads were then dereplicated, and error rates were learned from the data using the learnErrors function, which iteratively alternates between sample inference and error rate estimation until convergence. Following denoising, chimeras were detected and discarded using the "consensus" method (Callahan et al., 2016). This process generated amplicon sequence variants (ASVs) representing phylotypes with 100% nucleotide similarity, along with their representative sequences. After ASV inference, singletons and non-target sequences (mitochondria, chloroplasts) were removed.

Taxonomic classification was performed using the SILVA database (version SSU138.1) (http://www.arb-silva.de) for bacteria and archaea, and the NCBI-NT database (https://ftp.ncbi.nlm.nih.gov/blast/db/) for fungi, with the UCLUST algorithm at an 80% confidence threshold. All sequences are accessible in the NCBI Sequence Read Archive (SRA) under BioProject accessions PRJNA1280032 (bacteria), PRJNA1280037 (fungi), and PRJNA1280060 (archaea).

2.4. Microbial community structure, network topology properties, stability, keystone taxa, and assembly processes

We employed non-metric multi-dimensional scaling (NMDS) and analysis of similarities (ANOSIM) to assess the differences in soil microbial communities between croplands and adjacent planted forests. Network analysis was employed to decipher complex microbial interaction patterns. Specifically, co-occurrence networks were constructed for bacterial, fungal, and archaeal communities in both cropland and adjacent planted forest soils. Prior to network construction, microbial phylotypes with relative abundances below 0.005% were excluded (Liu et al., 2026). Pairwise Spearman correlations between ASVs were calculated, and only robust ($|r| > 0.50$) and statistically significant correlations (FDR-adjusted $P < 0.05$) were retained for network inference (Liu et al., 2026). The threshold ($|r| > 0.50$) is selected because it represents a balance between statistical robustness (capturing at least 25% shared variance) and network parsimony (filtering noise to reveal a clear, interpretable structure) (Liu et al., 2026). It ensures that the edges in the network represent moderate-to-strong relationships where the variables are genuinely and meaningfully associated. The resulting networks were visualized using Gephi (v0.10).

Key sub-network topology properties—including the number of nodes and edges, network density, average weight degree, clustering coefficient, and global efficiency—were extracted to characterize network structure. Finally, network complexity was quantified using the z-score mean method based on these topological metrics. Soil microbial community stability was assessed using the average variation degree (AVD), where a higher AVD value indicates greater community variability and thus lower stability (Xun et al., 2021). Consequently, community stability was quantitatively represented as 1-AVD, with higher values denoting greater stability.

Keystone taxa refer to critical nodes whose removal can destabilize modular network structures, including module hubs, network hubs, and connectors (Olesen et al., 2007; Deng et al., 2012; Shi et al., 2016). To identify them, we calculated the within-module connectivity (Zi) and among-module connectivity (Pi) for each node in the ecological network. Based on established thresholds (Guimerà and Nunes Amaral, 2005), nodes were classified into four topological roles: (1) peripherals

(Zi ≤ 2.5 and Pi ≤ 0.62), nodes with low connectivity; (2) connectors (Zi ≤ 2.5 and Pi > 0.62), which link different modules; (3) module hubs (Zi > 2.5 and Pi ≤ 0.62), which are highly connected within their own module; and (4) network hubs (Zi > 2.5 and Pi > 0.62), which are highly connected throughout the entire network.

To evaluate the relative importance of ecological processes in microbial community assembly, we employed a complementary two-method approach. First, a neutral community model (NCM) was fitted using nonlinear least-squares (NLS) to assess the role of neutral stochastic processes, by examining the relationship between ASV detection frequency and its relative abundance across the metacommunity (Sloan et al., 2006). Second, the relative contributions of five specific ecological processes (homogeneous selection, heterogeneous selection, homogenizing dispersal, dispersal limitation, and drift) were quantified using a phylogenetic-bin-based null model (Stegen et al., 2013, 2016; Huber et al., 2020).

2.5. Soil multifunctionality calculation and piecewise structural equation modeling

SMF in croplands and adjacent planted forests was quantified using an effective multifunctionality index (Byrnes et al., 2023; Li et al., 2023). This index integrated measurements from carbon (SOC, POC, MAOC, DOC, MBC, MNC), nitrogen (TN, NH_4^+-N, NO_3^--N), phosphorus (TP, AP), and potassium (TK, AK) pools, as well as the functional potential for microbial carbon (C), nitrogen (N), phosphorus (P), and sulfur (S) cycling. The traditional average multifunctionality index may obscure variations because high-performing functions can be offset by low-performing ones in the mean value (Delgado-Baquerizo et al., 2016; Xiao et al., 2025). Therefore, to better capture the integrated performance, we analyzed SMF using the effective number of functions and effective multifunctionality. This latter metric conceptually represents the cumulative performance of the system under a hypothetical condition where all functions are provided equally. To compute the effective number of functions, each of the 17 measured functions was first standardized to a common scale ranging from 0 to 1. In this scale, 0 indicates no detectable function, and 1 corresponds to the maximum observed level for that specific function. We further calculated effective multifunctionality across orders 0 through 5. The mean value of effective multifunctionality across all these orders was used as the final integrated SMF metric in this study. The detailed computational procedures and formulas for effective multifunctionality followed Li et al. (2023).

Subsequently, the direct and indirect effects of soil properties and microbial community properties on this multifunctionality index were assessed using a piecewise structural equation model (piecewiseSEM). To ensure the robustness and accuracy of the analysis, soil properties used in the calculation of SMF were excluded from the composite variable representing soil physicochemical properties in the piecewiseSEM. To deconstruct the complex causal relationships in our correlative dataset and partition the direct and indirect effects of predictors, we applied piecewiseSEM based on composite variables (Lefcheck, 2016; Liu et al., 2022, 2025). An a priori model, grounded in contemporary theory, was constructed. The model fit was evaluated with Fisher's C test, with a P-value range of 0.05–1.00 denoting acceptable fit (Liu et al., 2022; Wu et al., 2025; Xu et al., 2025). Subsequent refinements involved the addition of significant pathways ($P < 0.05$) to improve model performance, following established methodologies (Delgado-Baquerizo et al., 2020; Liu et al., 2025). The marginal R^2 (R^2_M) and conditional R^2 (R^2_C) represent the proportion of variance explained by all composite variables without and with accounting for random effects of the "sampling site", respectively (Nakagawa and Schielzeth, 2013). Multicollinearity was assessed for all variables in the final piecewiseSEM, with all variance inflation factor (VIF) values confirmed to be under the threshold of 7.0 (O'brien, 2007). This SEM analysis was implemented with the "piecewiseSEM" package in R (Lefcheck, 2016).

2.6. Statistical analysis

All data analysis and figure generation were carried out in R software (version 4.5.1) (R Core Team, 2025). We examined differences in the alpha diversity, Bray-Curtis dissimilarity, network complexity, and sub-network topology properties of soil microbial (bacterial, fungal, and archaeal) communities and SMF between croplands and adjacent planted forests using the Wilcoxon test, subsequent to testing for variance homogeneity (Levene's test) and residual normality (Shapiro-Wilk test).

Associations of soil multi-domain and multi-tiered microbial communities with soil properties were assessed with Mantel tests. Prior to these analyses, the data of soil properties were standardized using a Z-score for Euclidean distance computation, while the data of microbial community were Hellinger-transformed for Bray-Curtis distance calculation.

We employed hierarchical partitioning analysis to quantify the individual contributions of soil physicochemical properties and metallic elements in driving the divergence of soil multi-tiered microbial communities between croplands and adjacent planted forests. This analysis was performed using the "rdacca.hp" package (Lai et al., 2022a). The relative contributions of major drivers to SMF and microbial network complexity were quantified using the "glmm.hp" package (Lai et al., 2022b; Lai et al., 2023).

The Phylogenetic Investigation of Communities by Reconstruction of Unobserved States (PICRUSt2) based on the Kyoto Encyclopedia of Genes and Genomes (KEGG) was used to extrapolate bacterial and archaeal community functions (Langille et al., 2013). Then, the relative abundance of functional genes involved in the C, N, P, and S cycles was calculated to represent the functional potential of the microbial community in these biogeochemical processes.

