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RESEARCH

Deciphering soil nematode-bacteria-fungi community composition and functional dynamics in coffee agroecosystems under conventional and sustainable management practices in Costa Rica

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Abstract

Understanding the interactions between soil bacteria, fungi, and nematodes in coffee agroecosystems is crucial for optimizing sustainable agriculture. This study investigated the composition and functional dynamics of these communities under conventional and sustainable management systems. Soil samples were collected from three major coffee-growing regions in Costa Rica, representing different agricultural regimes. Nematode community was analyzed using optical microscopy, while microbial communities were analyzed using high-throughput sequencing. In both cases, bioinformatic tools were used for functional prediction based on taxonomy.. Herbivorous nematodes dominated both systems, while bacterivores (Rhabditidae, Cephalobidae) and fungivores (Aphelenchoidae) were significantly more abundant in soils subject to sustainable practice ($p < 0.05$). Nematode maturity indices and food web diagnostics showed no significant differences between systems, even though metabolic footprints related to organic matter decomposition varied ($p < 0.05$). Bacterial communities were dominated by the phyla Proteobacteria, Acidobacteria, and Chloroflexi, while the fungal community was largely composed of Ascomycota (53.21% in both systems). The fungal genus *Mortierella* was particularly prevalent. Soil pH, along with Ca, Mg, K, and extractable acidity, influenced community composition. Functional profiles revealed higher gene abundances linked to nutrient and energy cycling in sustainable systems, particularly phosphorus and sulfur metabolism. Saprotroph-symbiotroph fungi were more common in sustainable soils, while pathotrophic fungi dominated conventional systems. This is the first comprehensive analysis of bacteria, fungi, and nematodes across different agricultural practices in coffee agroecosystems in Costa Rica.

Keywords Biodiversity · Ecology · Microbiome · Rhizosphere · Soil

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Introduction

Coffee is the second most consumed beverage after water in the world (FAO 2023). Coffee (mainly *Coffea arabica* L.) is cultivated in over 50 countries, demonstrating that has been adapted to a range of environmental conditions and agricultural practices. Intensive agricultural practices, however, while boosting crop productivity, often damage chemical and physical soil properties (Dubey et al. 2019). Knowledge about soil and plant microbial communities is a trending topic in research, but the practical applications of microbiome data for more sustainable coffee agriculture has not been fully explored.

There is growing interest in studying the rhizosphere microbiome to understand community composition, biodiversity, and the impact of microbial interactions on plants (Trivedi et al. 2020; Morris and Blackwood 2024). The rhizosphere is highly heterogeneous, hosting diverse microbial communities that interact in various ways (Anthony et al. 2023). As a driving force behind nutrient cycling and ecosystem quality (Yadav et al. 2021), microbial communities are crucial for the health and productivity of ecosystems (Priya et al. 2021; Hartmann and Six 2022). They play an essential role in ecological and biogeochemical processes, including carbon and nitrogen cycling, and soil formation (Priya et al. 2021; Hartmann and Six 2022). Moreover, cross-kingdom interactions, i.e. complex relationships between organisms from different kingdoms, can be either beneficial or harmful (Cozim-Melges et al. 2025). On one hand, fungi play a crucial role in breaking down complex, recalcitrant carbon sources such as cellulose and lignin, whereas bacteria primarily utilize more readily soluble carbon sources like sugars and amino acids within the soil ecosystem (Frąc et al. 2018). These microbial processes are vital for enhancing soil fertility, ultimately supporting increased crop yields (Hartmann and Six 2022). On the other hand, nematodes are widely distributed at all nutrient levels in soil food webs (van den Hoogen et al. 2019). Some soil nematodes act as hubs, influencing bacteria and fungi diversity, preying on microorganisms, collaborating with other organisms, and impacting overall ecosystem function (Trivedi et al. 2016; Yang et al. 2021). They are commonly referred to as indicators of soil biodiversity and health in farmland, since they reflect the variation in soil´s environmental condition (Yeates 2003; Biswal 2022).

The diversity and composition of microbial communities are highly sensitive to environmental changes and anthropogenic disturbances, such as shifts in climate and land use (Banerjee et al. 2019). Agricultural practices including tillage, crop rotation, pesticide application, and fertilization also influence soil communities (Chen et al. 2021; Hartmann and Six 2022; Paudel et al. 2023). Soil microorganisms play a crucial role in promoting plant growth and health, while also contributing to crop quality (Banerjee and van der Heijden 2023). Recent research has illuminated the main factors shaping coffee-associated microbial communities, especially bacteria and fungi. These studies explore environmental conditions (Fulthorpe et al. 2019; Veloso et al. 2020), responses to agroecosystem management practices (Jurburg et al. 2020), the impact of coffee species on microbial community structures (de Sousa et al. 2023; Veloso et al. 2023), and the identification of core microbiome taxa in coffee rhizosphere soils (Bez et al. 2023). To the best of our knowledge, nonetheless, no research has yet examined interactions among bacterial, fungal, and nematode communities simultaneously.

Our understanding of key microbial taxa that significantly shape nutrient cycling and the overall rhizosphere environment, is still limited. Regarding how agricultural practices influence the interconnected networks of soil bacteria, fungi, and nematodes in coffee agroecosystems, it remains largely unknown whether these practices alter key taxa and subsequently their ecological functions. For this reason, extensive research is required. This study investigates the composition and functional dynamics of bacteria-fungi-nematode communities under two distinct agricultural management regimes in Costa Rican coffee soils. It uses both traditional morphologic identification and metagenomic tools, providing an in-depth examination of how agricultural strategies influence the soil microbiome.

Materials and methods

Description of the study area and sampling

Soil samples were collected from six Coffea arabica L. farms in Costa Rica, with agroecosystems varying in environmental, edaphic, and management characteristics.. The study area encompassed three major coffee-growing regions (Supplementary Fig. S1): León Cortés (9°39′ 37.54″ N, 84°4′ 16.31″W), Naranjo (10°10′ 4.57″ N, 84°22′ 56.24″W), and Turrialba (9°54′ 15.51″ N, 83°42′ 39.90″W). León Cortés is located at approximately 1,800 masl with Ultisols, while farms in Naranjo sit at medium elevations (1,000–1,400 masl) on volcanic Andisols. Turrialba features Inceptisols at altitudes ranging from 700 to 1100 masl (Mata et al. 2013).

The owner or manager of each farm was interviewed to gather information on field history, production duration, plant age, and pruning frequency. Two farms per region, representing conventional and sustainable management systems, were selected for comparison. Agricultural practices primarily referred to the use of fertilizers,

herbicides, and fungicides (details in Supplementary Table S1). Conventional management includes synthetic fertilizers (nitrogen, phosphorus pentoxide, and potassium oxide), along with bimonthly herbicide (glyphosate, paraquat) and fungicide (triazole compounds) applications. In contrast, sustainable management relies on alternating applications of green compost and biological inputs for fertilization, with mechanical weed control. The coffee variety Costa Rica 95 (Timor Hybrid 832/1×Caturra) was chosen for consistency across all farms in this study.

Soil samples were collected between September and November 2022, during coffee fruiting season. Prior to sampling, litter, living and dead vegetation were carefully removed from the soil surface. Within each farm ($n = 6$), a 100 m^2 plot was selected, from which three composite soil samples were collected (comprising 8–10 soil cores, 7 cm in diameter, taken from the rhizosphere of coffee plants). Edelman auger to a depth of 20 cm. These cores were then mixed to create a composite sample representative of each 100 m^2 plot. One-kilogram samples were placed in sterile plastic bags, stored at 4 °C, and transported to the laboratory. Upon arrival, each sample was divided into three subsamples: 400 g was partially air-dried for soil physicochemical analysis, 500 g was stored at 4 °C for nematode morphological identification, and 100 g was kept at -70 °C for subsequent DNA extraction. Soil sampling on farms (treatments) followed a completely randomized design.

