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Unlocking Mechanisms for Soil Fertility Enhancement in Tropical Forests Restored From Non-Native Rubber Plantations: Microbes as the Key Drivers

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ABSTRACT

Forest restoration is a well-established approach for effective soil rehabilitation, yet how soil microorganisms influence soil fertility at the soil aggregate microscale during tropical forest restoration remains unclear. We investigated the changes in soil microbial diversity and composition across four forest types: a tropical rainforest, a rubber monoculture plantation, and two restored types (natural restoration of rubber monoculture and natural restoration of rubber tree with tea tree intercropping). Results showed that soil fertility (soil organic C, total N, and total P), pH, and electrical conductivity (EC) exhibited increasing trends following forest restoration or decreasing soil aggregate fractions. Forest restoration and soil aggregate fractions were identified as the key predictors of microbial community structure. This relationship may be attributed to enhanced resource availability caused by increased plant diversity, pH, and EC in the restored forests. Smaller aggregates provide physical protection and retain more nutrients, thereby promoting microbial activity and diversity. PLS-PM showed that microbes constituted the primary contributor among all the factors driving soil fertility. Strong positive correlations were observed between soil fertility and microbial communities, particularly in the dominant phyla and microbial networks. Specifically, the abundance of r-strategy bacteria (Bacteroidota, Actinobacteria, and Proteobacteria) increased with forest restoration and decreasing aggregate size fractions. Similarly, fungal K-strategists (Basidiomycota) increased following forest restoration, whereas fungal r-strategists (Mortierellomycota) increased in the smaller aggregate size fractions. Microbial networks became more complex and tighter with forest restoration and decreasing aggregate size fractions. These shifts in microbial life strategies and co-occurrence patterns likely enhance the formation of microbial-derived organic matter, improve the efficiency of resource allocation and ecological signal transmission, and thereby promote soil fertility accumulation. Overall, this study highlights the critical role of forest restoration in abandoned rubber plantations in reshaping soil microbial communities and emphasizes the potential of soil microbes as indicators of soil resilience and health.

Xiaoyi Cai and Chunfeng Chen contribute equally.

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1 | Introduction

Microorganisms dominate soil health and play pivotal roles in sustaining biogeochemical cycling and regulating the response of the soil ecosystem to anthropogenic activities and environmental shifts (Qiu et al. 2021; Coban et al. 2022). Managing and maintaining soil microbial communities with reasonable structures can promote the restoration and holistic health of degraded ecosystems (Ma et al. 2022; Pedrinho et al. 2024). Soil erosion has become one of the greatest challenges in recent years (Coban et al. 2022; Hartmann and Six 2023), causing severe disasters (e.g., a decline in soil fertility and microbial diversity). These changes, such as soil organic matter sequestration and nutrient cycling, eventually influence the associated ecosystem services and land productivity (Qiu et al. 2021; Zhu et al. 2022; Philippot et al. 2024). To meet financial requirements and address the latex demand, rubber plantations have grown extensively worldwide, particularly in Southeast Asia, during the last few years, resulting in dwindling primary rainforests (Warren-Thomas et al. 2015; Zhang et al. 2019; Singh et al. 2021; Wang and Zhang 2025). Additionally, the crises of grievous soil erosion and structural degradation, soil nutrient loss, soil microbial community structure simplification, and biodiversity decline have started to emerge because of the single-vegetation composition, thinner ground cover, and heavy seasonal rainfall intensity in rubber plantation areas (Liu et al. 2016; Zhu et al. 2018; Cai et al. 2024; Wang and Zhang 2025). Consequently, native forest restoration may be an alternative approach to reconstruct the microbial community structure and mitigate soil quality decline and biodiversity loss in erosively degraded lands (Teng et al. 2019; Xu et al. 2022; Kang et al. 2024). However, it remains unclear how stepwise forest restoration affects soil fertility through its influence on soil microbial communities (Chen, Wang, et al. 2023; Zhang, Liu, et al. 2024).

Soil aggregates, which are fundamental components of soil structure and indicators of soil quality, play important roles in protecting soil organic matter, determining nutrient adsorption and desorption, influencing microbial community structure, and reducing runoff and erosion (Six et al. 2004). The formation and breakdown of soil aggregates are influenced by human-induced pressures such as agricultural management and intensive land utilization. The deforestation of primary forests and planting monocultures can significantly decrease the aggregation of soil particles (Gholoubi et al. 2019; Blanco-Canqui 2024). As a result, soil fertility is diminished, and the microbial community structure within aggregates is significantly altered (Gholoubi et al. 2019; Rui et al. 2022). As the primary drivers of soil carbon, nitrogen, and phosphorus cycling, microorganisms fundamentally regulate the storage and utilization of these key nutrients (Liao et al. 2018; Baumert et al. 2021). Additionally, soil aggregates of different sizes provide heterogeneous microenvironments and habitats with different physicochemical properties, which subsequently affect soil microbes and their functional roles in carbon, nitrogen, and phosphorus cycling (Liao et al. 2018; Chen, Wang, et al. 2023). However, little is known about how microbial co-occurrence patterns change and how soil nutrients and microbes are linked with different-sized soil aggregates in response to primary tropical rainforest conversion and restoration.

Forest restoration plays an essential role in the regulation of soil microbial communities and their distribution (Turley et al. 2020; Zhang et al. 2021). Furthermore, it significantly influences soil aggregation and nutrient cycling processes (Hu et al. 2023; Liu et al. 2025). Previous research has demonstrated that forest restoration changes bacterial composition and cross-kingdom coexistence patterns, as well as increases increased soil multifunctionality and soil fertility (Wang et al. 2022; Chen, Chi, et al. 2023; Zhang, Liu, et al. 2024). Another study found that forest restoration of bare land and farmland promoted soil fertility and enzyme activities, while fungi were more sensitive than bacteria to unique microenvironments within different-sized soil aggregates (Chen, Wang, et al. 2023). Notably, Liu et al. (2025) found that forest restoration of farmland led to a reduction in the average 16S rRNA operon copy number and the complexity of the functional network. The influence of forest restoration on soil microorganisms may be due to the recovered tree species, soil type, and microclimate. Most studies have focused on the restoration processes of bulk soil from bare land or farmland to forest, whereas dynamic changes in microbial communities within soil aggregates following forest restoration in the soil-depleted land of rubber plantations remain unclear.

In this study, three forest types were studied, including rubber monoculture plantation (RM), jungle rubber (JRM, natural restoration of rubber monoculture), and jungle rubber × *Camellia sinensis* mixed plantation (JRC). A tropical rainforest (RF) was used as the control. Using a space-for-time substitution approach, the four forest types were considered to have undergone degradation and restoration. The forest conversion pathway began with a transition from RF to RM (degradation). This was followed by a restoration transition from RM to JRM or JRC. Over extended temporal scales, these ecosystems were projected to undergo ecological succession from JRM or JRC towards RF. In addition, we aimed to investigate how forest restoration influences soil fertility in bulk soil and different-sized soil aggregates, with a particular emphasis on microbial community dynamics. Forest restoration improves soil structure and increases the diversity and quantity of nutrient inputs. This improved soil microenvironment stimulates microbial growth, particularly favoring r-strategy microbes (Shao et al. 2021; Duan et al. 2023), resulting in high micro-derived organic matter production and rapid nutrient turnover. The resultant nutrient-rich conditions reduced microbial competition, thereby fostering the development of more complex and stable co-occurrence networks. Such network optimization enhances nutrient use efficiency and facilitates greater sequestration of soil organic carbon and nutrients (Zhao et al. 2023). Furthermore, the unique physical structure of microaggregates likely provides enhanced protection for soil organic matter and facilitates greater microbial aggregation (Dorodnikov et al. 2009; Tiemann et al. 2015). Thus, three hypotheses were tested: (i) both forest restoration and smaller aggregate fractions enhance soil fertility indicators, (ii) forest restoration and smaller aggregate fractions foster greater microbial diversity, r-strategy microbes, and network complexity, and (iii) the resultant nutrient enrichment stems from modifications in microbial diversity, community composition, and interaction networks.