3. Results

3.1. Soil properties, microbial community diversity, and composition in croplands versus adjacent planted forests

Compared to adjacent planted forests, cropland soils exhibited significantly higher levels of SOC, POC, MAOC, MBC, EC, TP, AP, NO_3^--N, and SWC, while planted forests showed higher MNC/SOC ratio and NH_4^+-N (Table S1). Bacterial and archaeal alpha-diversity were significantly higher in croplands (Wilcoxon test, $P < 0.05$; Fig. 2a, c, and e), whereas fungal alpha-diversity showed no significant difference between land-use types ($P > 0.05$).

Analysis of the top 10 microbial taxa revealed distinct compositional shifts. At the bacterial phylum level, Acidobacteriota, Chloroflexi, Actinobacteriota, Bacteroidota, and Nitrospirota differed significantly between croplands and planted forests (Student's t-test, $P < 0.05$; Fig. 2b). For fungal class level, Sordariomycetes, Mortierellomycetes, Agaricomycetes, and Glomeromycetes showed significant differences (Fig. 2d), while for archaeal class level, Nitrososphaeria, Bathyarchaeia, Nanoarchaeia, Thermoplasmata, and Micrarchaeia differed significantly (Fig. 2f). Notably, substantial heterogeneity in the relative abundance of dominant taxa was observed across sampling sites, regardless of land-use type (Fig. S1).

3.2. Soil microbial community properties, keystone taxa, and assembly processes between croplands and adjacent planted forests

NMDS analysis revealed significant differences in bacterial, fungal, and archaeal community structure between croplands and planted forests (Fig. 3a-c), with Bray-Curtis dissimilarity significantly different for fungi and archaea (Wilcoxon test, $P < 0.001$; Fig. 3d). Network topology properties exhibited domain-specific patterns. For bacteria and archaea, cropland networks were more complex, with greater numbers of nodes, edges, and higher average weight degree compared to planted forests, whereas fungal networks in croplands showed fewer nodes and edges,

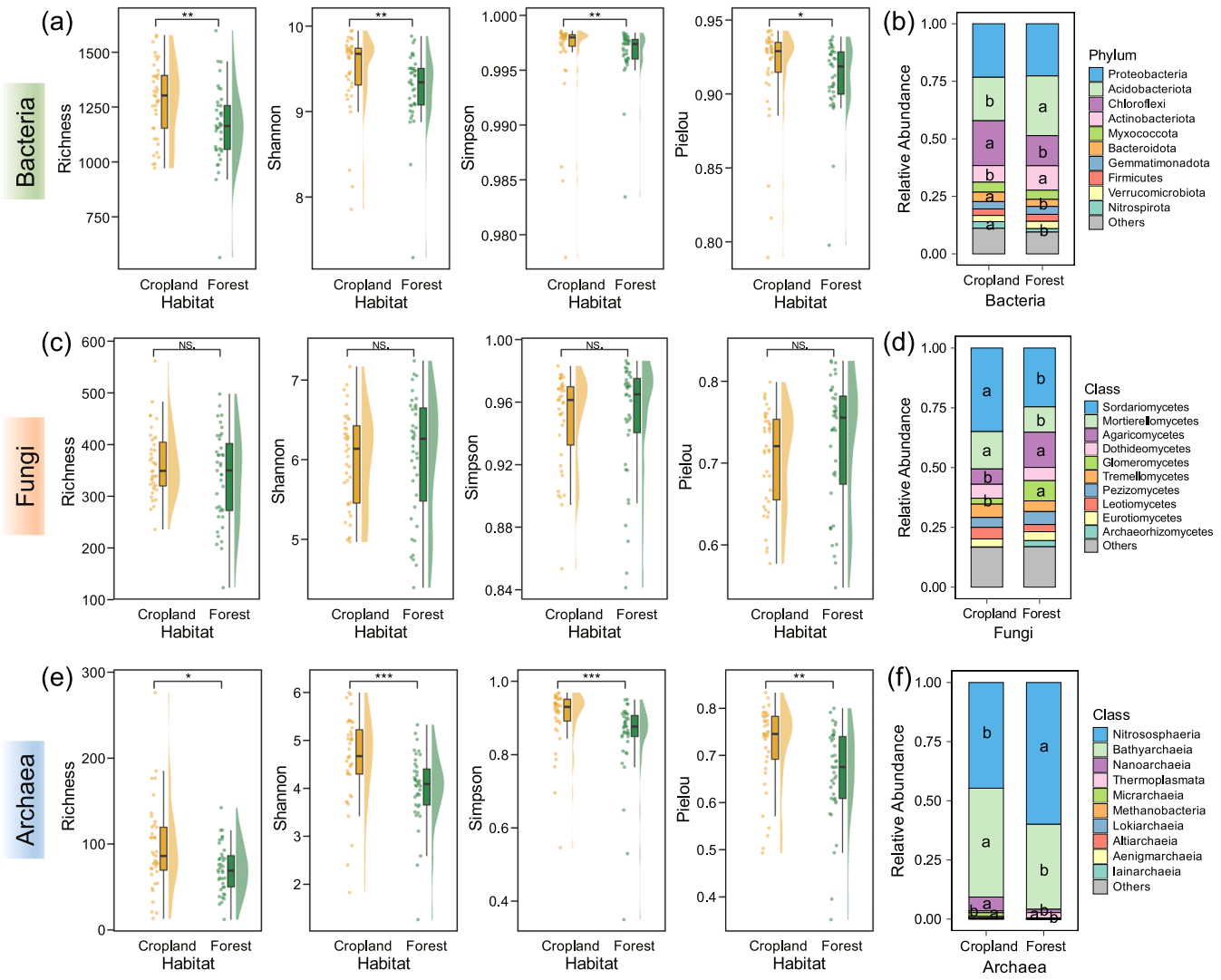

Fig. 2. Differences in soil microbial community diversity and composition between croplands and adjacent planted forests. (a) Bacterial alpha diversity; (b) Bacterial composition; (c) Fungal alpha diversity; (d) Fungal composition; (e) Archaeal alpha diversity; (f) Archaeal composition. The differences were tested using the Wilcoxon test (*: $P < 0.05$, **: $P < 0.01$, ***: $P < 0.001$, NS.: not significant). (b, d, f) Different lowercase letters within each column in the same sub-figure represent significant differences between croplands and adjacent planted forests (Student's *t*-test, $P < 0.05$).

lower modularity, and lower average clustering coefficient (Fig. 4a-f). This pattern of higher network complexity for bacteria and archaea but lower complexity for fungi in croplands was further reflected in sub-network topology properties (Fig. 4g-j). Strikingly, network complexity was positively correlated with Shannon diversity for all microbial domains in croplands—a relationship absent in planted forests (Fig. 4k).

The proportion and Shannon diversity of keystone taxa were consistently higher in croplands across all three microbial domains (Figs. 4a-f and S2a). ASV richness of keystone taxa was higher in croplands than in planted forests, with limited overlap between land-use types (Fig. 4l). Interestingly, the bacterial network complexity increased significantly with keystone taxa's Shannon diversity in adjacent planted forests. In contrast, archaeal network complexity increased significantly with keystone taxa's Shannon diversity in croplands (Fig. S2b). The dominant bacterial classes among keystone taxa differed markedly between land-use types, whereas fungal keystone genera were similar in composition but varied in relative abundance (Fig. S2c-d).

Analysis of soil microbial community stability showed a significant difference only for archaea, which was more stable in adjacent planted forests than in croplands (Fig. S3a). A significant negative correlation was observed between community stability and Shannon diversity across all microbial domains in both land-use types (Fig. S3b). Similarly, fungal and archaeal stability decreased with increasing network complexity, a pattern not seen in bacteria (Fig. S3c).

Significant differences in betaMNTD and betaNTI were observed between croplands and adjacent planted forests (Fig. 5a-b). Deterministic processes dominated bacterial assembly in both systems, whereas stochastic processes dominated fungal assembly (Fig. 5c-d). Archaeal assembly shifted from co-dominance in croplands to determinism in planted forests (Fig. 5e). The neutral community model showed a stronger fit to neutral processes of keystone taxa in planted forests compared to croplands (Fig. 5f-g), indicating that keystone taxa in planted forests were more strongly influenced by stochastic processes.