Soil properties

The Costa Rica Institute of Technology´s Agricultural Analysis Laboratory analyzed the physicochemical properties of the samples. For each farm, macronutrient and micronutrient analyses were performed for Ca, Mg, K, P, Zn, Mn, Cu, and Fe using the KCl and modified Olsen methods (Díaz-Romeu and Hunter 1978). The percentage of organic matter (OM) was also measured using the Walkley–Black method (Nelson and Sommers 1983). Soil pH and electrical conductivity (EC) were measured in a 1:5 (soil: water) suspension using a pH meter (Thermo Scientific, Waltham, MA, USA). In addition, the sum of base ratios (Ca/Mg, Ca/K, and Mg/K), base saturation, and cation exchange capacity (CEC) were analyzed. CEC was determined using the ammonium acetate (NH_4OAc) method at pH 7.0 (Chapman 1965). Aluminum saturation (%) was calculated by extracting exchangeable Al^{3+} with 1 M KCl and expressing it as a percentage of CEC (Sumner & Miller 1996). Soil texture, including clay, silt, and sand fractions, was assessed using the hydrometer method (Gee and Bauder 1979).

Nematode extraction, quantification, and specimen mounting

Nematodes were extracted from five 100 g subsamples of fresh soil for each treatment using modified gravitational sieving with 1 mm and 0.037 mm meshes (CDFA 2007) followed by sucrose centrifugation-flotation (Coolen 1979). Nematodes retained on the sieve were collected in a glass centrifuge tube. Extracted nematodes were counted under an inverted microscope (Olympus CKX41SF), heat-killed, fixed in 4% formaldehyde, and processed to pure glycerin using the Seinhorst method (Seinhorst 1966). They were then decanted into another counting chamber and at least 20% of the nematodes, selected in the order in which they were found, were permanently mounted on glass slides and identified by genus under a compound microscope (Olympus BX53, OMDS, Tokyo, Japan) at 100X magnification.. Their functional diversity was assigned based on trophic groups: bacterivores, fungivores, herbivores, omnivores, and predators, using stomatal and esophageal morphology (Bongers and Bongers 1998). Ecological and food web indices, such as the maturity index (MI), maturity index of nematodes in cp 2–5 (MI2-5), and plant-parasitic index (PPI) were calculated for each farm (Bongers and Bongers 1998). Channel index (CI), basal index (BI), enrichment index (EI), and structure index (SI) were used to estimate the dynamics of the soil food web and nematode community (Ferris 2010). Metabolic footprints were estimated per genus to assess carbon consumption throughout the nematode life cycle (Ferris et al. 2001). Metabolic footprints and indices were calculated using the Nematode Indicator Joint Analysis (NINJA) tool (Sieriebriennikov et al. 2014).

DNA extraction, library preparation, and sequencing

Total DNA was extracted from 500 mg of the composite soil samples, using a DNeasy UltraClean microbial kit (Qiagen, Hilden, Germany), according to the manufacturer's instructions. DNA integrity was evaluated by agarose gel electrophoresis, while quantity and purity were measured using a Nanodrop 8000 spectrophotometer (Thermo Fisher Scientific, MA, USA). Samples that exceeded a concentration of 20 ng/μL and had a 260/280 ratio in the range of 1.5–2.0 were selected.

Amplicon library preparation and sequencing were performed by the Novogene Corporation, Inc. (Beijing, China). The hypervariable regions V3–V4 of the 16S rRNA gene from prokaryotes were obtained using primers 341 F (5′-CCTAYGGGRBGCASCAG-3′) and 806R (5′-GGACTACNNGGGTATCTAAT-3′) (Yu et al. 2005). The fungal Internal Transcribed Spacer ITS1 domain was obtained

using primers ITS5-1737 F (5′-GGAAGTAAAAGTCGT AACAAGG-3') and ITS2-2043R (5′-GCTGCGTTCTTC ATCGATGC-3′) (Bellemain et al. 2010). Following successful PCR, amplicon libraries were prepared, pooled using Novogene's proprietary process, and sequenced on an Illumina NovaSeq (Illumina Inc., San Diego, CA, USA) using 2×250 bp paired-end chemistry.

Sequence data processing and bioinformatic analyses

Bacterial and fungal amplicon sequences were processed using QIIME2 version 2022.2 (Bolyen et al. 2019). Raw sequences were QC filtered, primers and barcode sequences removed, using FastQC (Cock et al. 2010) and Trimmomatic (Bolger et al. 2014). Denoising was performed using DADA2 (Callahan et al. 2016) as implemented in the QIIME2 pipeline. DADA2 uses a parametric model to infer true biological sequences from reads, remove chimeras and low-quality sequences, and merge paired end denoised sequences. Specifically, reads with a Phred quality score > 25 and a minimum fragment length of 240 bp were retained. The Amplicon Sequences Variants (ASVs) table was obtained using DADA2. Data were rarefied to the minimum size for each sample group, that is, 121,000 reads for 16S rRNA and 86,000 reads for ITS (Supplementary Table S2). Reading depth fidelity was evaluated using rarefaction curves (QIIME diversity alpha-rarefaction of QIIME2).

Furthermore, 16S rRNA ASVs were taxonomically assigned using the SILVA database (version 138) (Quast et al. 2013), whereas ITS1 sequences were taxonomically identified using the UNITE v8.2 classifier (Kõljalg et al. 2019) and the q2-classify-sklearn plugin. Cell organelles sequences (mitochondria and chloroplasts) were removed from downstream analyses. The dataset was imported into R using the package QIIME2R, and the subsequent analyses and plots were drawn using the phyloseq package (McMurdie and Holmes 2013). Phyloseq functions were used: import_biom() to import BIOM-formatted data, merge_phyloseq() to integrate OTU, taxonomy, and sample metadata, prune_samples() and prune_taxa() to filter out low-abundance samples and taxa, tax_glom() for taxonomic clustering, transform_sample_counts() for normalization, estimate_richness() to calculate alpha diversity indices, and ordinate() and plot_ordination() for ordination analyses such as PCoA. To visualize taxonomic composition, plot_bar() was used.

Predictive functional profiling of microbial communities

PICRUSt2 was used to estimate the potential functional contributions of bacterial communities (Douglas et al. 2020), based on the ASV previously identified. This software generates a genome abundance table, which is normalized based on 16S rRNA gene copy numbers to estimate genome content. Based on KEGG classification, level 3 of KEGG orthologs (KOs) was used for further analysis (Langille et al. 2013). The study specifically evaluated the effects of different agricultural management practices on the potential metabolism of C, N, P, and S. For fungal ASVs, functional guilds were assigned using FUNGuild (Nguyen et al. 2016), retaining only "probable" and"highly probable" matches, while excluding "possible" matches. ASVs were then filtered to include only those associated with the trophic modes of symbiotrophs, pathotrophs, and saprotrophs. Both FUNGuild and PICRUSt analyses were conducted using rarefied sequencing data.

Statistical analysis

Normality (Shapiro–Wilk test, $\alpha = 0.05$) and homoscedasticity (Levene's test) of the raw data were assessed. Since the data did not meet the assumption of normality, the non-parametric Kruskal–Wallis test was applied. One-way ANOVA was applied to analyze mean values for abundance, maturity indices, trophic network indices, and metabolic footprints, followed by Dunn's post hoc test for pairwise comparisons. Analyses were performed using JMP software (version 17.0) (SAS Institute Inc. USA). For alpha diversity analysis, Faith's phylogenetic diversity index (Faith 1992), Shannon index (Shannon 1948), Chao1 richness (Chao 1987), and Pielou´s evenness (Pielou, 1975) were calculated. Statistical analysis was performed using PERMANOVA (pseudo-F test) and a nonparametric Kruskal–Wallis test (Kruskal and Wallis 1952). Microbial beta diversity was analyzed using permutational analysis of variance (PERMANOVA) based on non-metric multidimensional scaling (NMDS) with Bray–Curtis distances. The Bray–Curtis distances were computed and visualized using functions from the phyloseq package. Redundancy analysis (RDA) was used to examine the relationships between community abundances and soil physicochemical properties. Spearman rank correlation analysis was used to study the correlation between nematode families, and soil bacterial and fungal community diversity and composition. All statistical analyses and visualizations were carried out using JMP software (version 17.0), along with the R packages *vegan* and *ggplot*. In addition, the Venny 2.1 program (Oliveros 2015) was used to create Venn diagrams of unique and shared phyla between the management systems and between samples.