2 | Materials and Methods

2.1 | Description of Research Site and Soil Sampling

The research site is located in four long-term forest monitoring stations in the Xishuangbanna in Yunnan Province, China (21°55′39″ N, 101°16′34″ E, 101°15′55″ E). Mean annual temperature at these stations was between 24°C and 29°C, whereas the average annual precipitation was 1475 mm. The soils are classified as laterites (Oxisols) (Chen et al. 2019). RF is a climatic climax community consisting of *Pometia tomentosa*, *Garcinia cowa*, *Ficus subulate*, *Baccaurea ramiflora*, and *Pteridrys cnemidaria*. Rubber trees at RM were cultivated with a 2.5 × 3.0 m spacing on land cleared of native rainforest. Each pair of double rows is separated by a gap of 18.0 m. Synthetic fertilizer, which contained N, P, and K, was applied at an annual rate of 200 kg ha^{-1} in mid-October in the RM. Rubber tapping was performed on alternate days, starting in late April and continuing until mid-November. The shrubs and herbs were regularly cleared using herbicides. JRM and JRC communities were established in aged rubber plantations and aged rubber × tea plant (*Camellia sinensis*) intercropped plantations, respectively. Additionally, JRM and JRC have experienced natural succession for 10 years and have formed multi-layered vegetation (tree, herb, and shrub layers). All rubber trees were planted in 1962, after the deforestation of a native rainforest. In 2005, tea trees were planted in 18-m-wide gaps between the rows of rubber trees.

We established four 20 × 20 m sampling plots at each forest site in February 2023. Composite soil samples were prepared for each plot by collecting and homogenizing five topsoil cores (0–20 cm depth). The homogenized soil was then sieved through a 4 mm sieve to exclude roots and rocks. In addition, the sieved soils were stored at 4°C for approximately 7 days, allowing soil moisture content to decrease to approximately 10% in preparation for the soil aggregate fractionation experiments. To minimize perturbation of soil microbial communities during isolation, soil aggregates were separated using a modified dry-sieving protocol (Wang et al. 2015; Yuan et al. 2021; Zhang, Song, et al. 2024): large macroaggregates (LMA) exceeding 2000 μm, small macroaggregates (SMA) between 250 and 2000 μm, and microaggregates (MI) smaller than 250 μm. In addition, we maintained the bulk soil for analysis. Bulk soil and separated soil aggregates were freeze-dried. The freeze-dried soils were stored at −80°C and 4°C and used for genomic DNA and soil properties analysis, respectively. The pH and electrical conductivity (EC) were measured in a soil: water (*w/v*, 1:2.5) mixture using a glass-electrode meter. Soil organic C (SOC) content was determined using a dichromate wet oxidation approach described by Vitti et al. (2016). The total N (TN) was measured using a CN elemental analyzer (Vario MAX, Elementar, Germany). Total P (TP) was measured using ICP-AES (ICAP6300, Thermo Fisher Scientific, USA) after pre-digestion with a mixed acid (nitric acid, hydrogen fluoride, and perchloric acid).

2.2 | DNA Extraction and Sequencing

DNA was extracted from each subsample (0.5 g) using the CTAB/SDS method. The bacteria-specific V4 hypervariable region of the 16S rRNA gene was amplified with the primer pairs 341F/806R (5′-CCTAYGGGRBGCASCAG-3′/5′-GGACTACNNGGGTATCTAAT-3′) (Klümper et al. 2015). The fungal ITS1 region was amplified using the primer pairs ITS1F/ITS2R (5′-CTTGGTCATTTAGAGGAAGTAA-3′/5′-GCTGCGTTCTTCATCGATGC-3′) (Ranjard et al. 2000). The mixture of amplicon was analyzed using the Illumina NovaSeq platform (Illumina, San Diego, CA, USA). The bacterial V4 and fungal ITS sequences were analyzed and filtered using QIIME 2. After denoising with DADA2, final amplicon sequence variants (ASVs) and feature lists were generated for subsequent analysis. Functional predictions for bacteria and fungi were generated using PICRUSt and FUNGuild v 1.0, respectively. In total, 5,510,394 and 5,519,118 high-quality reads were obtained from bacteria (67,323–97,189 reads per sample) and fungi (70,976–96,109 reads per sample), respectively, from 48 soil samples. To reduce taxonomic bias, the microbial diversity was assessed using random subsample sequence sets to ensure rarefaction curve saturation. Downstream analyses used rarefied datasets with 67,323 sequences of soil bacteria and 70,976 sequences of soil fungi. From the 48 soil samples, we identified 51,007 bacterial and 15,683 fungal ASVs. Following singleton removal, the ASV tables were normalized to uniform observation counts. Raw sequence data were deposited in NCBI SRA (PRJNA1200975 and PRJNA1201057).

2.3 | Microbial Network Construction

Spearman's rank coefficient of correlation (*r*) was used to construct the co-occurrence networks of bacteria and fungi. To reduce the redundancy of rare OTUs, the OTUs detected in fewer than eight samples from the microbial datasets were removed. Correlations of $|r| > 0.8$ and $p < 0.01$ were used to construct networks. Network parameters were evaluated using the “igraph” package. Furthermore, sub-networks of individual soil samples were obtained using the subgraph extraction, as described by Ma et al. (2016). The parameters of the sub-networks in each sample, including nodes, edges, average degree, and modularity, were calculated. Gephi 0.10.1 was used to visualize microbial networks.

2.4 | Data Analysis

Given that all data satisfied the criteria for homogeneity of variance and normality, they were directly applied to the statistical analysis. The effects of forest types and/or soil aggregates on soil properties, the community diversity of microbes, and the relative abundance of microbial phyla were evaluated using one-way or mixed-effects analysis of variance (ANOVA) and Duncan's test. The *F* and *p values* of ANOVA were calculated using the aov() function. One-way and mixed-effect ANOVA allowed us to examine whether the effects of forest types and forest types varied with the size of soil aggregates, respectively. Alpha diversity indices, including the abundance-based coverage estimator (ACE) and Shannon indices, were calculated using the “vegan” package. Principal coordinates analysis (PCoA), permutational multivariate analysis (PERMANOVA), and Bray–Curtis dissimilarity were used to investigate the dissimilarities in microbial community structures (“vegan” package). Microbial diversity was compared using Duncan's test. We applied the Mantel test (“vegan” package) and Pearson's correlation analysis (“psych”