3.3. *Influencing factors of soil multi-domain and multi-tiered microbial community divergence between croplands and adjacent planted forests*

Influencing factors of microbial community divergence varied markedly by community tier (whole community, core abundant taxa, keystone taxa) and land-use type (Fig. 6). For whole community, pH was identified as the predominant influencing factor of divergence between

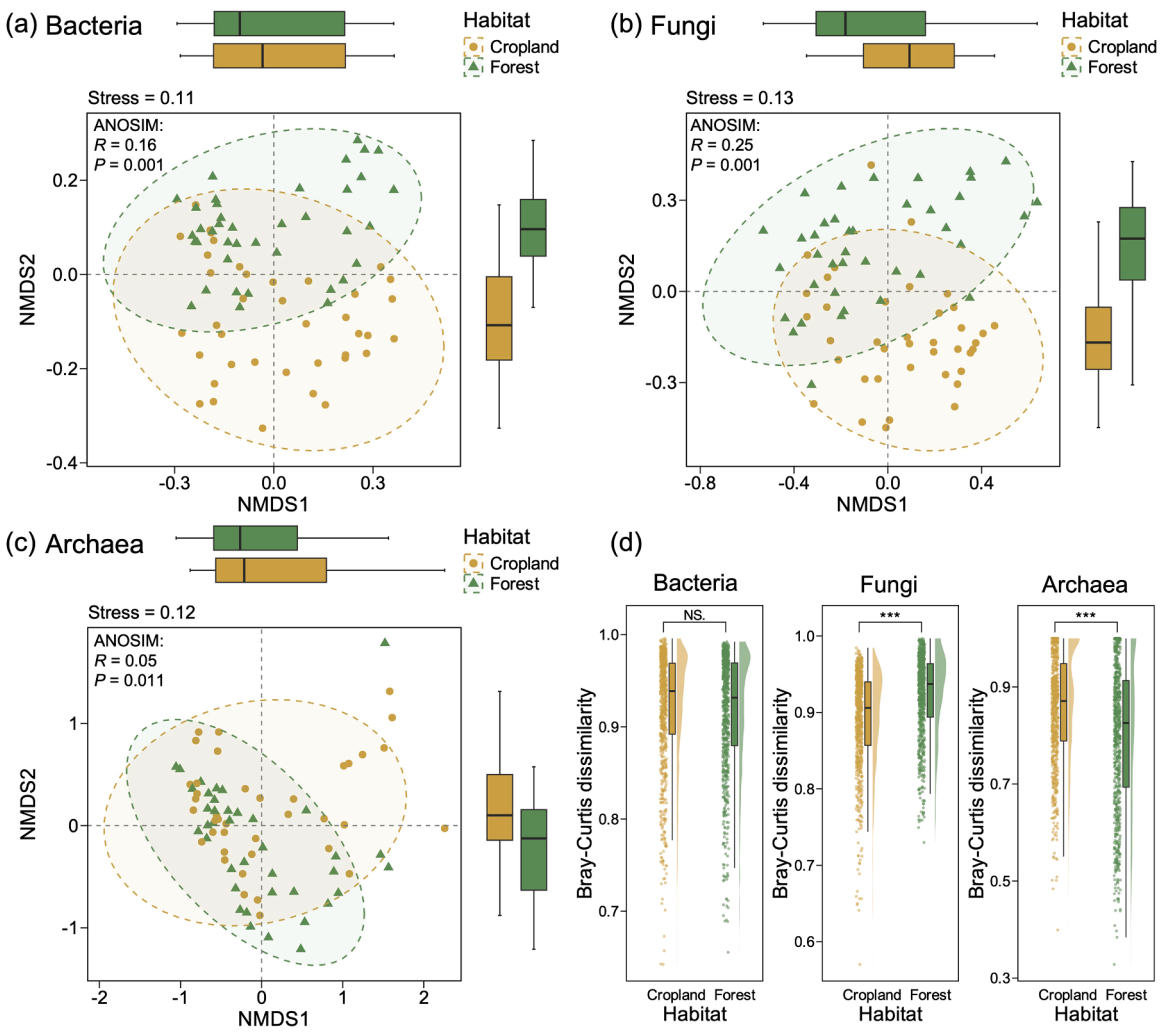

Fig. 3. Differences in soil microbial community structure and Bray-Curtis dissimilarity between croplands and adjacent planted forests. (a) Bacteria; (b) Fungi; (c) Archaea; (d) Differences in Bray-Curtis dissimilarity of soil microbial communities between croplands and adjacent planted forests were tested using the Wilcoxon test (***: $P < 0.001$, NS.: not significant).

croplands and planted forests across all three microbial domains (Fig. 6a-c). In croplands, whole community correlated significantly with SOC, SWC, DOC, TN, EC, and soil texture, while in planted forests, correlations were observed with SOC, NH_4^+-N, and Cu (Fig. S4a-b).

For core abundant taxa, the major influencing factors differed by domain. Bacterial divergence was influenced by SWC, SOC, and pH. Fungal divergence was influenced by pH, TP, and AP. Archaeal divergence was influenced by SWC, sand, and SOC (Fig. 6d-f).

For keystone taxa, soil metallic elements (Cr, Mn, Ca) emerged as the dominant influencing factors of divergence across all three domains (Fig. 6g-i). Cropland keystone taxa correlated positively with SOC and SWC, whereas planted forest keystone taxa correlated with NH_4^+-N, Ca, Mg, and Cu (Fig. S4e-f).

3.4. Quantifying the relative importance of major influencing factors for soil multifunctionality and microbial network complexity in croplands and adjacent planted forests

SMF was significantly higher in croplands than in planted forests (Fig. 7c). In croplands, SMF was primarily promoted by archaeal keystone taxa's diversity, bacterial network complexity, and fungal community structure (Fig. 7a). In planted forests, SMF was predominantly influenced by fungal community structure and archaeal network complexity (Fig. 7b).

The influencing factors of microbial network complexity also differed markedly between land-use types. In croplands, bacterial network complexity was negatively influenced by clay content and positively influenced by bacterial Shannon diversity (Fig. 7d). Fungal network complexity was influenced primarily by fungal Shannon diversity, followed by AK and Mn (Fig. 7e). Archaeal network complexity was most strongly influenced by archaeal Shannon diversity, followed by archaeal community structure and archaeal keystone taxa's Shannon diversity (Fig. 7f). In planted forests, bacterial network complexity was positively influenced by bacterial keystone taxa's diversity and negatively by bacterial community structure (Fig. 7g). Fungal network complexity was influenced by fungal community structure (positive) and pH (negative) (Fig. 7h), whereas archaeal network complexity was most influenced by pH (negative) and its own Shannon diversity (positive) (Fig. 7i).

3.5. Direct and indirect effects of soil properties and microbial community properties on soil multifunctionality in croplands and adjacent planted forests

The piecewiseSEM revealed distinct influencing pathways underlying SMF between croplands and planted forests. In croplands, soil physicochemical properties exerted the strongest direct and total effects on SMF (path coefficient = 0.410, $P < 0.01$), followed by archaeal