Results

Nematode community composition

A total of 28 nematode families, representing five trophic groups, were morphologically identified across coffee

farms under two different agricultural management systems (Supplementary Table S3). Notably, the families Steinernematidae and Nordiidae were absent on conventional farms. Mean abundances were higher under sustainable management (ranging from 87 to 293 nematodes per 100 g of soil) compared to conventional practices (ranging from 51 to 275 nematodes per 100 g of soil). For bacteria-feeding nematodes, Cephalobidae and Rhabditidae were the dominant families in both management systems. Among herbivores, Hoplolaimidae, Pratylenchidae, Heteroderidae, Longidoridae, and Tylenchidae were the most prevalent, with only Heteroderidae and Hoplolaimidae showing significant differences in abundance between management systems (Kruskal–Wallis $\chi^2 = 4.74$, $p < 0.05$ and $\chi^2 = 4.38$, $p < 0.05$, respectively). Aporcelaimidae and Dorylaimidae were the dominant omnivorous families across both systems. Aphelenchidae was the most common frugivorous family and showed significant variation between management regimes (Kruskal–Wallis $\chi^2 = 11.70$, $p < 0.05$). Mononchidae and Mylonchulidae, both predatory nematodes, were the most frequently observed across both systems.

Bacterivorous nematodes were the dominant feeding group (n = 10 families) across both management types, followed by herbivores nematodes (n = 9 families) (Fig. 1A). Bacterivores (Kruskal–Wallis $\chi^2 = 7.38$, $p < 0.05$) and fungivores (Kruskal–Wallis $\chi^2 = 11.81$, $p < 0.05$) showed significant variation depending on the agricultural management system. However, no significant differences were found for omnivores (Kruskal–Wallis $\chi^2 = 0.34$, $p > 0.05$), herbivores (Kruskal–Wallis $\chi^2 = 3.14$, $p > 0.05$), or predators (Kruskal–Wallis $\chi^2 = 2.79$, $p > 0.05$). According to the colonizer-persister (cp) classification, nematodes from cp class 3 were more prevalent in conventional management (45.0%) compared to sustainable systems (32.9%) (Fig. 1B). In contrast, cp classes 1–2 were more abundant in sustainable management systems (44.4%) than in conventional (31.4%).

The soil food web indices were generally similar across agricultural management regimes, with no significant differences in maturity or food web indices ($p > 0.05$) (see Supplementary Table S4). Conventional coffee farms had higher MI25, PPI, CI, and SI values, while sustainable farms showed higher values for MI, BI, and El, indicating differences in soil health metrics between the two management approaches. Metabolic footprints were used as indicators of functional guilds, alongside nematode biomass. Across both management systems, there were no significant differences in the composite (Kruskal–Wallis $\chi^2 = 0.4134$, $p = 0.5202$) and structure (Kruskal–Wallis $\chi^2 = 3.1075$, $p = 0.0779$) footprints. However, the enrichment footprint was higher in sustainable coffee farms (Kruskal–Wallis $\chi^2 = 4.39$, $p = 0.0362$) (Fig. 2A). When analyzed by trophic group, fungivores (Kruskal–Wallis $\chi^2 = 11.70$, $p = 0.0006$) and bacterivores (Kruskal–Wallis $\chi^2 = 4.38$, $p = 0.0362$) showed significantly higher metabolic footprints under sustainable management. In contrast, no significant differences were found for omnivores (Kruskal–Wallis $\chi^2 = 0.34$, $p > 0.05$), herbivores (Kruskal–Wallis $\chi^2 = 3.14$, $p > 0.05$), or predators (Kruskal–Wallis $\chi^2 = 2.79$, $p > 0.05$) (Fig. 2B).

Microbiome community assessment

Prokaryote diversity was studied with high-throughput sequencing, a total of 21,141 ASVs were identified from soil samples. Conversely, fungal diversity analysis only yielded 5,075 ASVs. As sequencing depth increased, rarefaction curves for high-throughput sequencing flattened, indicating that all samples reached the saturation point and most of

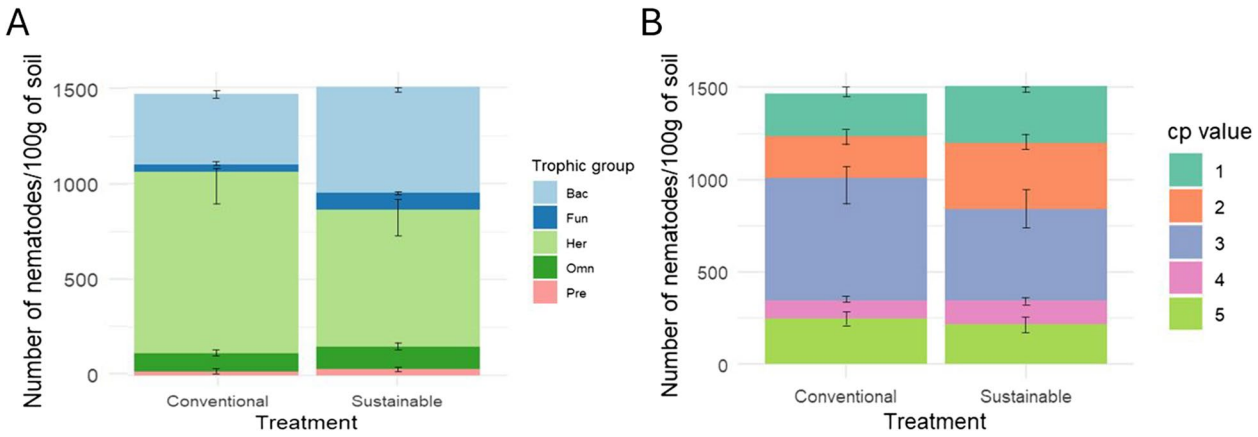


Fig. 1 Stacked bar plot of nematode abundance based on (**A**) feeding habit (Bacterivores, Bac; Predators, Pre; Fungivores, Fun; Omnivores, Omn; and Herbivores, Her), and (**B**) colonizer-persister (cp) groups in coffee farms under two different agricultural management systems. The bars in the graph represent the mean ± SD of data from the respective treatments

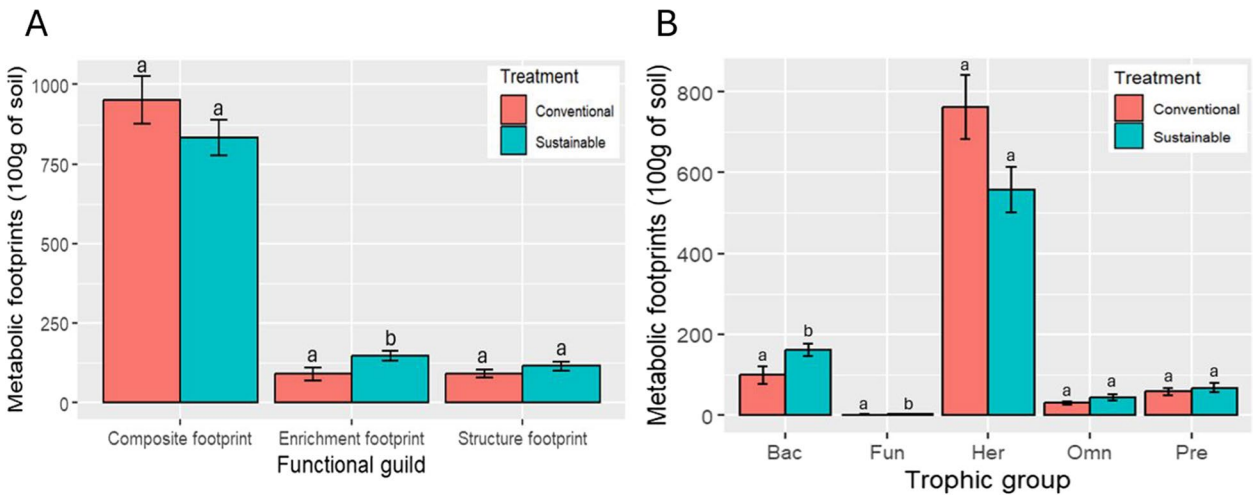


Fig. 2 Distribution of footprint values from coffee farms under different agricultural management systems (conventional and sustainable) in Costa Rica. (**A**) composite, enrichment, and structure footprints. (**B**) Metabolic footprints for each trophic group (Bacterivores, Bac; Fungivores, Fun; Herbivores, Her, Omnivores, Omn; Predators, Pre). Columns with the same letter(s) indicate no statistical significance ($p < 0.05$) between treatments, as determined by Dunn's test

the biodiversity present in the samples was captured and assigned to an ASV (Supplementary Fig. S2).