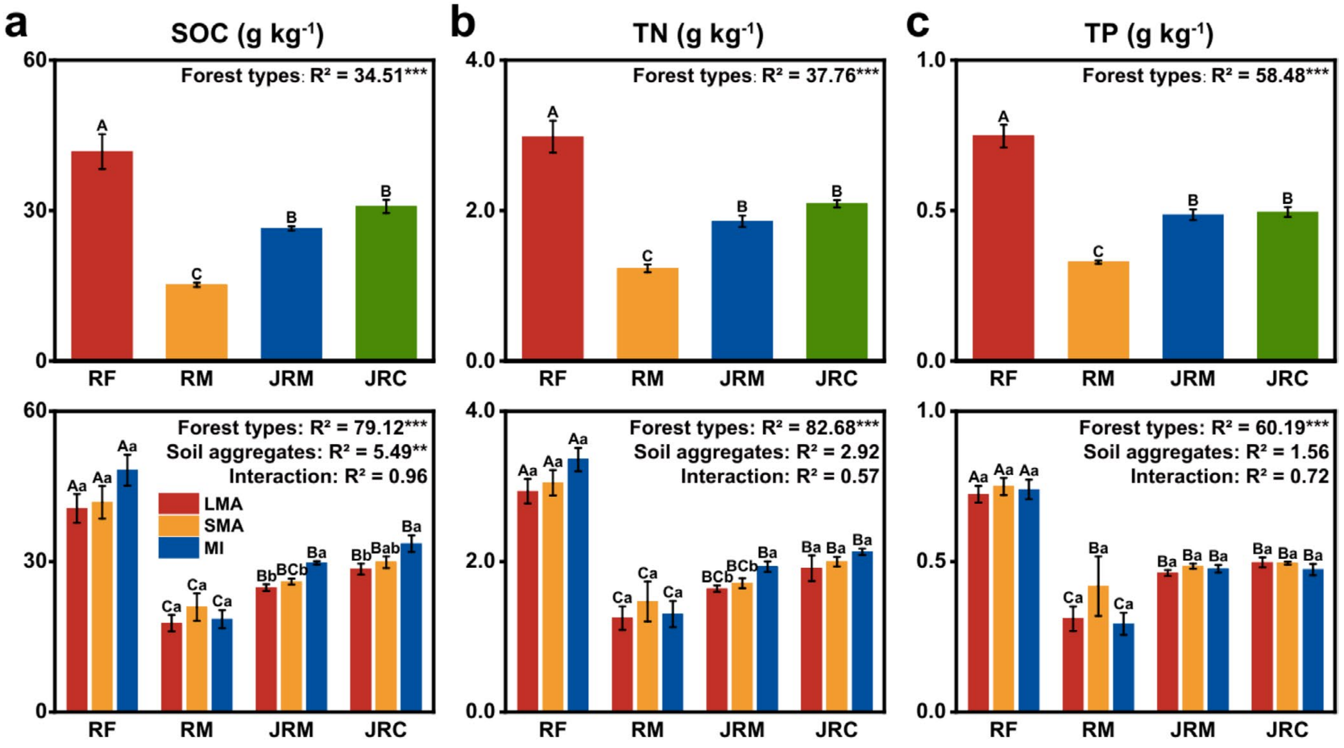

FIGURE 1 | Soil fertility across various forest types. Soil organic carbon (a), total nitrogen (b), and total phosphorus (c) in the bulk soil and soil aggregates. RF, rainforest; RM, rubber monoculture; JRM, jungle rubber mixed; JRC, jungle rubber × *Camellia sinensis* mixed; LMA, large macroaggregate; SMA, small macroaggregate; MI, microaggregate. Capital letters indicate the significant difference in the different forest types of the same soil size (Duncan test, $p < 0.05$); Lowercase letters indicate the significant difference in the different soil aggregates of the same forest type (Duncan test, $p < 0.05$). [Colour figure can be viewed at wileyonlinelibrary.com]

package) to examine the relationship between soil properties and microbial composition and the correlations within the soil properties, respectively. We applied the random forest analysis ("rfPermute" package) to estimate the importance of forest types, soil aggregates, pH, EC, bacterial community indices, and fungal community indices for soil fertility. In addition, redundancy analysis (RDA) ("vegan" package) was applied to explore the relationships between soil properties and soil microbes. Finally, the partial least squares path modeling (PLS-PM) was conducted in the "plspm" package to determine the main path of forest restoration, soil aggregates, pH, EC, and microbial communities to the soil fertility. A goodness of fit index (GFI) > 0.36 was used to examine model fitting (Zhu et al. 2022; Wang, He, et al. 2023).

3 | Results

3.1 | Soil Physicochemical Properties in Bulk Soil and Different-Sized Soil Aggregates Among Different Forest Types

Soil pH of both the bulk soil and soil aggregates decreased in the sequence of RF, JRC, RM, and JRM (Table S1). Similarly, EC exhibited the highest value for RF, followed by JRC, RM, and JRM. Soil fertility in the bulk soil and soil aggregates decreased in the order of RF, JRC, JRM, and RM (Figure 1). Across all forest types, soil pH, SOC, and TN decreased in the orders of MI, SMA, and LMA (Figure 1 and Table S1).

3.2 | Soil Microbial Diversity in Bulk Soil and Different-Sized Soil Aggregates Among Different Forest Types

The bacterial alpha diversity and fungal ACE index of bulk soil and soil aggregates decreased in the following order: JRC, JRM, RF, and RM (Figure 2a,b). The bacterial alpha diversity and fungal ACE index of different soil aggregate size fractions within the same forest type were in the decreasing order of MI, SMA, and LMA (Figure 2c,d). The soil pH, EC, and soil fertility were positively correlated with the bacterial Shannon and fungal ACE indices (Figure 5a). The same correlation was shown between SOC and bacterial Shannon index for different aggregate size fractions (Figure S1).

The microbial compositions (beta diversity) in the bulk soil and soil aggregates differed significantly between the forest types (Figure 2a,b). In addition, microbial community composition showed positive correlations with pH, EC, and soil fertility (Figures 5b and S2).

3.3 | Microbial Presence and Relative Abundance in Bulk Soil and Different-Sized Soil Aggregates Among Different Forest Types

In bulk soil, the relative abundances of Acidobacteria and Chloroflexi showed a decline in the following sequence: RM, JRM, JRC, and RF (Figure 3a and Table S2). Conversely, the