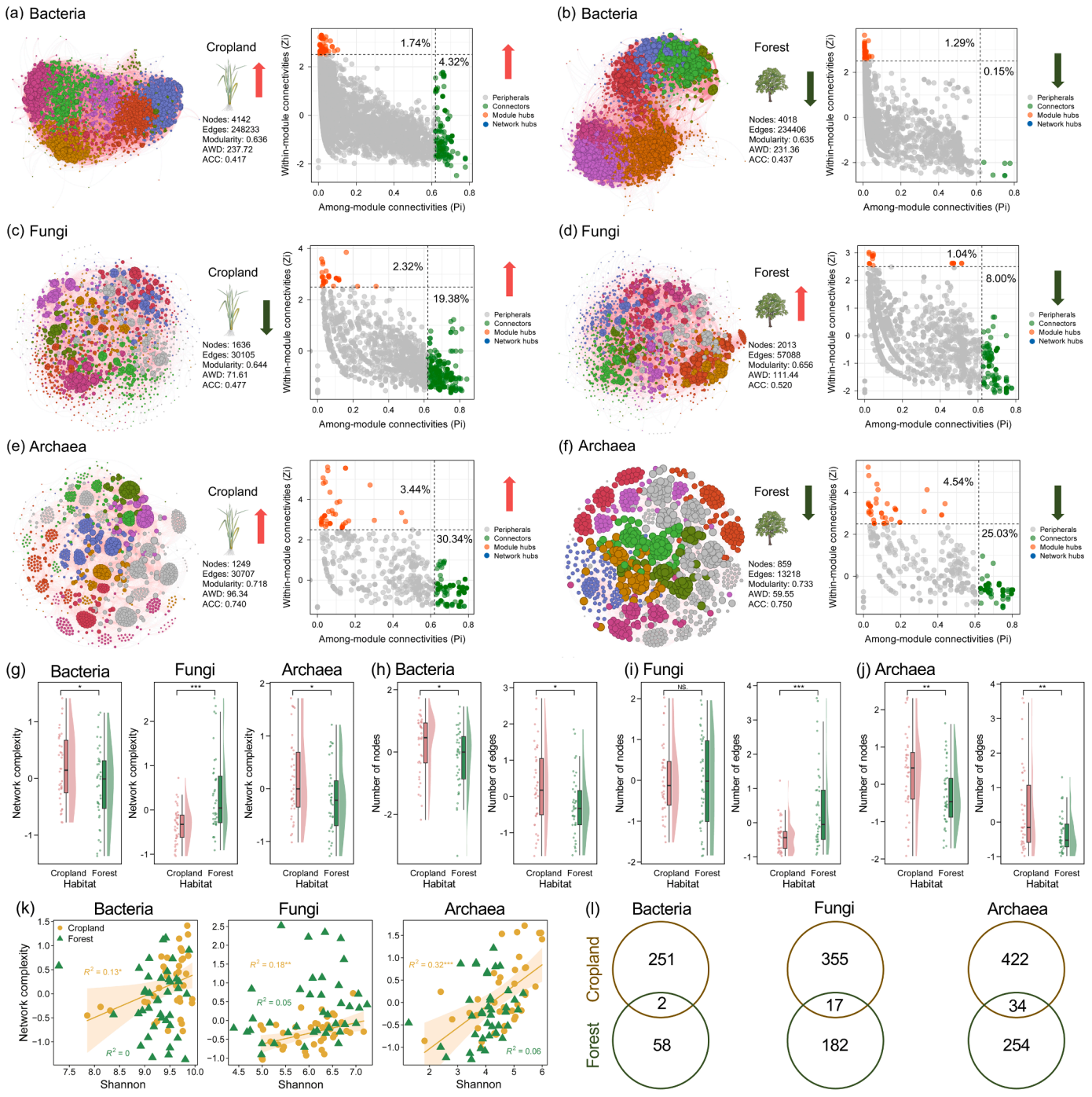

Fig. 4. Soil microbial network properties between croplands and adjacent planted forests. Co-occurrence networks and module connectivity of soil (a, b) bacteria, (c, d) fungi, and (e, f) archaea. Networks were constructed based on significant Spearman correlations ($|r| > 0.50$, $P < 0.05$), where node size corresponds to connectivity (i.e., weight degree), and edges depict positive (red) and negative (green) interactions. Nodes are colored by their assigned module. AWD, average weight degree; ACC, average clustering coefficient. Zi-Pi plots reveal the topological roles of individual ASVs, identifying potential keystone taxa. Differences in soil microbial (g) network complexity and (h-j) partial sub-network topology properties between croplands and adjacent planted forests were tested using the Wilcoxon test (*: $P < 0.05$, **: $P < 0.01$, ***: $P < 0.001$, NS.: not significant). (k) Linkages between soil microbial network complexity and Shannon diversity. The solid line represents the trends, and the shaded area represents the standard error of the estimate. *: $P < 0.05$, **: $P < 0.01$, ***: $P < 0.001$. (l) Venn diagram showing the unique and shared ASVs among the keystone taxa of bacteria, fungi, and archaea.

community properties (0.381, $P < 0.01$) and metallic elements (0.371, $P < 0.01$). Soil physicochemical properties also had significant positive direct effects on bacterial and fungal community properties (Fig. 8a and c).

In planted forests, soil physicochemical properties again exhibited the strongest direct and total effects on SMF (0.388, $P < 0.05$), followed by fungal community properties (0.321, $P < 0.05$). Although the direct effect of metallic elements was minor, their total effect was substantial (standardized effect = 0.332). Soil physicochemical properties also had a significant positive direct effect on bacterial community properties (Fig. 8b and d).

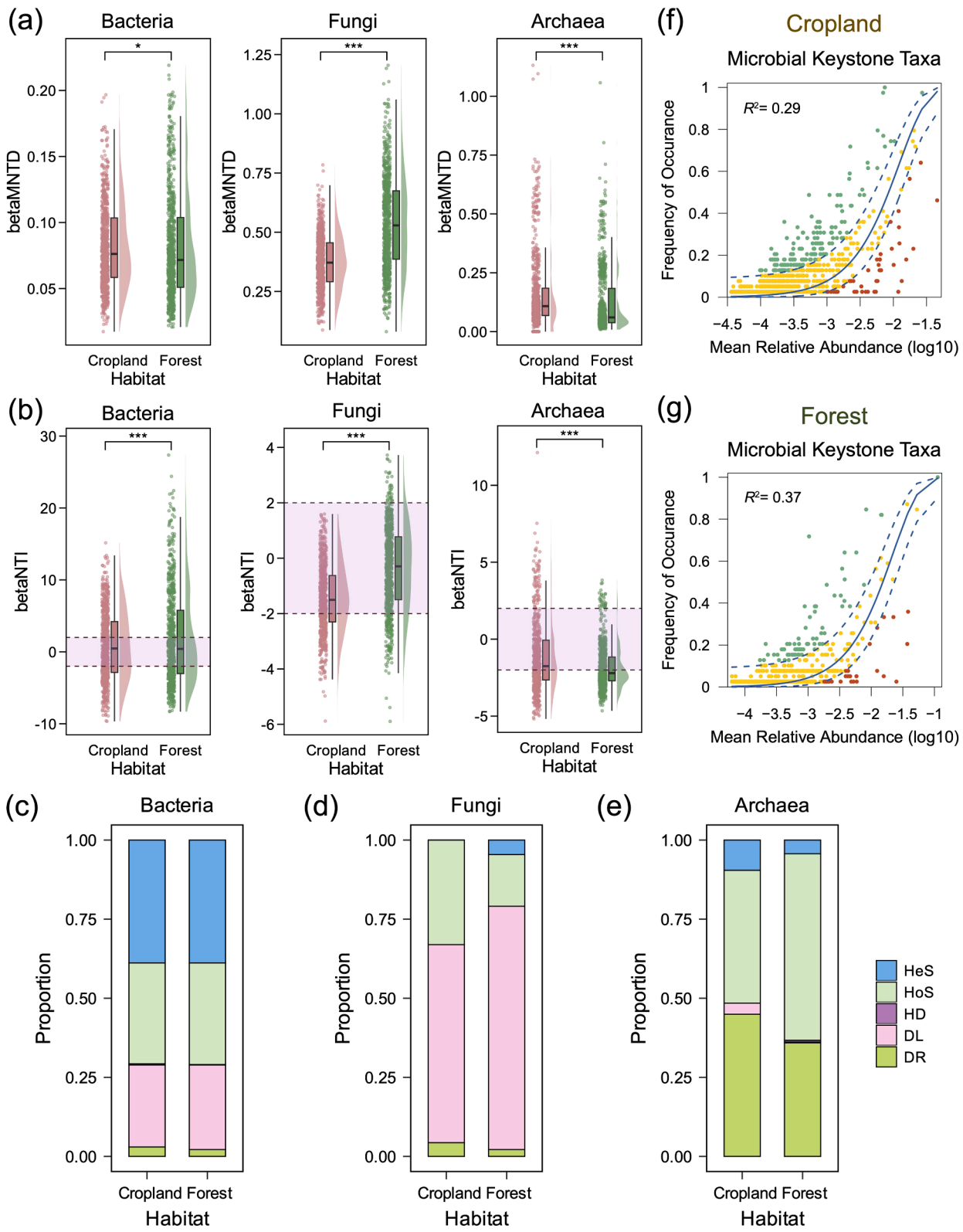

Fig. 5. Assembly processes of soil microbial communities between croplands and adjacent planted forests. (a) betaMNTD and (b) betaNTI distributions and differences for bacteria, fungi, and archaea between croplands and adjacent planted forests. *: $P < 0.05$, ***: $P < 0.001$. (c-e) Quantify the relative importance of ecological processes in microbial community assembly between croplands and adjacent planted forests. HeS, heterogeneous selection; HoS, homogeneous selection; HD, homogenizing dispersal; DL, dispersal limitation; DR, drift. Fit of the neutral community model (NCM) of soil microbial (bacterial-fungal-archaeal) keystone taxa's community assembly between (f) croplands and (g) adjacent planted forests. The solid blue line is the best fit to the neutral community model (NCM), and the dashed blue line indicates 95% confidence intervals around the NCM prediction. ASVs occurring more or less frequently than predicted by the NCM are shown in green and red, respectively; those falling within the predicted range are shown in yellow. R^2 represents the goodness of fit to this model, with a higher R^2 indicating closer proximity to the neutral community model, meaning that the construction of the community is more influenced by stochastic processes and less by deterministic processes, that is, the closer it is to the neutral community model.