Alpha diversity indices of microbial communities

In terms of alpha diversity, there was a trend towards greater diversity within samples from sustainably managed coffee soils compared to conventionally managed (Table 1). Similarly, higher bacterial and fungal Pielou's evenness was found in soils from sustainable farms compared to conventional ones.

Beta diversity indices of microbial communities

Beta diversity refers to the similarity or dissimilarity between biological communities, based on their taxonomic composition, which differed between individual sites (farms), but did not show a consistent difference with land use (Fig. 3). The PERMANOVA test revealed no statistically significant differences in either bacterial (pseudo-F = 0.890, $p = 0.793$) or fungal (pseudo-F = 1.001, $p = 0.294$) communities.

Characterization of soil microbial communities

In the soil samples, 40 bacterial phyla were detected under sustainable management, while 43 phyla were identified under conventional practices. The top 10 phyla that dominated soil bacterial communities were Proteobacteria (26.90–29.34%, sustainable and conventional management, respectively), Acidobacteria (18.86–22.19%), Chloroflexi (15.54–9.39%), Actinobacteria (12.62–8.70%), Methylomirabilota (2.62–4.96%), Gemmatimonadota (3.39–3.31%), Verrucomicrobia (3.87–2.31%), Myxococcota (2.79–2.75%), Bacteroidota (1.93–2.43%), and Firmicutes (1.98–0.52%)

Table 1 Alpha diversity indices for bacterial and fungal communities in coffee soil under sustainable and conventional management

Kingdom	Index	Sustainable Mean ± SD	Conventional Mean ± SD	X^2	*p*-value*
Bacteria	Shannon	10.40 ± 0.30	10.17 ± 0.35	1.1904	0.2752
	Faith	247.96 ± 33.02	258.96 ± 31.78	1.1904	0.2752
	Evenness	0.95 ± 0.04	0.86 ± 0.04	0.4285	0.5126
	Chao1	3,535.81 ± 2,180.92	3,634.89 ± 2,255.61	0.0476	0.8273
Fungi	Shannon	4.73 ± 0.36	4.09 ± 1.03	1.1904	0.2752
	Faith	199.44 ± 115.58	326.25 ± 97.21	2.3333	0.1266
	Evenness	0.68 ± 0.11	0.60 ± 0.06	1.1904	0.2752
	Chao1	1,091.67 ± 158.22	855 ± 507.36	0.4286	0.5127

*The measures were statistically compared using the Kruskal–Wallis nonparametric test of means, considering a *p*-value ≤ 0.05 as statistically significant

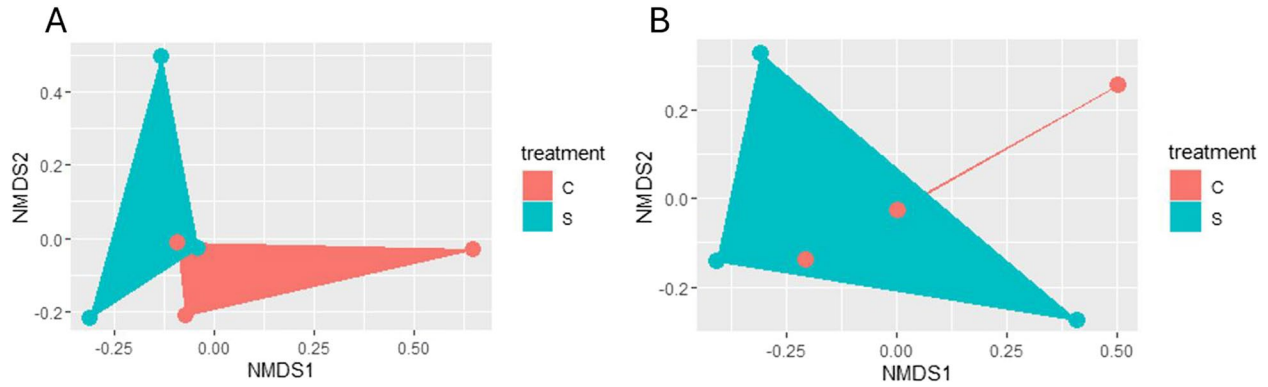


Fig. 3 Non-metric multidimensional scaling (NMDS) analysis of the bacterial (**A**) and fungal (**B**) beta diversity of soil based on Bray–Curtis distances between (stress 0.32 and 0.26, respectively), under two agricultural management treatments: conventional (**C**) and sustainable (S)

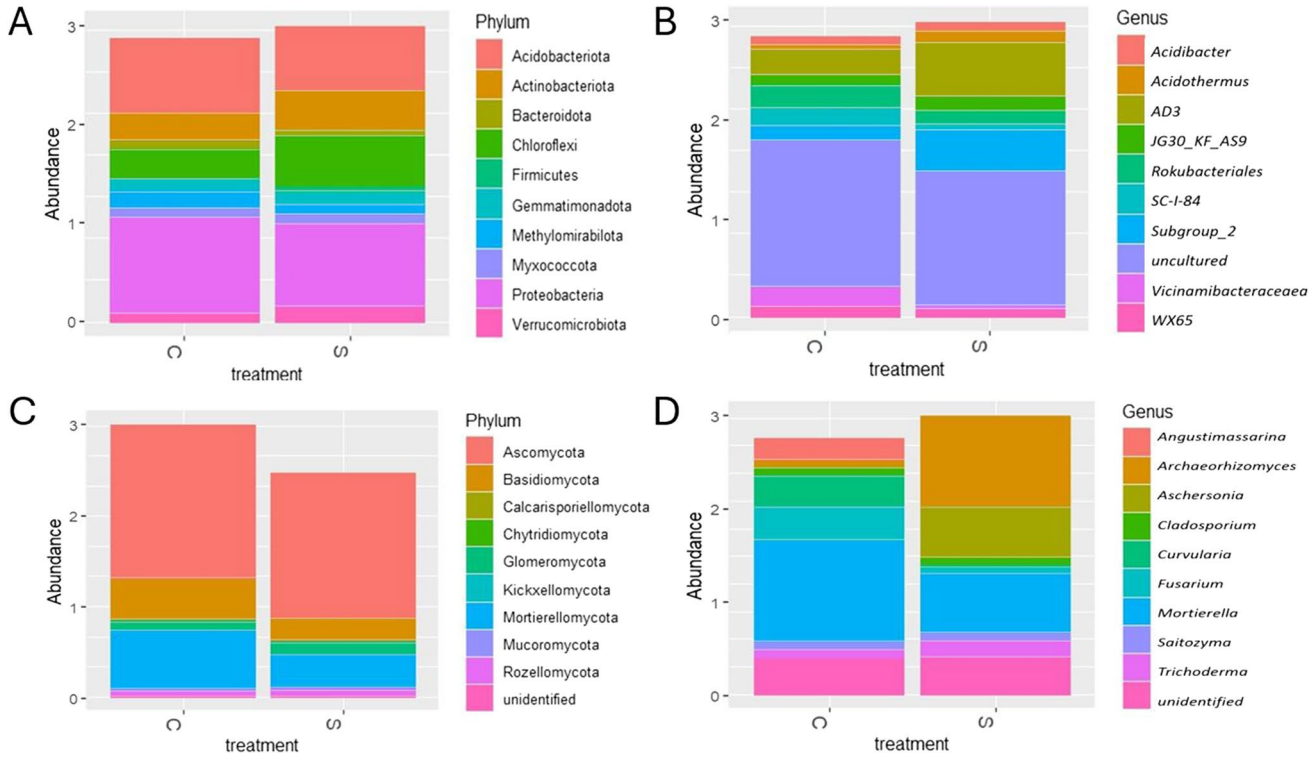


Fig. 4 Relative abundance of the 10 most abundant taxa in coffee rhizosphere soils under sustainable and conventional management. Bars represent the relative abundance at the phyla (**A**) and genus (**B**) levels based on 16S rRNA sequencing, as well as at the phylum (**C**) and genus (**D**) levels based on ITS1 sequencing

(Fig. 4A). At the genus level, the following genera dominated soil bacterial communities: AD3, *Rokubacteriales,* JG30-KF-AS9, SC-I-84, *Vicinamibacteraceae, Acidibacter, Acidothermus* (Fig. 4B).