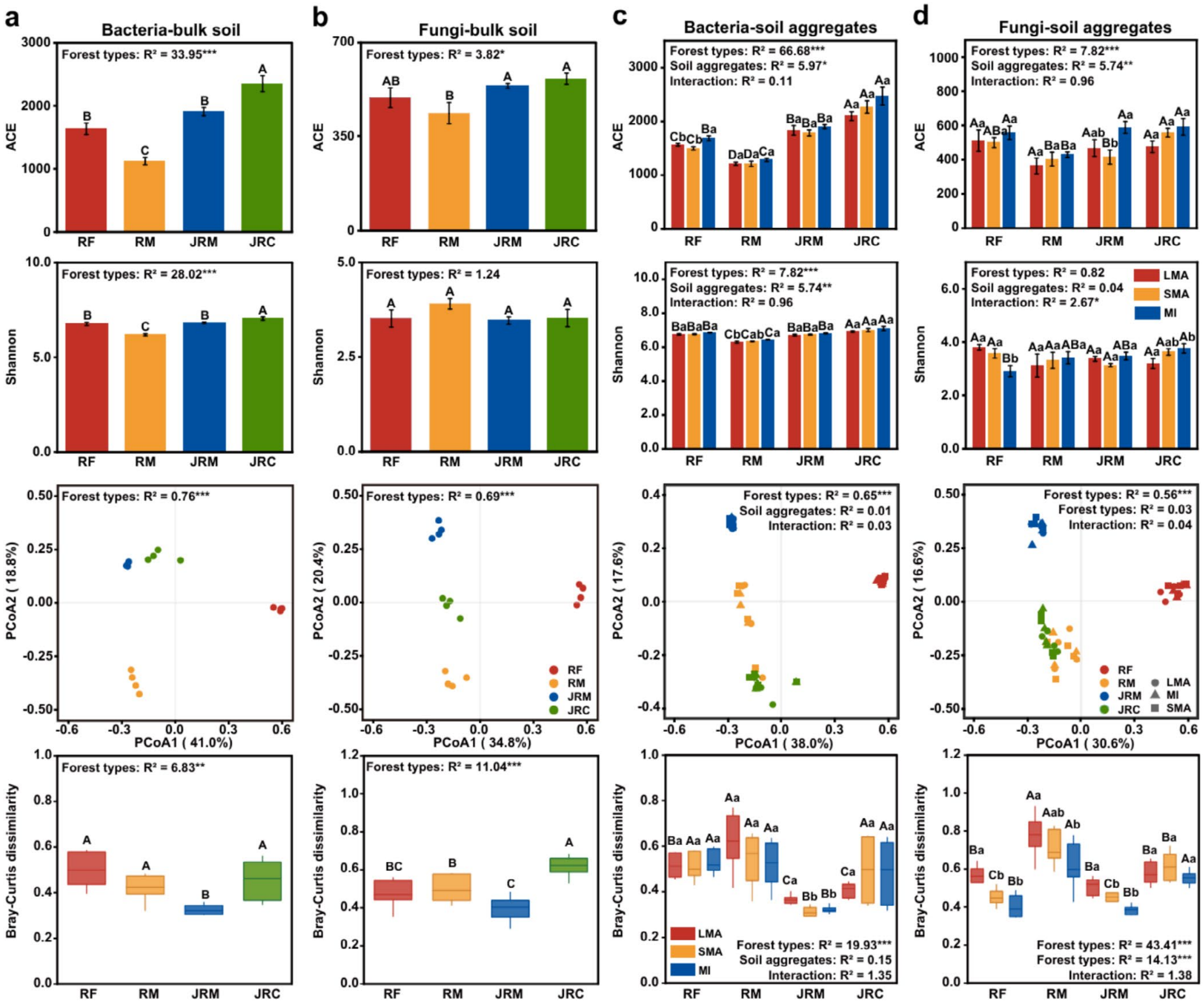

FIGURE 2 | Bacterial and fungal alpha and beta diversity in bulk soil and soil aggregates across various forest types. ACE index, Shannon index, PCoA, and Bray–Curtis dissimilarity of bacteria (a) and fungi (b) in the bulk soil. ACE index, Shannon index, PCoA, and Bray–Curtis dissimilarity of bacteria (c) and fungi (d) in different-sized soil aggregates. RF, rainforest; RM, rubber monoculture; JRM, jungle rubber mixed; JRC, jungle rubber × *Camellia sinensis* mixed; LMA, large macroaggregate; SMA, small macroaggregate; MI, microaggregate. Capital letters indicate the significant difference in the different forest types of the same soil size (Duncan test, $p < 0.05$); Lowercase letters indicate the significant difference in the different soil aggregates of the same forest type (Duncan test, $p < 0.05$). [Colour figure can be viewed at wileyonlinelibrary.com]

abundance of Bacteroidota, Actinobacteria, Latescibacterota, and Methylomirabilota showed a decline in the following sequence: RF, JRC, JRM, and RM (Figure 3a and Table S2). The order of decreasing Proteobacteria abundance in the bulk soil was JRC, followed by JRM, RF, and RM (Figure 3a and Table S2). Additionally, the relative abundances of Acidobacteria, Verrucomicrobiota, and Chloroflexi increased with larger aggregate size fractions within the same forest type, whereas Proteobacteria and Actinobacteria showed the opposite trend (Figure 3a and Table S2). Notably, the relative abundances of Acidobacteria and Chloroflexi were negatively correlated with pH, EC, and soil fertility (Figures 5a and S3). Furthermore, the abundances of Proteobacteria, Bacteroidota, and Actinobacteriota were positively correlated with the soil properties (Figure S3).

The abundance of Basidiomycota showed a decline in the following sequence: JRC, JRM, RM, and RF in the bulk soil, whereas Ascomycota showed a decrease in the sequence of RM, JRM, JRC, and RF (Figure 3b and Table S3). The abundances of Ascomycota and Basidiomycota increased with an increase in aggregate size fractions in the same forest type, whereas Mortierellomycota exhibited the opposite trend (Figure 3b and Table S3). The abundances of Ascomycota and Basidiomycota were negatively correlated with pH, EC, and soil fertility in different-sized soil aggregates, whereas Mortierellomycota was positively correlated with these soil physicochemical attributes (Figures 5a and S4).

3.4 | Soil Microbial Networks in Bulk Soil and Different-Sized Soil Aggregates Among Different Forest Types

Among the forest types, JRC showed higher microbial network complexity for both bacteria and fungi compared to JRM and RM

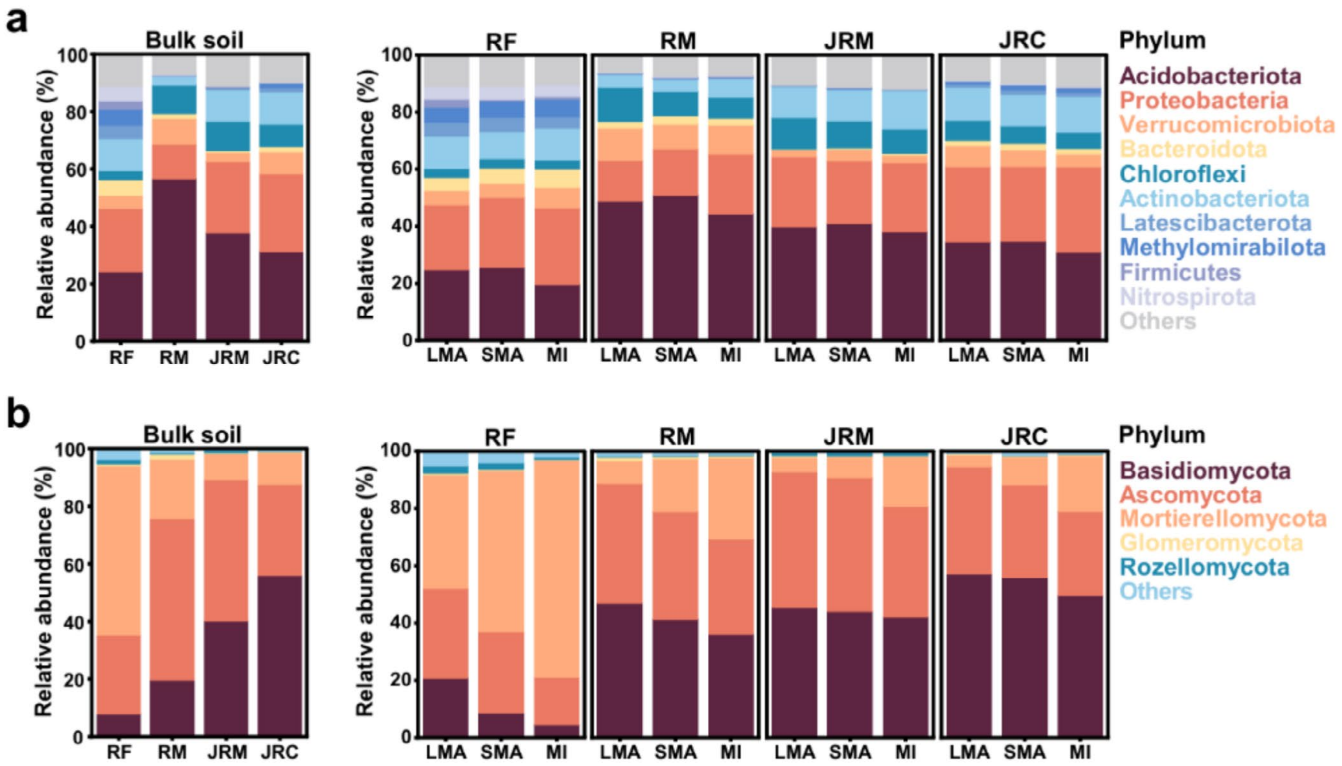

FIGURE 3 | The dominant microbial phyla composition and abundance. Soil bacterial relative abundance in bulk soil and soil aggregates across various forest types (a). Soil fungal relative abundance in bulk soil and soil aggregates across various forest types (b). RF, rainforest; RM, rubber monoculture; JRM, jungle rubber mixed; JRC, jungle rubber × *Camellia sinensis* mixed; LMA, large macroaggregate; SMA, small macroaggregate; MI, microaggregate. [Colour figure can be viewed at wileyonlinelibrary.com]

(Figure 4a). The percentage of positive links in the bacterial networks followed the gradients of JRC, RF, JRM, and RM, whereas fungal networks followed the gradients of JRM, RF, JRC, and RM (Table S4). In bulk soil, bacterial networks demonstrated greater complexity than the fungal networks (Figure 4b and Table S5). Notably, microbial network complexity progressively increased with decreasing soil aggregate size fraction. Pearson correlation analysis revealed significant relationships between bacterial network complexity and the measured soil properties (Figures 5a and S5).

3.5 | Soil Microbial Functions in Different-Sized Soil Aggregates Among Different Forest Types

The bacterial and fungal functions exhibited distinct patterns across forest types and aggregate size fractions (Figures S6 and S7). Undefined saprotrophs, soil saprotrophs, and plant saprotrophs in the bulk soil showed a decline sequence: RF, JRC, RM, and JRM (Figure S6b). Notably, the relative abundances of fungal parasites and endophytes showed consistent reductions with increasing aggregate size fractions within each forest type, following the order: MI, SMA, and LMA (Figure S7d).