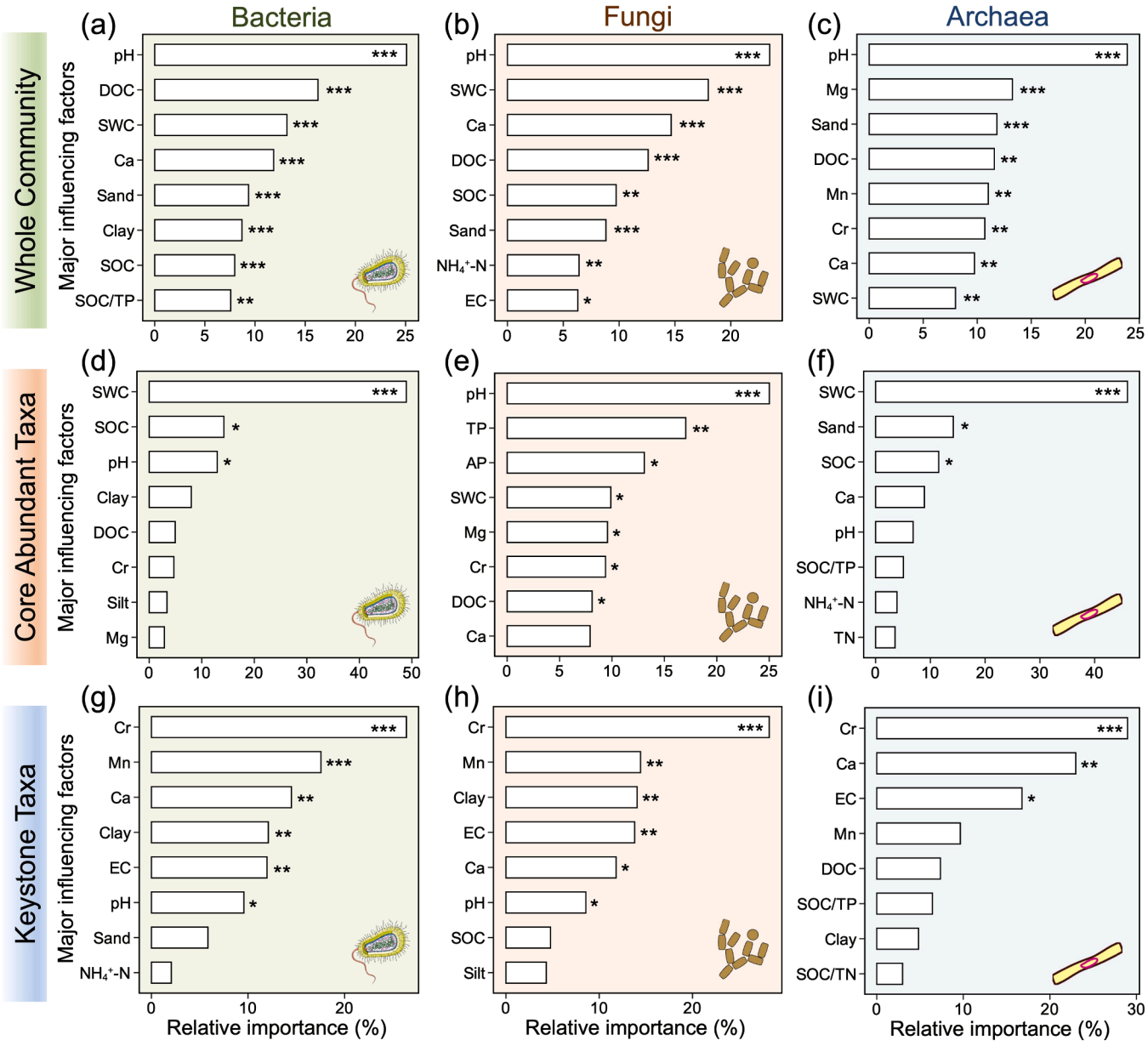

Fig. 6. Relative importance of major influencing factors (soil physicochemical properties and metallic elements) in shaping differences in soil multi-domain (bacteria, fungi, archaea) and multi-tiered (whole community, core abundant taxa, keystone taxa) microbial communities between croplands and adjacent planted forests. (a, d, g) Bacteria; (b, e, h) Fungi; (c, f, i) Archaea; (a, b, c) Whole community; (d, e, f) Core abundant taxa; (g, h, i) Keystone taxa. SOC, soil organic carbon; DOC, dissolved organic carbon; SOC/TN, SOC to TN ratio; SOC/TP, SOC to TP ratio; SWC, soil water content; TN, total nitrogen; NH_4^+-N, ammonium nitrogen; TP, total phosphorus; AP, available phosphorus; EC, electrical conductivity. Bars marked with "*", "**", and "***" represent variables that are significant at the < 0.05, < 0.01 and < 0.001 level, respectively.

4. Discussion

4.1. Reconfiguration of soil multi-domain and multi-tiered microbial communities after cropland-to-planted forest conversion

We observed that bacterial and archaeal alpha diversity were significantly higher in croplands than in adjacent planted forests. This finding challenges the common perception that agricultural practices universally reduce soil microbial diversity (Tsiafouli et al., 2015; Banerjee et al., 2019, 2024). This pattern can be attributed to the intensive management in croplands, including regular fertilization and irrigation, which creates a resource-rich environment that supports a wider spectrum of prokaryotic microorganisms (Zhang et al., 2025; Zhou et al., 2025). The higher availability of nutrients such as SOC, TN, and TP in cropland soils likely sustains a more diverse bacterial and archaeal community by providing a broader niche space for metabolic specialization. In contrast, the planted forests, characterized by more oligotrophic conditions and dependent on litter-derived organic matter, may impose stronger environmental filtering on these microbial domains (Zhang et al., 2025). This interpretation aligns with previous studies reporting higher bacterial alpha diversity in croplands than in forests (Xiao et al., 2023; Zhou et al., 2025), as well as research indicating that high nutrient inputs in farmlands favor "fast-growing" r-strategist microbes, in contrast to pristine soils that sustain