Taxonomic analysis of the fungal communities in the soil samples identified 12 phyla under sustainable management and 14 phyla under conventional. The difference in fungal community abundance at the phylum level was greater in conventional management when compared to sustainably managed soil (Fig. 4C). Ascomycota was the most abundant group in all samples, representing 59.23% with sustainable management and 47.19% with conventional management. The Mortierellomycota phylum was detected at a lower proportion (10.94% and 18.41%) in sustainable and conventional management, respectively. Basidiomycota was detected at 8.86% and 12.33%, respectively. Glomeromycota, Rozellomycota, Chytridiomycota, Mucoromycota, Calcarisporiellomycota, Kickxellomycota, Aphelidiomycota,

were also detected. At the genus level, the most abundant taxa in both management approaches were *Mortierella*, *Aschersonia*, *Archaeorhizomyces*, *Fusarium*, *Curvularia*, and *Trichoderma* (Fig. 4D).

Unique taxonomic composition of soil under different management systems

A total of 325 bacterial families were shared between both management systems, accounting for 75.8% of total bacterial families (Fig. 5A). At the phylum level, Abditibacteriota was exclusive to sustainably managed soils, while Lainarchaeota, Dadabacteria, Aenigmarchaeota, and DTB120 were found only in conventionally managed farms. Among fungal families, 147 families were common to both soil management systems, representing 62.6% of the total fungal families (Fig. 5B). At the phylum level, Entorrhizomycota and Blastocladiomycota were uniquely associated with sustainably managed soils. When comparing to common nematode families, 26 families were found to be shared in both soils (Fig. 5C). Steinernematidae and Nordiidae were two nematode families not observed in conventionally managed farms.

Relationships between soil properties and soil bacterial and fungal phyla with nematode communities

Physicochemical soil analysis revealed no statistically significant differences between coffee agricultural management systems (Supplementary Table S5). However, conventional soils were slightly more acidic, with lower pH, base sum, and base saturation values compared to sustainably managed soils. In contrast, organic matter and organic carbon levels were higher in the latter. The RDA analysis revealed that pH, Ca, Mg, K, and extractable acidity were the primary factors influencing microbial community composition (Fig. 6). Together, axes 1 and 2 accounted for 83.65%, 90.86%, and 86.61% of the total variation within bacterial, fungal, and nematode communities, respectively. Soil Mg, Ca, and pH were positively correlated with Chloroflexi, while K and extractable acidity were associated with Actinobacteria (Fig. 6A). In fungal communities, Ascomycota, Glomeromycota, and Basidiomycota were strongly linked to Mg and Ca, and to a lesser extent, to extractable acidity and K (Fig. 6B). In nematode communities, Mg, K, and extractable acidity were strongly associated with Rhabditidae (Fig. 6C).

Relations between the relative soil bacterial and fungal phyla with nematode communities

Pairwise comparison was performed to establish Spearman's rank correlation between soil bacterial and fungal phyla with the top 10 nematode families, according to agricultural management (Fig. 7). In conventionally managed soil, the relative abundance of Acidobacteria showed a strong positive correlation with both Aphelenchidae ($r = 0.999$, $p < 0.05$) and Hoplolaimidae ($r = 0.994$, $p < 0.05$). Similarly, Crenarchaeota was positively correlated with Heteroderidae ($r = 0.959$, $p < 0.05$). In contrast, Tylenchidae was negatively correlated with Bacteroidota ($r = -0.992$, $p < 0.05$), and Verrucomicrobiota showed a negative correlation with Dorylaimidae ($r = -0.998$, $p < 0.05$). In sustainably managed soil, the relative abundance of Dorylaimidae exhibited a significant positive correlation with Proteobacteria ($r = -0.994$, $p < 0.05$), but a negative correlation with Gemmatimonadota ($r = -0.998$, $p < 0.05$). Similarly, Longidoridae was positively correlated with Actinobacteria ($r = 0.998$, $p < 0.05$), and negatively correlated with Myxococcota ($r = -0.997$, $p < 0.05$) (Fig. 7A).

In conventionally managed soil, nine significant correlations were observed between fungal taxa and nematodes (Fig. 7B). The relative abundances of Kickxellomycota ($r = 0.993$, $p < 0.05$), Calcarisporiellomycota ($r = 0.986$, $p < 0.05$), and Basidiomycota ($r = 0.691$, $p < 0.05$) were positively correlated with Rhabditidae. Likewise, Dorylaimidae showed a negative correlation with Kickxellomycota ($r = -0.994$, $p < 0.05$) and Chytridiomycota ($r = -0.999$, $p < 0.05$). Additionally, Aporcelaimidae and Longidoridae were positively correlated with Ascomycota ($r = 0.998$, $p < 0.05$, and $r = 0.969$, $p <$

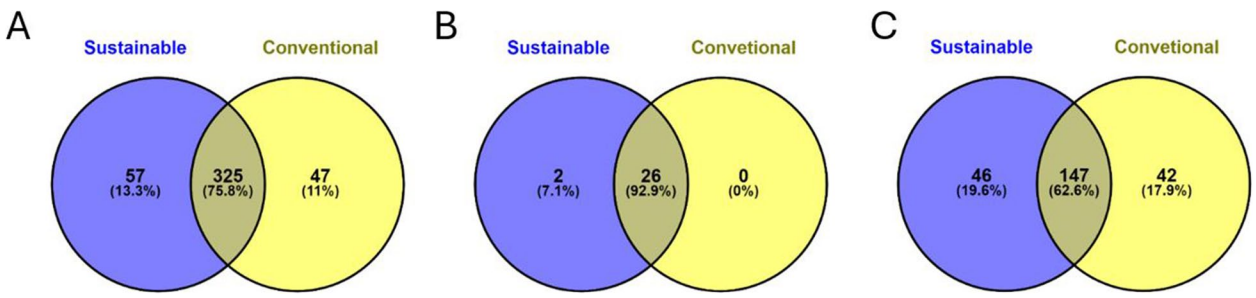


Fig. 5 Venn diagram of ASV distribution for bacteria (**A**), fungi (**B**) and nematodes (**C**) at the family level in coffee plantations managed under both sustainable and conventional regimes