3.6 | Comprehensive Relationships Between Abiotic Factors, Biotic Factors, and Soil Fertility

Both random forest and RDA models revealed that forest types, pH, EC, bacterial composition, and fungal composition were significantly associated with soil fertility (Figure 6A,B and Table S6). Specifically, pH and EC exhibited strong correlations with both bacterial and fungal community structures across all aggregate size classes and forest types (Figure 6b and Table S6). PLS-PM analysis revealed the positive and negative effects of forest restoration and soil aggregates on pH/EC and soil microbes, respectively (Figure 7a). Soil pH and EC positively influenced soil microbes, which in turn directly enhanced soil fertility. Notably, soil microbes exhibited the strongest total effect on soil fertility among all factors examined (Figure 7b).

4 | Discussion

4.1 | Soil Physicochemical Properties

In this study, an increase in soil fertility was noted in the bulk soils of restored forests compared with that of rubber monoculture plantation (Figure 1), which is consistent with previous reports on soil quality improvement in rubber-based agroforestry systems (Chen et al. 2019; Zeng et al. 2021). Rubber monoculture plantations typically exhibit severe soil degradation, manifested through erosion, topsoil loss, nutrient depletion, carbon depletion, and biodiversity reduction (Coban et al. 2022). Forest restoration can enhance the soil quality through multiple pathways. First, increased vegetation diversity and plant-derived organic matter inputs, combined with reduced anthropogenic disturbances (e.g., the application of compound fertilizer and sulfur powder) and improved soil hydrological structure, collectively contribute to elevated

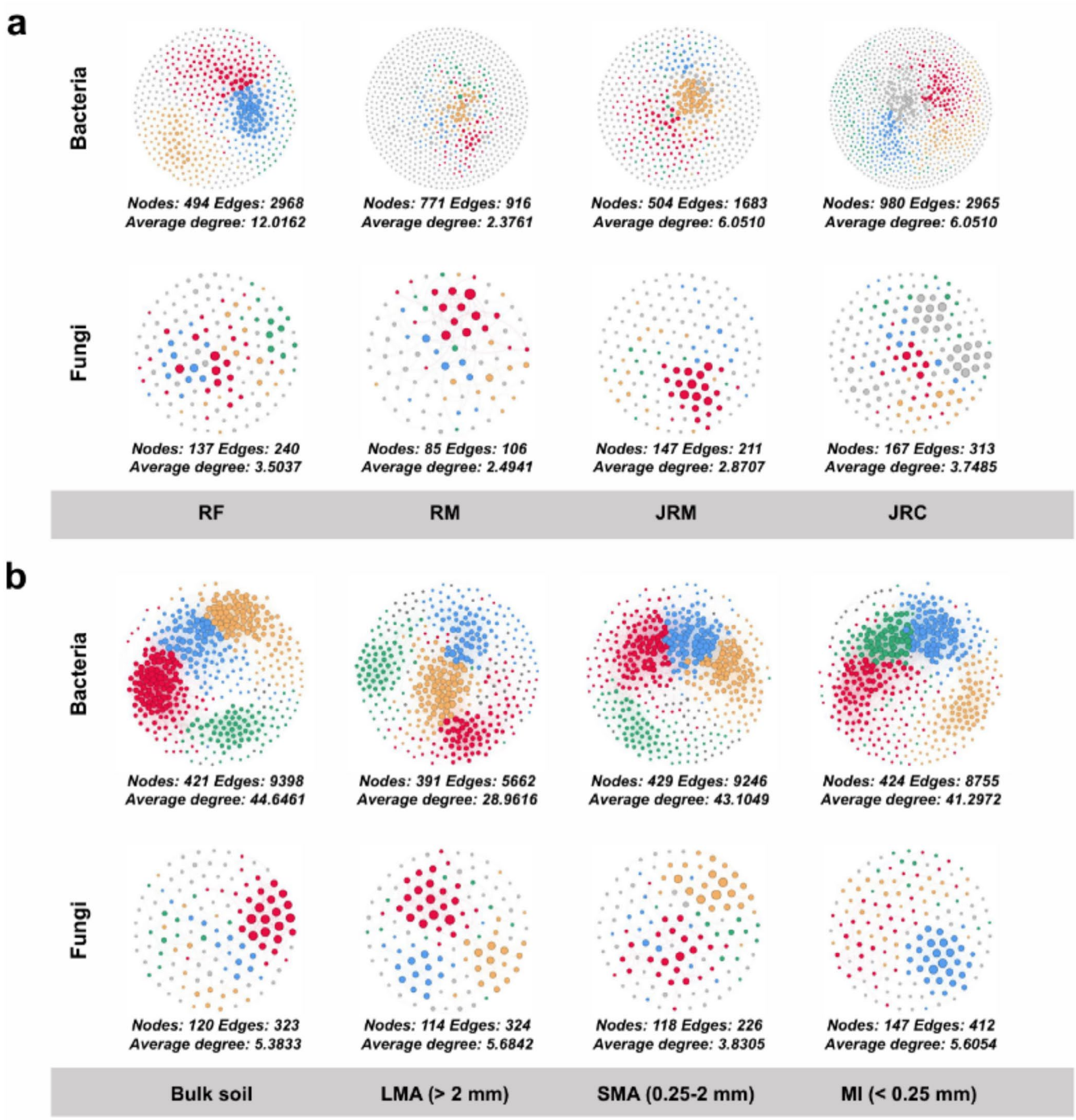

FIGURE 4 | Soil microbial co-occurrence networks. The co-occurrence networks of bacteria and fungi in bulk soils (a). The co-occurrence networks of bacteria and fungi in different-sized soil (b). RF, rainforest; RM, rubber monoculture; JRM, jungle rubber mixed; JRC, jungle rubber × *Camellia sinensis* mixed; LMA, large macroaggregate; SMA, small macroaggregate; MI, microaggregate. [Colour figure can be viewed at wileyonlinelibrary.com]

pH, EC, organic carbon, and nutrient (N and P) levels in restored forest soils (Zhu et al. 2019; Zeng et al. 2021). Second, elevated soil pH in tropical restored forests may reduce the priming effect intensity by alleviating microbial phosphorus limitation and decreasing enzyme secretion to decrease the decomposition of organic matter (Liu et al. 2019, 2023; Wang and Kuzyakov 2024; Zou et al. 2025).

Our results revealed significantly higher SOC and TN concentrations in microaggregates than in macroaggregates (Figure 1), which is consistent with prior findings (Tiemann et al. 2015; Han et al. 2021, 2024). This distribution pattern can be attributed to several unique physicochemical and biological properties of smaller soil aggregates. Primarily, microaggregates exhibit high extracellular enzyme activity, which accelerates the decomposition of externally sourced organic matter, leading to increased soil available carbon and nitrogen (Han et al. 2024). These available nutrients are ultimately assimilated by soil microorganisms and stored within living biomass. Additionally, relatively higher microbial biomass