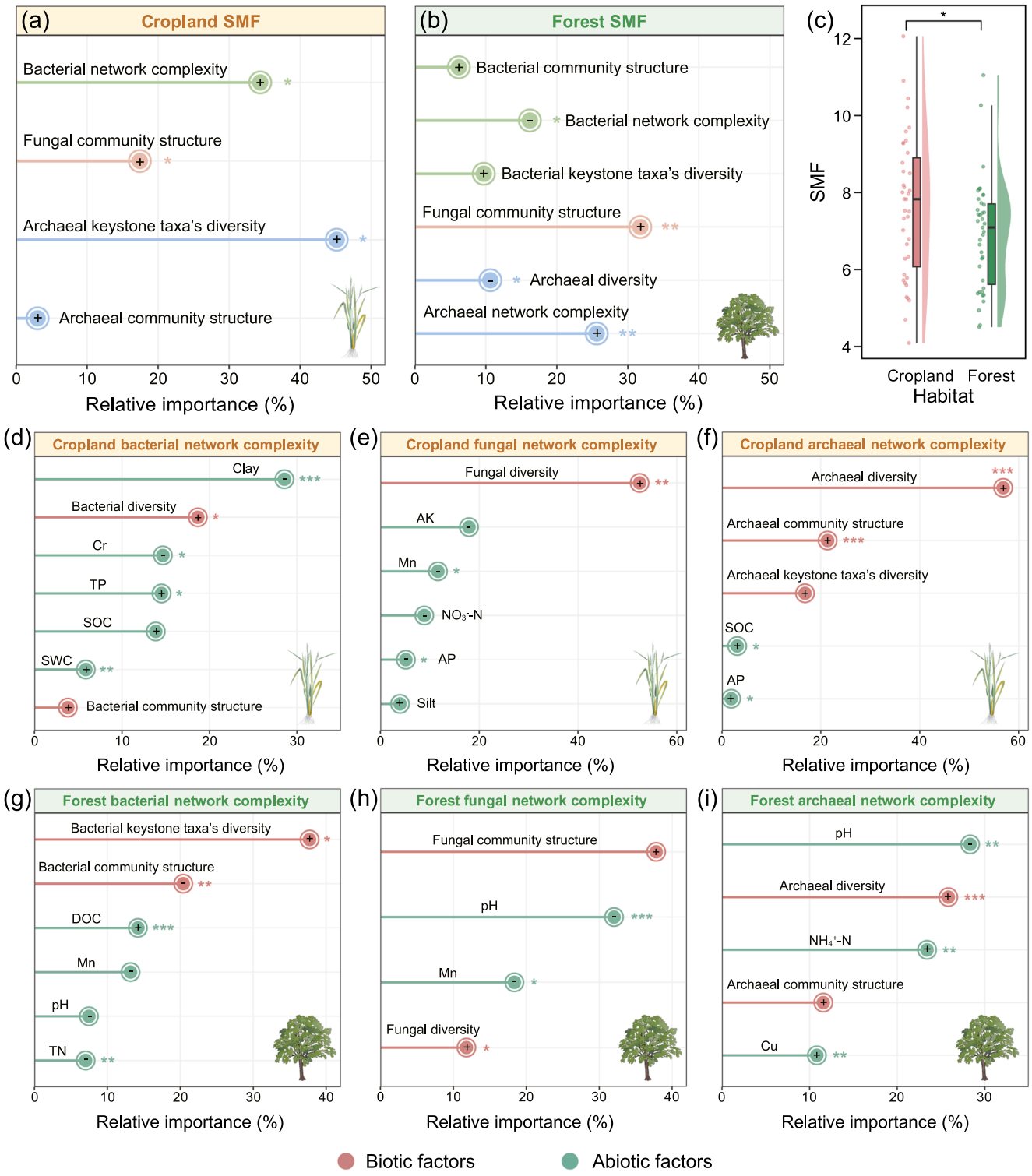

Fig. 7. Relative importance of major influencing factors for (a, b) soil multifunctionality (SMF) and (d-i) microbial network complexity in croplands and adjacent planted forests. Relative importance of microbial (bacterial, fungal, and archaeal) community properties for SMF in (a) croplands and (b) adjacent planted forests. (c) Differences in SMF between croplands and adjacent planted forests were tested using the Wilcoxon test (*: $P < 0.05$). Relative importance of soil physicochemical properties, metallic elements, and microbial community structure and diversity (whole community, keystone taxa) for soil microbial network complexity in (d-f) croplands and (g-i) adjacent planted forests. Lollipops marked with "*", "**", and "***" represent variables that are significant at the < 0.05, < 0.01 and < 0.001 level, respectively. SOC, soil organic carbon; DOC, dissolved organic carbon; SWC, soil water content; TN, total nitrogen; NH_4^+-N, ammonium nitrogen; NO_3^--N, nitrate nitrogen; TP, total phosphorus; AP, available phosphorus; AK, available potassium.

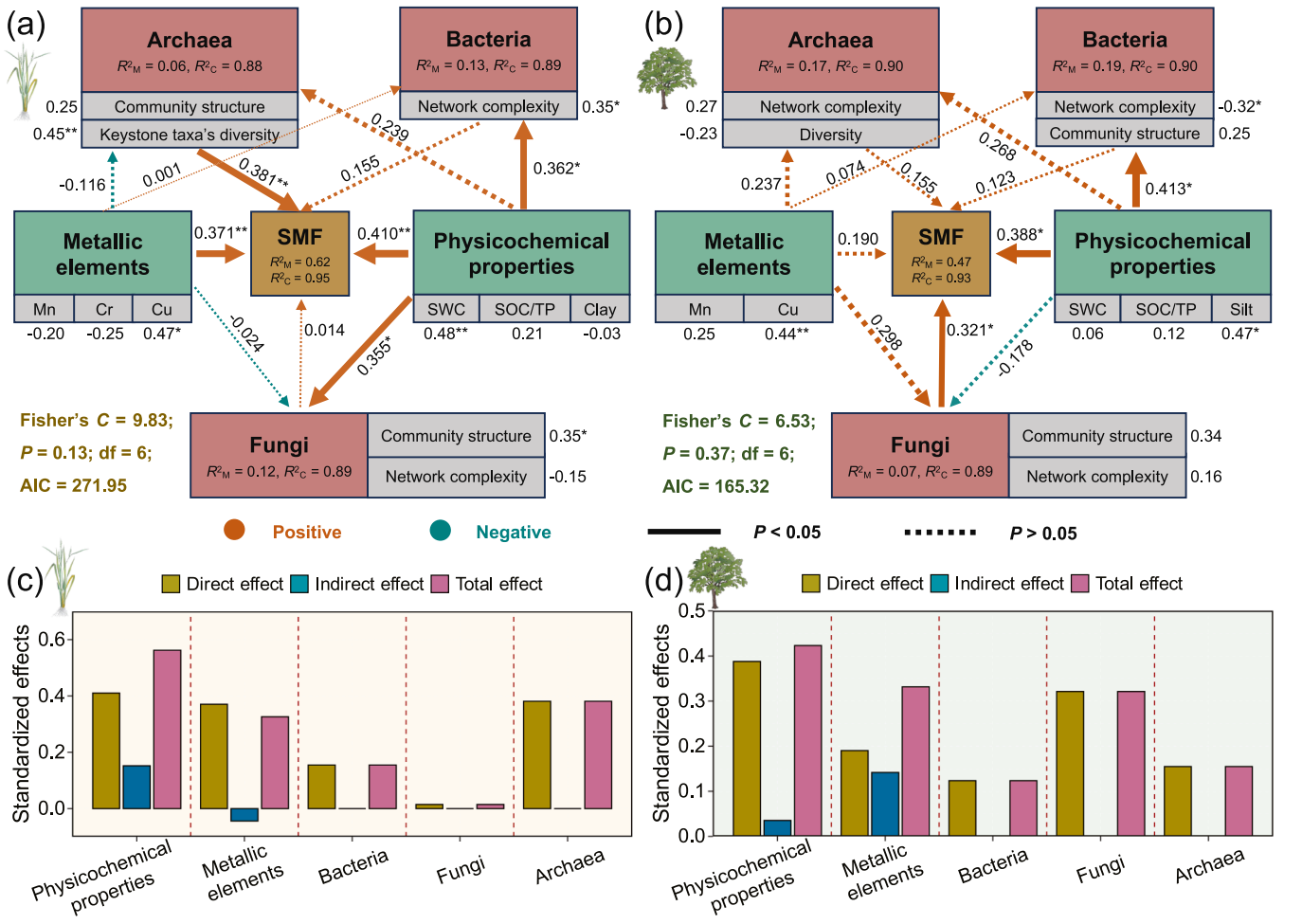

Fig. 8. Piecewise structural equation modeling (piecewiseSEM) accounting for the direct and indirect effects of soil properties (physicochemical properties and metallic elements) and microbial (bacterial, fungal, and archaeal) community properties on soil multifunctionality (SMF) in (a, c) croplands and (b, d) adjacent planted forests. Numbers adjacent to arrows are path coefficients (partial regression), which represent the directly standardized effect size of the relationship. The standardized path coefficients in the paths are shown in red if positive or in green if negative. Significant paths ($P < 0.05$) are represented by solid lines, and non-significant paths ($P > 0.05$) are represented by dashed lines in the figure. Significance levels of each predictor are $^*P < 0.05$, $^{**}P < 0.01$. Standardized effects (total, direct, and indirect effects) based on piecewiseSEM are shown in the figure at the bottom. The marginal R^2 (R^2_M) and conditional R^2 (R^2_C) represent the proportion of variance explained by all composite variables without and with accounting for random effects of the "sampling site", respectively. df, degree of freedom; AIC, Akaike information criterion; SWC, soil water content; SOC/TP, SOC to TP ratio.

"resource-efficient" K-strategists (He et al., 2025a). However, our findings contrast with a previous study showing higher bacterial alpha diversity after afforestation compared to croplands (Zhao et al., 2018), suggesting that the direction of diversity change may depend on factors such as climate, soil type, stand age, and land-use history.