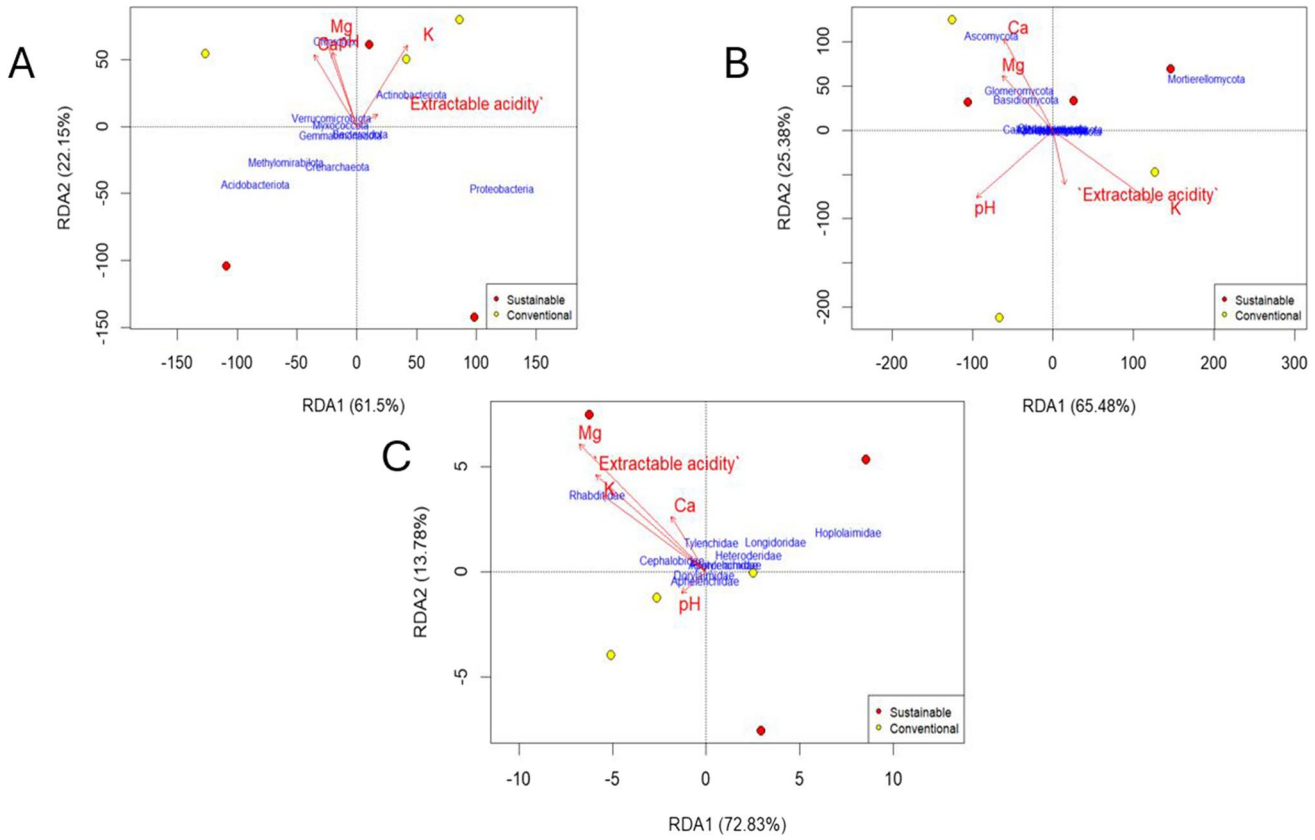


Fig. 6 Redundancy analysis (RDA) plots show the relationships between soil physicochemical properties and the top 10 soil bacteria (**A**), fungal phyla (**B**), and nematode families (**C**) across two different agricultural systems. The RDA was performed using the relative abundances of ASVs and corresponding soil properties. The arrows in the RDA plots represent the direction and magnitude of measurable variables associated with each community structure

0.05, respectively). In sustainable soil management, the fungal community showed a significant positive correlation between Pratylenchidae and Glomeromycota ($r = 0.989$, $p < 0.05$), Chytridiomycota ($r = 0.997$, $p < 0.05$), and Ascomycota ($r = 0.970$, $p < 0.05$). Conversely, Rhabditidae was negatively correlated with Rozellomycota ($r = -0.996$, $p < 0.05$), Mucoromycota ($r = -0.923$, $p < 0.05$), Calcarisporiellomycota ($r = -0.993$, $p < 0.05$), and Aphelidiomycota ($r = -0.768$, $p < 0.05$). Likewise, Dorylaimidae displayed a negative correlation with Ascomycota ($r = -0.538$, $p < 0.05$).

Soil bacterial potential functions based on PICRUSt2

Functional predictions were generated from the KEGG database using the 16S metagenome data, and resulted in 7621 KEGG Orthology IDs (KOs), including 556 KEGG pathways. The abundance of KOs related to carbon, nitrogen, phosphorus, and sulfur metabolism showed no functional differences by agricultural system (Fig. 8). The abundance of KOs related to carbon metabolism (K00615) and nitrogen metabolism (K000459) was 15.2% and 15.1%, respectively, being 7.6% and 7.8% for conventional and sustainable management systems, respectively (Fig. 8A and B). On the other hand, the abundance of sulfur metabolism (K01738) was 8.9% in conventional soils and 9.9% in sustainable management soils, showing a higher presence in the latter (Fig. 8C). A similar trend was observed for phosphorus metabolism (K03823), with an abundance of 27.9% in conventional and 30.6% in sustainable soils (Fig. 8D).

Soil fungal potential functions based on FUNGuild

The fungal ASVs were categorized into ecological functional groups using the FUNGuild tool. In this study, a total of 2,547 ASVs were identified in seven trophic groups, with pathotrophs, saprotrophs, and symbiotrophs as the major components (Supplementary Fig. S3). The analysis revealed that both sustainable and conventional treatments had similar abundances across the

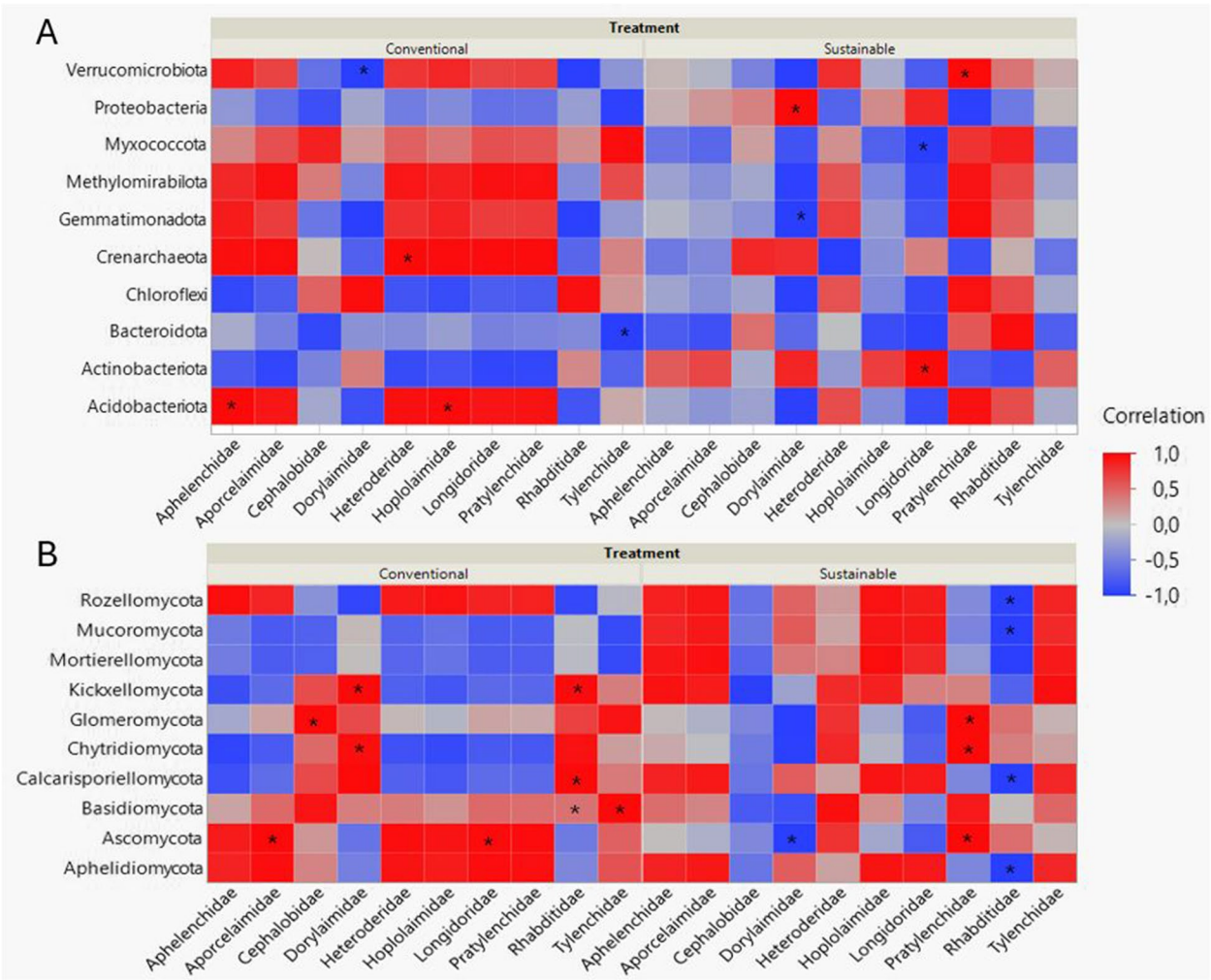


Fig. 7 Spearman correlation heatmap shows the relationships between the top 10 soil bacteria (**A**) and fungal phyla (**B**) with the top 10 nematode families under two different agricultural managements. Negative correlations are indicated in blue, positive correlations in red, with darker shades representing stronger correlations. Significant correlations ($p < 0.05$) are marked with an asterisk (*)

different functional guilds. However, the saprotroph-symbiotroph guild was the most prevalent trophic mode under conventional management, comprising 27.06% of the community. In contrast, saprotrophs were dominant in sustainable management, making up 34.50% of the total community.