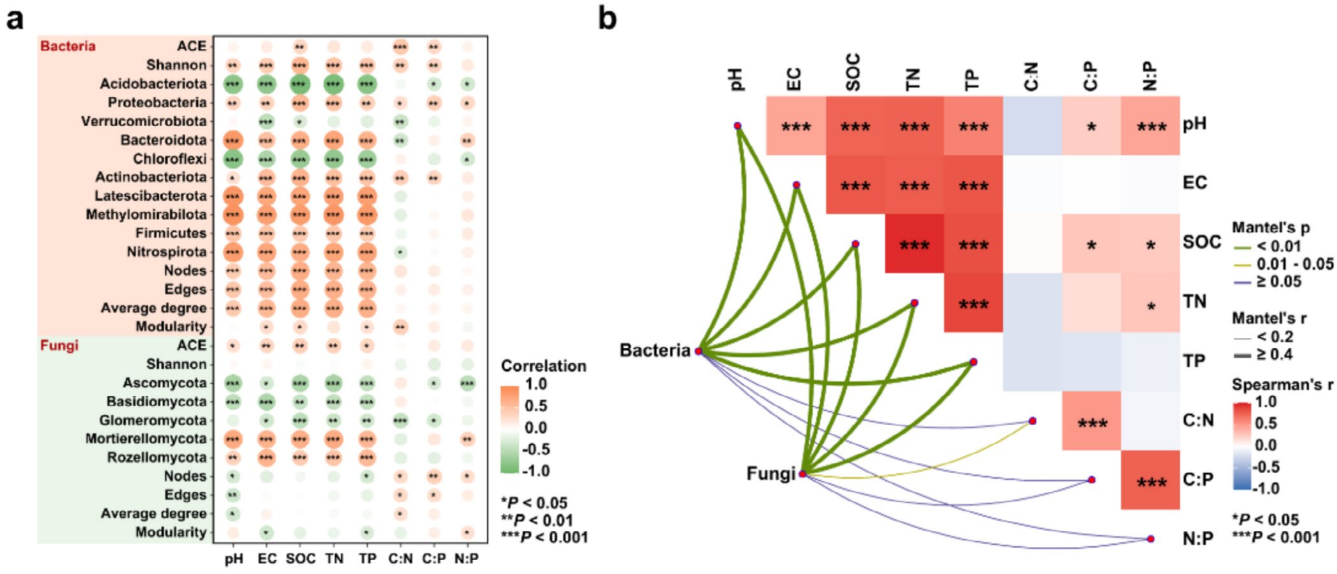

FIGURE 5 | Relationships between soil properties and microbial communities. The Pearson correlation coefficients between microbial alpha diversity, dominant phyla, network parameters, and soil properties (a). Mantel test among soil properties and between soil properties and bacterial and fungal composition (b). EC, electrical conductivity; SOC, soil organic carbon; TN, total nitrogen; TP, total phosphorus; C:N, the ratio of SOC to TN; C:P, the ratio of SOC to TP; N:P, the ratio of TN to TP. [Colour figure can be viewed at wileyonlinelibrary.com]

within microaggregates may enhance microbial necromass accumulation, potentially contributing to stable organic carbon formation (Wang et al. 2015, 2021; Zhao et al. 2023). Furthermore, organic matter tends to be older and is more effectively protected through mineral associations in microaggregates than in macroaggregates, resulting in reduced accessibility (Tiemann et al. 2015).

4.2 | Forest Restoration and Soil Aggregates Reshaped Soil Microbial Communities

In our study, forest restoration significantly enhanced soil microbial communities, including alpha diversity and network complexity (Figures 5 and 7a), primarily mediated through pH and EC modifications. Compared to degraded rubber plantations, restored forests exhibited greater plant diversity, which enhanced resource availability for soil microbes and consequently increased microbial activity, biomass, community stability, and network complexity (Qiu et al. 2021; Duan et al. 2023). Soil pH and EC are established key drivers of microbial community assembly (Liu et al. 2019; Fu et al. 2020; Zhang, Ji, et al. 2024), although their influence varies with soil type (Zeng et al. 2020). Crucially, forest restoration increases soil pH and EC in acidic rubber plantation soils, potentially improving microbial nutrient use efficiency while reducing maintenance energy costs, thereby promoting greater microbial biomass and diversity (Aye et al. 2017; Liu et al. 2019). These findings support our hypothesis (ii), indicating that increases in pH and EC during forest restoration may generate favorable conditions for soil microbial communities in former rubber monocultures.

Notably, the microbial communities in the microaggregates showed greater diversity and network complexity than those in the macroaggregates (Figures 2 and 4). This distribution pattern of microbial communities is likely due to larger specific surface areas and more soil nutrients in smaller aggregates (Chen, Wang, et al. 2023). Additionally, the presence of numerous small pores in the microaggregates provides physical protection to microbes against protozoan predation (Dorodnikov et al. 2009).

4.3 | Microbial Diversity, Composition, Networks, and Functions in Soil Fertility Regulation

Soil microorganisms play a pivotal role in regulating soil organic matter dynamics and nutrient cycling processes (Figure 7b; Liu et al. 2023). Our findings demonstrated that forest restoration significantly enhanced microbial diversity, which is closely associated with improved soil quality (Figure 5a; Wang, Mishra, and Yang 2023). Specifically, we observed marked increases in copiotrophic bacterial phyla (Bacteroidota, Actinobacteria, and Proteobacteria), which were positively correlated with soil fertility indicators (Figures 3a and 5a). These r-strategists thrive in organic-rich environments, where they contribute to the biodegradation of organic matter and nutrient cycling through extracellular enzyme production and rapid biomass turnover (Yang et al. 2022; Zhao et al. 2023). Conversely, oligotrophic K-strategists (Acidobacteriota and Chloroflexi) showed reduced abundance in the restored forests, likely due to the altered physicochemical conditions characterized by elevated pH, EC, and nutrient availability.

Fungal community composition exhibited parallel shifts during ecosystem recovery, transitioning from Ascomycota-dominated (r-strategy) to Basidiomycota-rich (K-strategy) assemblages, consistent with the results reported by Liu et al. (2020) and He et al. (2022). This transition reflects