In contrast to prokaryotes, fungal alpha diversity showed a non-significant trend toward higher diversity in planted forests. This divergent response can be explained by the ecological role of fungi as key decomposers of complex plant polymers (Qu et al., 2025; Zhou et al., 2025). The shift from herbaceous to woody vegetation provides distinct substrate types, particularly lignin-rich litter, that favor fungal-dominated decomposition pathways. The significant changes in the relative abundances of Sordariomycetes, Mortierellomycetes, Agaricomycetes, and Glomeromycetes between land-use types further support this interpretation, indicating functional reorganization of the fungal community in response to altered carbon sources and root associations. Additionally, in our study, compared to croplands under conventional tillage, the planted forests established on former croplands experience reduced anthropogenic disturbance, creating a low-disturbance soil environment that is more conducive to fungal growth and diversity—particularly decomposers such as Agaricomycetes and arbuscular mycorrhizal fungi like Glomeromycetes—as soil fungi are particularly susceptible to agricultural tillage (Banerjee et al., 2024). This finding aligns with previous studies showing that agricultural intensity adversely affects cropland fungal richness compared to non-cropland habitats (Banerjee et al., 2024). However, our findings diverge from previous research reporting lower fungal diversity in forests compared to croplands (Labouyrie et al., 2023). This contrast may be explained by differences in environmental context. Labouyrie et al. (2023) attributed higher fungal diversity in croplands to greater niche availability from crop rotation, whereas forests were described as highly competitive environments with limited niche opportunities. In our study, however, the planted forests are relatively young (15 ± 5 years) and may not yet have developed such competitive exclusion, while the croplands are dominated by rice paddies or rice-wheat rotations, which may differ from the arable systems examined previously. These differences highlight the context-dependent nature of fungal community responses to land-use change.

We found that cropland-to-planted forest conversion influences soil multi-tiered microbial communities through distinct mechanisms. Notably, the proportion of keystone taxa was higher in croplands across all three microbial domains, and these keystone taxa showed extremely low overlap between the two land-use types. This fundamental restructuring of soil microbial keystone taxa highlights their central role

in maintaining network stability and ecosystem functioning. Such turnover may have profound implications for the long-term stability of ecosystem functions following afforestation. The differential response of keystone taxa compared to other community tiers can be explained by their distinct environmental factors. While soil properties such as pH, SWC, and SOC were the primary factors influencing differences in both the whole community and core abundant taxa between land-use types (Zhou et al., 2020; Bastida et al., 2021; Guo et al., 2021; Zhong et al., 2023), metallic elements served as the main factors influencing differences in keystone taxa. This hierarchical response pattern indicates that environmental filtering operates differently across multi-tiered microbial communities, with keystone taxa being particularly sensitive to micronutrient availability and potentially heavy metal stressors (Dai et al., 2023). Keystone taxa may occupy distinct metabolic niches tied to metal-dependent enzymes or may be more vulnerable to metallic elements due to their central network positions and potentially higher metabolic activity. This interpretation is supported by previous research showing that cropland-to-planted forest conversion profoundly reshapes bacterial communities and increases their sensitivity to soil nutrients (Kong et al., 2022), accompanied by a significant decrease in β-diversity and a tendency toward homogenization of keystone taxa and functional groups. Similarly, research has found that conversion of natural forests to croplands reduces soil keystone taxa, primarily due to increased soil TP content (Ding et al., 2024).

4.2. Changes in microbial network topology properties and domain-specific community assembly processes

We observed that cropland soils showed more complex bacterial and archaeal networks compared to planted forests, whereas fungal networks showed the opposite pattern. This domain-specific response can be attributed to the distinct ecological strategies of these microbial groups. The higher bacterial and archaeal network complexity in croplands suggests that agricultural practices may foster tighter cooperative or competitive interactions among specific microbial taxa in response to relatively high-frequency disturbances and resource fluctuations (Chen et al., 2024; Long et al., 2025). This interpretation aligns with previous research showing that prokaryotic microbial network complexity in wheat croplands was higher than in natural grasslands with lower levels of human disturbance, attributed to more abundant nutrient supply and greater microbial functional redundancy in wheat fields (Cornell et al., 2023). However, intensive agricultural management can also compromise network stability despite enhancing complexity (Long et al., 2025). In contrast, the higher fungal network complexity in planted forests likely reflects that tree roots and litter inputs provide a more stable and heterogeneous habitat, facilitating the expansion of fungal mycelial networks and specific interactions among species (Kong et al., 2022).

We found a positive correlation between microbial diversity and network complexity in croplands—a relationship that became uncoupled in planted forests. This decoupling reflects a fundamental shift in microbial community structure following land-use change. In cropland ecosystems, consistent nutrient inputs and regular disturbance regimes appear to create conditions where higher diversity naturally translates into more complex interaction networks (Cornell et al., 2023). This coupling suggests that cropland microbial communities operate under resource competition paradigms where diverse taxa establish structured interactions to optimize resource utilization in a relatively predictable environment. The disappearance of this relationship in planted forests indicates a disruption of the mechanisms linking diversity to network structure. The transition to litter-based nutrient cycling, increased spatial heterogeneity, and reduced management intensity in planted forests may create environmental conditions where historical relationships between diversity and network complexity break down (Kong et al., 2022). This decoupling may reflect an unstable, transitional state of the microbial community after afforestation, or it may be because the ecological functions of the 10–20 year-old planted forests have not yet been restored to the level of a natural forest. Our findings also revealed that in croplands, the diversity of bacteria, fungi, and archaea exhibited higher relative contributions to their network complexity, whereas in planted forests, the community structure of these microbial domains contributed more to network complexity. Several studies confirm the positive influence of microbial diversity on network complexity (Chen et al., 2022; He et al., 2025b).

The contrasting responses in community assembly processes across microbial domains reveal fundamental differences in their ecological strategies. We found that deterministic processes consistently dominated bacterial assembly across both land-use types, indicating strong environmental filtering on bacterial communities regardless of ecosystem type (Peng et al., 2025; Riddley et al., 2025). This reflects the high niche differentiation among bacterial taxa and their rapid response to environmental conditions, particularly soil pH and organic matter quality. For fungi, we observed that stochastic processes dominated in both systems, but with increased deterministic influence in croplands. This pattern highlights the importance of dispersal limitation and ecological drift in fungal biogeography, and the stronger deterministic component in croplands suggests that agricultural management imposes stronger environmental filtering on fungal communities—potentially through tillage disturbance and nutrient amendments that reduce the importance of random dispersal events (Osburn et al., 2021; Peng et al., 2025). Our findings align with a recent study conducted along a 1300-km climate and land-use gradient in Australia, which found that soil bacterial communities were primarily governed by deterministic processes, while fungal communities were mainly dominated by stochastic processes (Du et al., 2026). The most striking shift occurred in archaeal communities, which transitioned from co-dominance in croplands to deterministic dominance in planted forests. This transition suggests that afforestation increases the strength of environmental selection on archaeal communities, possibly through changes in ammonia availability, soil acidity, or organic matter composition (Zhang et al., 2024b).

4.3. The decline in soil multifunctionality after cropland-to-planted forest conversion

Significantly lower SMF was observed in planted forests compared to croplands. This finding presents an apparent paradox, as afforestation is generally expected to enhance ecosystem functioning (Cheng et al., 2024). This pattern can be understood by considering the different functional priorities of these ecosystems. Croplands are managed for intensive nutrient cycling and rapid decomposition to support plant productivity, resulting in high scores for nutrient-related functions. Planted forests, in contrast, prioritize aboveground carbon sequestration and storage (Cheng et al., 2024), which may come at the cost of reduced nutrient cycling rates. This interpretation is consistent with a previous study that observed higher SMF in croplands than in planted forests (Hao et al., 2024). However, other research has reported decreased SMF after forest-to-cropland conversion, mainly due to intensified agricultural management (Ding et al., 2024). Our findings diverge from a previous 20-year afforestation study in the semi-arid Loess Plateau of China, which showed higher topsoil SMF in planted forests than in croplands (Kong et al., 2022). This discrepancy may be attributed to fundamental differences in climatic conditions (subtropical humid vs. semi-arid), land-use history (paddy rice and rice-wheat rotation systems vs. upland), and soil texture between the studied regions (Jiao et al., 2018; Zhong et al., 2020; Kong et al., 2022; Zhang et al., 2023).