A significantly higher percentage of symbiotrophic groups was found in the sustainably managed soil compared to the conventional soil (Fig. 9A), with the Glomeraceae family being the most abundant in both managements. Pathogens were more abundant in sustainable farms, while their diversity was greater under conventional management (Fig. 9B). Among the pathotrophic genera, *Aschersonia* dominated in sustainable farm soils, whereas *Cylindrocarpon* was more prevalent in conventional soils. The saprotrophic group had a lower relative abundance than the other groups did and was more frequent in conventionally managed fields (Fig. 9C), with the Mariannae family being the most abundant. *Mortierella* (Fig. 9D) was representative of the saprotrophic-symbiotrophic mode across both treatments. The pathotroph-saprotroph-symbiotroph group showed a lower relative abundance in sustainable farm soils. Within this trophic mode, *Fusarium* was predominant under conventional management, whereas *Trichoderma* dominated sustainable practices (Fig. 9F).

Discussion

Characterization of soil microbial and nematodes communities

In coffee agroecosystems, comparisons between sustainable and conventional management systems revealed similar nematode community structures in terms of abundance,

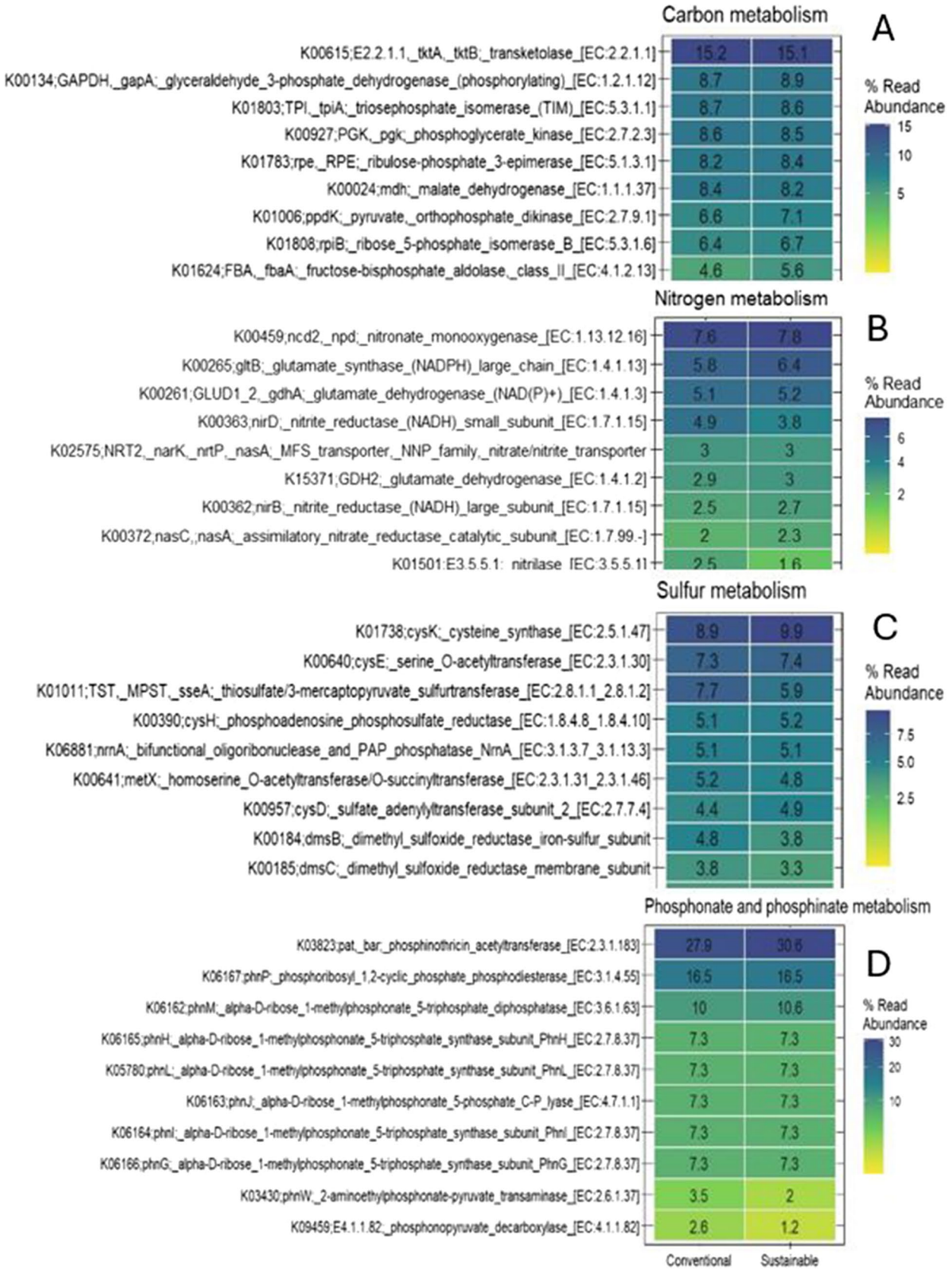
genus dominance, and ecological indices. Twenty-eight nematode families were detected in samples from sustainable farms and 26 families in samples from conventional farms, the latter of which exceeds reported values from other studies (Peraza-Padillla 2010; Júnior et al. 2021). Bacterivore and fungivore abundances were significantly higher under sustainable management compared to conventional systems (Sauvadet et al. 2019). Opportunistic bacterivores, such as Rhabditidae, Cephalobidae, and Panagrolaimidae, prevailed, likely due to moisture-rich conditions and easily degradable organic matter. These findings align with (Júnior et al. 2021), who observed a greater presence of these nematode families in coffee plantations with higher organic matter availability. The predominant fungivore family recorded was Aphelenchoideae, also aligning with anothers findings (Júnior et al. 2021). The genus *Aphelenchus*, part of the fungivorous trophic group, is commonly found in soils rich in recalcitrant organic matter, typical of habitats in advanced ecological succession (Bongers and Bongers 1998; Porazinska et al. 1999). The abundances of herbivorous nematodes, particularly from the Heteroderidae and Hoplolaimidae, varied across different management regimes. These plant-parasitic nematodes, including the genera *Meloidogyne* and *Helicotylenchus*, prosper in environments with high organic matter and dense root systems; therefore, they are commonly found in coffee crops worldwide (Villain et al. 2018; Bell et al. 2018) and in Costa Rica (Peraza-Padillla 2010).

Nematodes in the cp-1 and cp-2 categories responded significantly to agricultural management (Maina et al. 2022; Karuri 2023). Cp-2 nematodes are described as opportunists, while cp-1 nematodes, enrichment opportunists and r-strategists, are indicators of soils enriched with organic matter (Bongers and Bongers 1998). Sustainable practices in coffee farming may boost soil fertility by encouraging these nematodes, aligning with findings who also reported higher cp-1 and cp-2 abundances (van den Hoogen et al. 2019; Dioh Lobe et al. 2023). The MI of the soil samples in this study varied between 2.19 and 2.42, suggesting ecological succession due to soil enrichment (Bongers et al. 1997). Both management systems showed reduced MI and MI2-5 after chemical fertilizer and organic amendment use, aligning with previous studies (Forge et al. 2005; Maina et al. 2022). The decrease in MI suggests a higher density of opportunistic nematodes (Júnior et al. 2021), particularly *Rhabditis*, known for its short generation time, excessive egg production, and rapid population growth in nutrient-enriched conditions (Bongers et al. 1997). The study found that the enrichment footprint is generally larger in sustainable agricultural systems that utilize cover crops and organic matter. These findings are supported by the abundance of bacterivores and fungivores, crucial for decomposition and nutrient cycling. Their presence indicates quality and availability of food resources in the soil (Yeates et al. 1993).