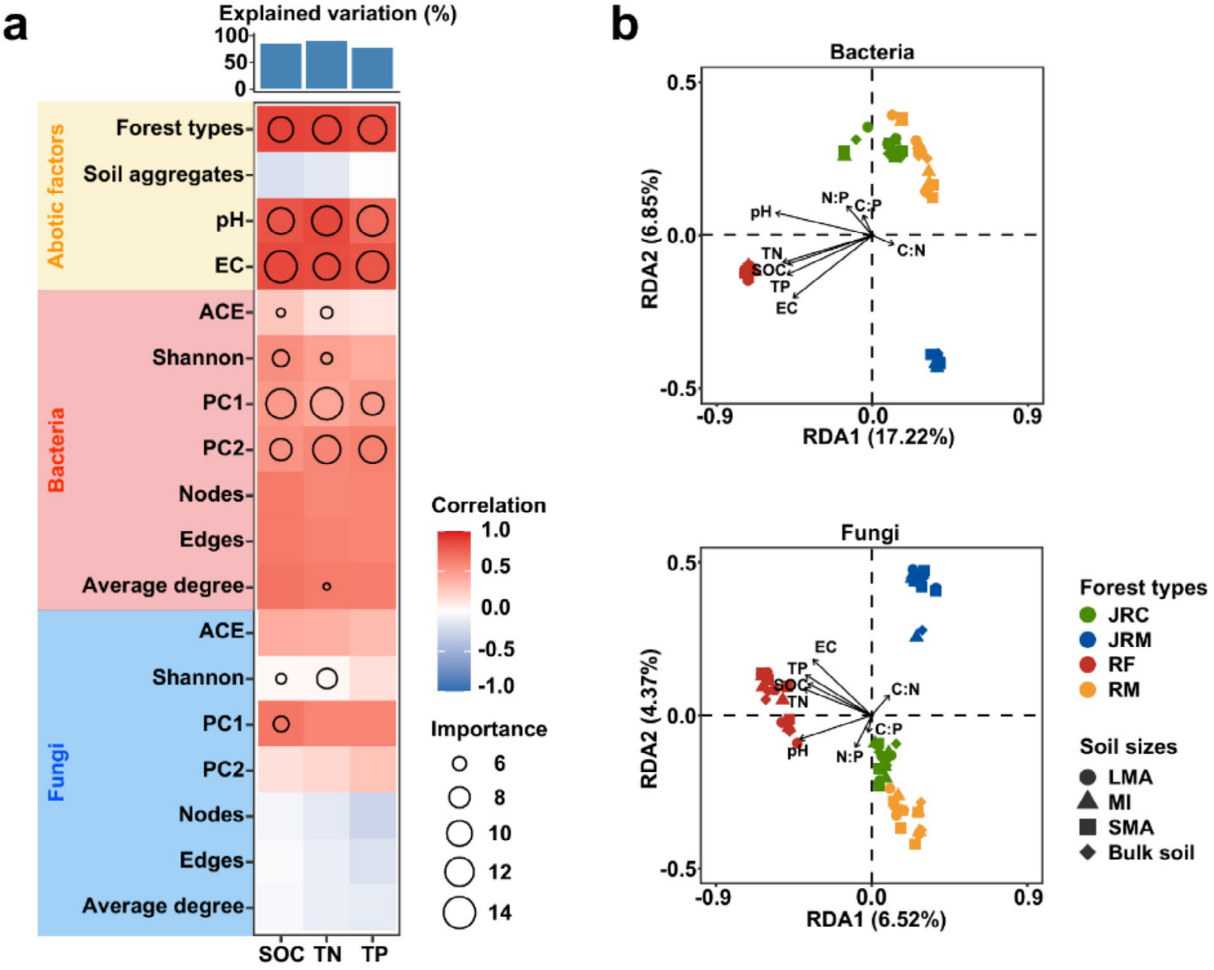

FIGURE 6 | Relationships between soil fertility and abiotic and biotic factors. Contributions of abiotic and biotic factors to soil fertility based on Pearson's correlation and random forest model (a). The redundancy analysis (RDA) shows the relationship between soil bacterial and fungal communities and the physicochemical properties in bulk soil and in different-sized soil aggregates (b). EC, eletrical conductivity; SOC, soil organic carbon; TN, total nitrogen; TP, total phosphorus; C:N, the ratio of SOC to TN; C:P, the ratio of SOC to TP; N:P, the ratio of TN to TP; PC1, the first component from the principal coordinate analysis conducted for microbial ASVs (i.e., the variation in microbial community); PC2, the second component from the principal coordinate analysis conducted for microbial ASVs (i.e., the variation in microbial community). Circle size represents the variables' importance (i.e., percentage of increase of mean square error calculated via random forest model). [Colour figure can be viewed at wileyonlinelibrary.com]

changing litter quality, with Basidiomycota abundance increasing in response to the accumulation of recalcitrant organic matter (Jiang et al. 2021; Yang et al. 2022). The elevated abundance of Basidiomycota further promotes SOC formation during forest restoration by enhancing the development of mycorrhizal hyphae and the production of mucilage and polysaccharides (Zheng et al. 2022). Notably, rainforest ecosystems harbored distinct microbial communities characterized by elevated Mortierellomycota abundance (Figure 3b), which likely contributes to phosphorus mineralization through organic acid production (Wang et al. 2020; Duan et al. 2023). Importantly, microaggregates emerged as critical hotspots for copiotrophic microbial activity, showing particularly strong associations between r-strategist abundance and soil fertility parameters (Figure 3). These findings collectively support hypotheses (ii) and (iii), highlighting how forest restoration drives coordinated shifts in bacterial and fungal communities, which collectively enhance soil fertility through modified nutrient cycling pathways. The preferential colonization of microaggregates by copiotrophic microbes appears to be particularly important for stabilizing microbial-derived organic matter and maintaining nutrient pools in restored ecosystems.

Complex microbial networks reflect soil microbial adaptability and directly influence biomass production, respiration, and carbon use efficiency, thereby regulating nutrient cycling and ecosystem functions (Maynard et al. 2017; Qiu et al. 2021). Our study revealed that restored forests exhibited more intricate microbial networks with a higher proportion of positive interactions (indicating enhanced interspecific cooperation) compared to rubber monocultures (Table S4). Such network complexity improves nutrient use efficiency, accelerates cycling processes, and promotes organic carbon and nutrient accumulation (Liu et al. 2023; Wang, Zhang, et al. 2023; Zhao et al. 2023). Significantly, microaggregates harbored more complex microbial networks than macroaggregates (Table S5), likely because of their greater surface area and resource availability, which foster microbial interactions

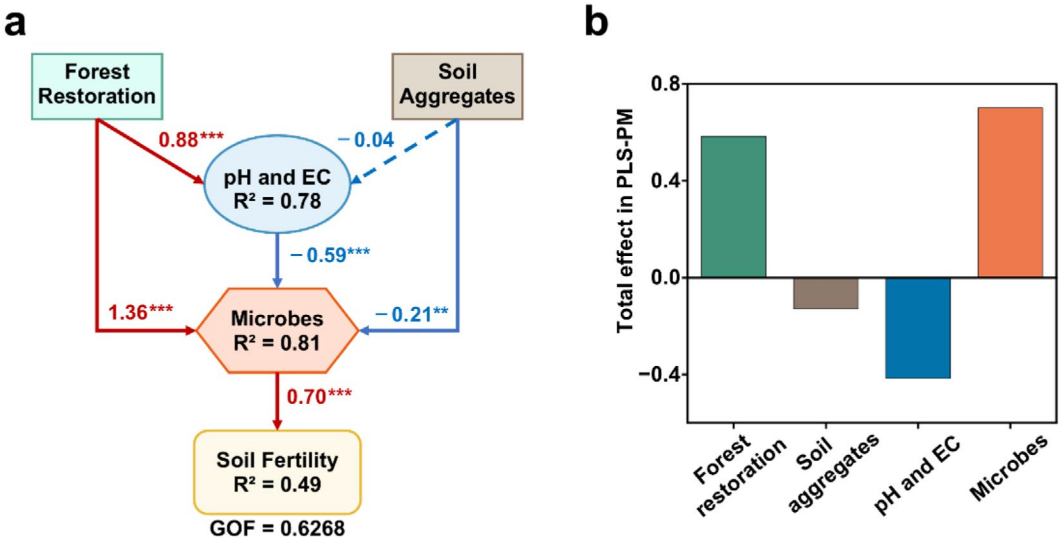

FIGURE 7 | Partial least squares path model (PLS-PM) analysis. PLS-PM of forest restoration, soil aggregates (i.e., soil aggregate sizes), soil pH and EC, microbes (i.e., microbial alpha diversity, composition, and network complexity), and soil fertility (i.e., SOC, TN, and TP) (a). Total effect coefficients of each variable on soil fertility (b). Red and blue arrows reflect positive and negative relationships, respectively. Significant and non-significant paths are denoted by solid and dashed arrows, respectively. R^2 values show the percentage of the total variance that each variable contributes to. **$p < 0.01$, ***$p < 0.001$. [Colour figure can be viewed at wileyonlinelibrary.com]

and nutrient turnover (Wang, Zhang, et al. 2023). Contrary to previous findings (Yang et al. 2022, 2024), fungal network complexity showed weaker associations with soil fertility parameters than with bacterial networks, likely reflecting the greater microenvironmental sensitivity of bacteria compared with the broader environmental tolerance of fungi (Yuste et al. 2011; Barnard et al. 2013; Sun et al. 2017). Notably, functional microbes including fungal parasites and soil saprophytic fungi were preferentially enriched in small aggregates (Figure S7d), where they respectively facilitate plant nutrient metabolism and drive humus decomposition (Zhang et al. 2022; Wei et al. 2024). These findings provide strong support for hypothesis (iii), demonstrating that the enhanced complexity and stability of microbial co-occurrence networks in both restored forests and small soil aggregates significantly improved the efficiency of resource allocation and ecological signal transmission. This network optimization promoted functional diversification within the microbial communities, ultimately leading to more robust nutrient cycling processes and greater soil organic matter accumulation.

4.4 | Limitations and Perspectives of the Research

Current microbial function prediction tools (e.g., PICRUSt, Tax4Fun2, and FUNGuild) have significant limitations in accurately characterizing soil microbial functional potential (Sun et al. 2020; Toole et al. 2021). These tools may systematically underestimate the abundance of genes involved in key biogeochemical processes, particularly those related to soil carbon and nitrogen cycling (Toole et al. 2021). Consequently, the functional predictions derived in this study, which rely on these methods, should be interpreted with caution. Therefore, shotgun metagenomic sequencing should be used in future studies to overcome these limitations.

Although this study demonstrated that forest restoration can effectively enhance soil fertility by regulating soil microbial community composition, the limited spatial scale and homogeneous edaphic conditions within our study area may have reduced the environmental heterogeneity typically required for robust ecological inferences (Hurlbert 1984). Therefore, caution should be exercised when extending these findings to other regions and ecosystems. Future research should investigate dynamic changes in microbial communities and their mechanistic roles in regulating soil nutrient cycles at broader spatial and temporal scales.