The fundamental reorganization of SMF drivers between land-use types provides mechanistic insights into this functional trade-off. We found that in croplands, SMF was driven by a collaborative model where archaeal keystone taxa diversity, bacterial network complexity, and fungal community structure jointly support multiple functions. This integrated approach allows cropland systems to maintain high levels of simultaneous functioning across different process types. In planted

forests, we observed a shift to fungal community structure and archaeal network complexity as primary SMF drivers. This shift reflects a different functional strategy: the increased dependence on fungal processes aligns with the slower decomposition pathways and organic matter accumulation characteristic of forest ecosystems (Guan et al., 2025). While this strategy enhances carbon storage, it may reduce the efficiency of nutrient cycling processes, resulting in lower overall SMF when considering the broad suite of functions measured. Our findings align with previous studies showing that microbial network complexity and diversity improve ecosystem function through enhanced functional coordination, demonstrating the important role of network complexity and diversity in driving SMF (Wagg et al., 2019; Chen et al., 2022; Wang et al., 2023b).

Our structural equation modeling results further elucidate that soil physicochemical properties had the strongest total effects on SMF in both systems, albeit through different pathways. In croplands, multiple direct pathways from archaeal communities, physicochemical properties, and metallic elements to SMF indicate distributed functioning. In planted forests, the more focused pathways through fungal communities and physicochemical properties suggest a more specialized functional configuration. This interpretation is supported by a separate afforestation study conducted in semi-arid uplands, which highlighted the significant influence of soil nutrients on SMF (Kong et al., 2022). Another study based on multiple land-use types found that SWC and microbial community properties interactively and substantially influenced SMF (Hao et al., 2024). Similarly, research on croplands in Eastern China revealed that soil properties and soil biodiversity exert considerable influence on SMF, with soil multitrophic network complexity enhancing the linkage between soil biodiversity and SMF (Jiao et al., 2022). Our findings contrast with a previous study on post-agricultural ecological restoration in the Qinling Mountains, which found that soil microbial network complexity significantly negatively influenced SMF (Chen et al., 2023). In that study, this negative relationship was attributed to environmental stresses during restoration (e.g., reduced nutrient content and lower water availability), which may destabilize networks through co-oscillation of positively correlated taxa. In contrast, our study was conducted in the warmer and more humid Yangtze River Delta region, where planted forests (stand age approximately 15 $\pm$ 5 years) experience less environmental stress compared to the early successional stages (e.g., 5-year grasslands) examined by Chen et al. (2023). This contextual difference likely explains the contrasting relationships between network complexity and SMF, highlighting the strong ecosystem-dependence of this association.

4.4. Implications, limitations, and future directions

Our comprehensive study demonstrates that cropland-to-planted forest conversion triggers a systematic reconfiguration of soil microbial communities across multiple tiers, altering their assembly processes and ultimately reshaping the influencing factors of SMF. The findings reveal complex and often contrasting responses among bacterial, fungal, and archaeal communities to this ecosystem transformation, providing new insights into the ecological consequences of afforestation on former croplands. For management and evaluation of afforestation projects, these results suggest that comprehensive microbial assessments should incorporate multiple domains and community levels to fully understand ecosystem impacts. The identification of metallic elements as main influencing factors of keystone taxa differences highlights a previously underappreciated aspect of afforestation ecology, suggesting that micronutrient management may be crucial for maintaining key microbial functions during land-use transition. Additionally, the uncoupling of diversity-network complexity relationships in planted forests indicates that diversity-based assessments alone may be insufficient for evaluating microbial community responses to afforestation (Xiao et al., 2025). It is essential to look beyond changes in microbial diversity and focus more critically on the structural stability and complexity of their interaction networks and the turnover of keystone taxa (Ding et al., 2024; Long et al., 2025; Xiao et al., 2025).

From a practical perspective, these results suggest that management strategies aimed at enhancing SMF in planted forests should focus on supporting fungal community development and maintaining appropriate archaeal network complexity. This could involve selective retention of tree species that support diverse mycorrhizal associations, maintenance of coarse woody debris, and careful consideration of soil amendment practices that influence metal availability (Tang et al., 2024; Tripathi et al., 2025). The functional trade-off observed between carbon sequestration and nutrient cycling functions underscores the importance of defining clear management objectives for afforested lands. Where multiple ecosystem services are desired, management strategies may need to explicitly address the compromise between carbon storage and nutrient cycling capacity, potentially through mixed-species plantings or targeted interventions to maintain critical microbial functions (He et al., 2025b).

One limitation of this study is that our sampling was confined to the surface layer. While this depth captures the direct effects of land-use conversion on soil microbial communities, land-use may also influence deeper soil horizons. Future studies incorporating depth profiles would provide a more complete understanding of how afforestation influences soil microbial communities throughout the soil profile. Additionally, the cross-sectional nature of our sampling (a single time point) and the variable stand ages of planted forests (15 $\pm$ 5 years) introduce potential temporal confounding, limiting our ability to infer causal dynamics over time. Moreover, the functional profiles of bacterial and archaeal communities in this study were predicted using PICRUSt2 based on 16S rRNA gene data and KEGG pathways. This approach provides only indirect inferences and should be considered highly speculative, as it represents a predicted functional profile rather than direct measurements of true microbial functions. Furthermore, the relationships between microbial community properties and SMF, although assessed using hierarchical partitioning and piecewiseSEM, are derived from observational data and therefore remain inherently correlative rather than causal. Future research combining long-term monitoring with metagenomic and metatranscriptomic techniques would be valuable to more directly reveal the expression of microbial functional genes and their dynamics, thereby enabling a more precise dissection of the causal pathway from microbial communities to underlying ecosystem functions. Meanwhile, controlled experiments (e.g., in situ manipulative field experiments) are needed to validate causal relationships between microbial community properties and SMF. Finally, although we implemented strict pairwise sampling, the potential influence of inherent site-specific differences cannot be entirely ruled out, and this study was conducted within ecological-functional planted forests. Future studies are needed to determine the applicability of these findings to other planted forest types (e.g., erosion-control forests), which may differ in management priorities and environmental constraints.

5. Conclusions

Our study reveals that converting croplands to planted forests induces a comprehensive restructuring of soil multi-domain and multi-tiered microbial communities, accompanied by a significant decline in SMF. This transition reduced bacterial and archaeal diversity and network complexity while enhancing fungal network complexity, signaling a fundamental shift in belowground ecosystem organization. A key finding is the decoupling of the diversity-network complexity relationship in planted forests, suggesting a disruption of established microbial interactions after afforestation. Moreover, archaeal community assembly shifted from a balance of stochastic and deterministic processes to deterministic dominance, reflecting altered ecological rules influencing community formation. The influencing factors of SMF also underwent substantial reconfiguration between the two land-use types. Cropland SMF was influenced by a collaborative model involving

archaeal keystone taxa's diversity and bacterial network complexity, whereas planted forest SMF relied more heavily on fungal community structure and archaeal network complexity. This functional reorganization, coupled with the observed decline in overall SMF in planted forests, highlights an important ecological trade-off: the enhancement of aboveground carbon sequestration potential in forest systems appears to come at the expense of the intensive nutrient cycling capacity maintained under agricultural management. These findings underscore the need to integrate multi-domain and multi-tiered microbial assessments into the evaluation of afforestation projects. Our study further suggests that management strategies targeting specific microbial components—particularly fungal communities and keystone taxa—could help optimize ecosystem service delivery in planted forests established on former croplands.

CRediT authorship contribution statement

Jie Liu: Writing – original draft, Writing – review & editing, Data curation, Investigation, Software, Methodology, Formal analysis, Validation, Visualization, Conceptualization, Project administration. **Lin Yang:** Writing – review & editing, Supervision, Conceptualization, Resources, Project administration, Funding acquisition. **Jie Wang:** Writing – review & editing, Investigation. **Ren Wei:** Writing – review & editing, Investigation. **Yongqi Qian:** Writing – review & editing, Investigation. **Lei Zhang:** Writing – review & editing, Supervision. **Chenghu Zhou:** Writing – review & editing, Supervision, Resources.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Acknowledgements

This work was supported by the National Natural Science Foundation of China (grant number 42471468); the Fundamental Research Funds for the Central Universities (grant number 0209–14380115); and the Postgraduate Research & Practice Innovation Program of Jiangsu Province (grant number KYCX25_0209).

Appendix A. Supplementary data

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

Appendix A. Supporting information

Supplementary data associated with this article can be found in the online version at doi:10.1016/j.agee.2026.110553.

Data availability

Data will be made available on request.

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