Consistent with previous studies (Zhang et al. 2021; Wang et al. 2022; Guo et al. 2024), our findings demonstrated that forest restoration in degraded rubber plantations significantly improved soil properties and shifted the microbial community structure toward a state approaching that of the climax rainforest ecosystem. Our previous studies have demonstrated the emergence of primary rainforest species (e.g., *Baccaurea ramiflora* and *Pteridrys cnemidaria*) in restored forests (Zeng et al. 2021; Cai et al. 2024), providing direct evidence of progressive plant succession. Considering the established role of soil microbial networks and keystone taxa in driving plant community assembly and stability (Qiang et al. 2021; Zandt et al. 2023), our findings collectively suggest that forest restoration initiates coupled plant–soil–microbiome feedback that may facilitate the recovery of degraded lands toward the original rainforest state. Future studies should prioritize temporal tracking of restored forests and integrate functional genomics to elucidate the microbial mechanisms underpinning plant establishment.

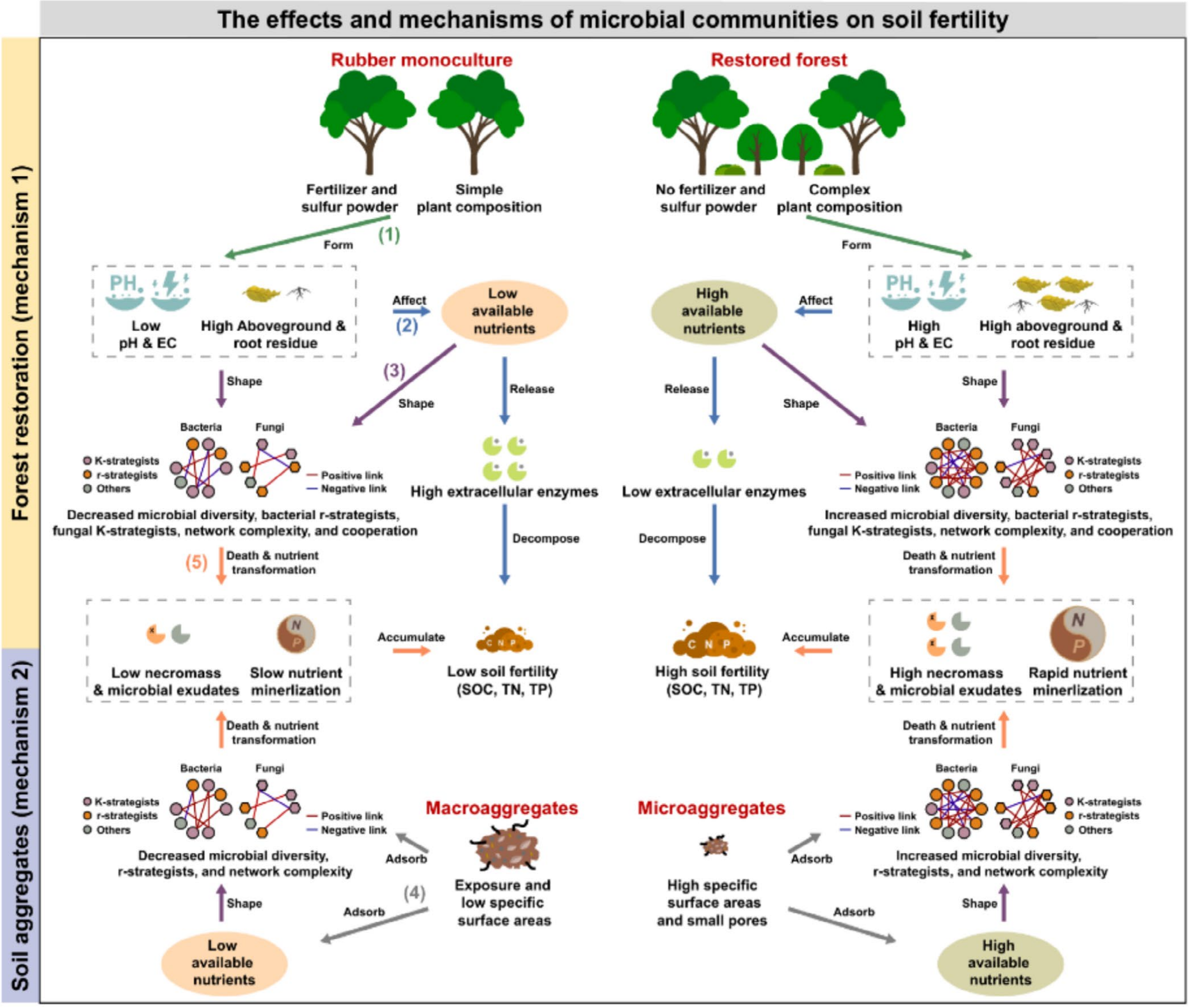

FIGURE 8 | Schematic diagram illustrating the key factors and mechanisms affecting soil fertility during forest restoration. Reduced field management and increased plant diversity during forest restoration enhanced soil pH, EC, and plant residue input (1). These improvements in the soil environment increased nutrient availability and alleviated microbial nutrient limitations, thereby reducing the secretion of extracellular enzymes by native microbial communities for organic matter decomposition (2). The resulting nutrient-rich conditions promoted the restructuring of microbial communities, characterized by higher diversity, increased abundance of bacterial r-strategists and fungal K-strategists, and the formation of more complex and cooperative co-occurrence networks (3). Meanwhile, smaller soil aggregates, characterized by a larger specific surface area and greater microporosity, retained more available nutrients and provided favorable microhabitats for microbial communities. Their composition and structure gradually resembled those found in restored forests (4). Ultimately, these reconstructed microbial communities supported rapid microbial metabolism and nutrient turnover, leading to significant accumulation of soil organic carbon, nitrogen, and phosphorus (5). [Colour figure can be viewed at wileyonlinelibrary.com]

5 | Conclusions

Our study elucidated the key mechanistic pathways by which forest restoration enhances soil fertility in degraded rubber plantations (Figure 8). We demonstrated that forest restoration, along with soil aggregates, pH, and EC, significantly influenced soil microbial community and soil fertility. Compared with rubber monocultures, restored forests developed more favorable soil pH and EC conditions, along with higher nutrient availability, a change attributable to the reduced application of fertilizer and sulfur powder and increased inputs of plant-derived organic matter. These improved soil conditions alleviate microbial nutrient limitations and indirectly reduce microbial maintenance energy costs, promoting greater microbial diversity and fostering a more complex community dominated by fast-growing bacterial r-strategists and fungal K-strategists. Such shifts in microbial life-history strategies and co-occurrence relationships are likely to enhance the production of microbial exudates and microbial-derived carbon, as well as improve ecological signal transmission, thereby stimulating microbial biomass turnover, increasing nutrient use efficiency, and promoting the sequestration of soil carbon, nitrogen, and phosphorus. Furthermore, the enrichment of available nutrients and small pores provided sufficient substrates and physical protection for microorganisms and reshaped the microbial composition within smaller soil aggregate fractions. This unique microenvironment increased microbial diversity and the prevalence of r-strategists and fostered stable co-occurrence patterns, which significantly contributed to higher microbial biomass and enhanced nutrient cycling, thereby supporting the accumulation of organic carbon and nutrients in smaller soil aggregates. These findings suggest that microbial diversity, life-history strategies, and interactions serve as key indicators of alterations in organic carbon and nutrient storage. In summary, this study revealed the effects of forest restoration and soil intrinsic heterogeneity (associated with soil aggregates) on microbial communities and soil fertility, underscoring the critical role of soil microbes in modulating soil health.

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Data Availability Statement

The data that support the findings of this study are available from the corresponding author upon reasonable request.

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Supporting Information

Additional supporting information can be found online in the Supporting Information section. **Data S1:** ldr70215-sup-0001-supinfo.docx.