Proteobacteria, a Gram-negative bacterial phylum, is the most abundant microorganism in coffee agroecosystem soils, playing key roles in carbon, nitrogen, and sulfur cycling (Duong et al. 2020; Andrade et al. 2023; Bez et al. 2023; Veloso et al. 2023). The second most abundant group, Acidobacteria, contributes to nutrient mineralization, especially through nitrite use as a nitrogen source, making them crucial for nitrogen supply (Kielak et al. 2016; Veloso et al. 2023; Gómez-Godínez et al. 2024). Coffee-growing regions, characterized by acidic soils with high H^+ and manganese (Mn) levels, favor acidophilic bacteria like *Acidibacter* species (Caldwell et al. 2015; Bez et al. 2023). The ratio of Proteobacteria to Acidobacteria serves as a key indicator of soil nutrient availability, with Proteobacteria dominating in nutrient-rich soils and Acidobacteria more common in nutrient-poor environments (Sun et al. 2022; Ge et al. 2023). Our data showed higher Proteobacteria levels across both agricultural systems, suggesting that synthetic fertilizers in conventional farming enhanced soil nutrient availability and drove this shift. These results align with those observed in conventional coffee systems (Jurburg et al. 2020; Martinez et al. 2023).

Chloroflexi, the third most abundant group, thrives in nutrient-poor environments and plays a key role in the carbon cycle by breaking down plant materials like cellulose and starch, also promoting plant growth (Hug et al. 2013; Ochoa-Henriquez et al. 2024). Our findings found a higher abundance of Chloroflexi in agricultural soils compared to less disturbed soils. Actinobacteria assist in organic matter cycling and in the production of humic acid and melanin (Jung et al. 2024). Previous studies have emphasized the prevalence of Actinobacteria in the coffee soil microbiome (Fulthorpe et al. 2019; Ge et al. 2023).

In this study, the fungal community was dominated by the phyla Ascomycota, Mortierellomycota, and Basidiomycota across both management systems, consistent with previous findings in coffee soils (Veloso et al. 2023; Kutos et al. 2024). In a recent study on soil fungi across various coffee-growing regions of Colombia (Gómez-Godínez et al. 2024) reported that approximately 64% of the fungal abundance was attributed to Mortierellomycota. Ascomycota, the most dominant phylum, plays a key role in promoting root and plant establishment, nutrient cycling, and improving soil structure. Saprotrophs are crucial for decomposing organic matter (Frac et al. 2018; Rao et al. 2020; Zhao et al. 2024). Additionally, a study in Costa Rica found that Ascomycota were positively associated with organic matter and nitrogen available in organic coffee plantations (Sternhagen et al. 2020). Although no significant differences in organic matter or nitrogen were observed in our study, this may


Carbon metabolism
A
K00615;E2.2.1.1,_tktA,_tktB;_transketolase_[EC:2.2.1.1]
K00134;GAPDH,_gapA;_glyceraldehyde_3-phosphate_dehydrogenase_(phosphorylating)_[EC:1.2.1.12]
K01803;TPI,_tpiA;_triosephosphate_isomerase_(TIM)_[EC:5.3.1.1]
K00927;PGK,_pgk;_phosphoglycerate_kinase_[EC:2.7.2.3]
K01783;rpe,_RPE;_ribulose-phosphate_3-epimerase_[EC:5.1.3.1]
K00024;mdh;_malate_dehydrogenase_[EC:1.1.1.37]
K01006;ppdK;_pyruvate,_orthophosphate_dikinase_[EC:2.7.9.1]
K01808;rpiB;_ribose_5-phosphate_isomerase_B_[EC:5.3.1.6]
K01624;FBA,_fbaA;_fructose-bisphosphate_aldolase,_class_II_[EC:4.1.2.13]
15.2 15.1
8.7 8.9
8.7 8.6
8.6 8.5
8.2 8.4
8.4 8.2
6.6 7.1
6.4 6.7
4.6 5.6
% Read Abundance
15
10
5
Nitrogen metabolism
B
K00459;ncd2,_npd;_nitronate_monooxygenase_[EC:1.13.12.16]
K00265;gltB;_glutamate_synthase_(NADPH)_large_chain_[EC:1.4.1.13]
K00261;GLUD1_2,_gdhA;_glutamate_dehydrogenase_(NAD(P)+)_[EC:1.4.1.3]
K00363;nirD;_nitrite_reductase_(NADH)_small_subunit_[EC:1.7.1.15]
K02575;NRT2,_narK,_nrtP,_nasA;_MFS_transporter,_NNP_family,_nitrate/nitrite_transporter
K15371;GDH2;_glutamate_dehydrogenase_[EC:1.4.1.2]
K00362;nirB;_nitrite_reductase_(NADH)_large_subunit_[EC:1.7.1.15]
K00372;nasC,,nasA;_assimilatory_nitrate_reductase_catalytic_subunit_[EC:1.7.99.-]
K01501;E3.5.5.1;_nitrilase_[EC:3.5.5.1]
7.6 7.8
5.8 6.4
5.1 5.2
4.9 3.8
3 3
2.9 3
2.5 2.7
2 2.3
2.5 1.6
% Read Abundance
6
4
2
Sulfur metabolism
C
K01738;cysK;_cysteine_synthase_[EC:2.5.1.47]
K00640;cysE;_serine_O-acetyltransferase_[EC:2.3.1.30]
K01011;TST,_MPST,_sseA;_thiosulfate/3-mercaptopyruvate_sulfurtransferase_[EC:2.8.1.1_2.8.1.2]
K00390;cysH;_phosphoadenosine_phosphosulfate_reductase_[EC:1.8.4.8_1.8.4.10]
K06881;nrnA;_bifunctional_oligoribonuclease_and_PAP_phosphatase_NrnA_[EC:3.1.3.7_3.1.13.3]
K00641;metX;_homoserine_O-acetyltransferase/O-succinyltransferase_[EC:2.3.1.31_2.3.1.46]
K00957;cysD;_sulfate_adenylyltransferase_subunit_2_[EC:2.7.7.4]
K00184;dmsB;_dimethyl_sulfoxide_reductase_iron-sulfur_subunit
K00185;dmsC;_dimethyl_sulfoxide_reductase_membrane_subunit
8.9 9.9
7.3 7.4
7.7 5.9
5.1 5.2
5.1 5.1
5.2 4.8
4.4 4.9
4.8 3.8
3.8 3.3
% Read Abundance
7.5
5.0
2.5
Phosphonate and phosphinate metabolism
D
K03823;pat,_bar;_phosphinothricin_acetyltransferase_[EC:2.3.1.183]
K06167;phnP;_phosphoribosyl_1,2-cyclic_phosphate_phosphodiesterase_[EC:3.1.4.55]
K06162;phnM;_alpha-D-ribose_1-methylphosphonate_5-triphosphate_diphosphatase_[EC:3.6.1.63]
K06165;phnH;_alpha-D-ribose_1-methylphosphonate_5-triphosphate_synthase_subunit_PhnH_[EC:2.7.8.37]
K05780;phnL;_alpha-D-ribose_1-methylphosphonate_5-triphosphate_synthase_subunit_PhnL_[EC:2.7.8.37]
K06163;phnJ;_alpha-D-ribose_1-methylphosphonate_5-phosphate_C-P_lyase_[EC:4.7.1.1]
K06164;phnI;_alpha-D-ribose_1-methylphosphonate_5-triphosphate_synthase_subunit_PhnI_[EC:2.7.8.37]
K06166;phnG;_alpha-D-ribose_1-methylphosphonate_5-triphosphate_synthase_subunit_PhnG_[EC:2.7.8.37]
K03430;phnW;_2-aminoethylphosphonate-pyruvate_transaminase_[EC:2.6.1.37]
K09459;E4.1.1.82;_phosphonopyruvate_decarboxylase_[EC:4.1.1.82]
27.9 30.6
16.5 16.5
10 10.6
7.3 7.3
7.3 7.3
7.3 7.3
7.3 7.3
7.3 7.3
7.3 7.3
3.5 2
2.6 1.2
% Read Abundance
30
20
10
Conventional
Sustainable

◂**Fig. 8** Relative abundance of predicted soil bacterial functions associated with Carbon (**A**), Nitrogen (**B**), Sulfur (**C**), Phosphonate, and Phosphinate (**D**) metabolism, as classified by the Kyoto Encyclopedia of Genes and Genomes (KEGG) pathways, in coffee plantations under two different agricultural management systems

reflect ongoing changes due to organic inputs in the sustainable system. Mortierellomycota is known to promote phytohormone production (e.g., gibberellins and indoleacetic acid), enhance phosphorus availability, and release organic acids that dissolve recalcitrant phosphorus (Zhu et al. 2022; Gómez-Godínez et al. 2024). Basidiomycota, the third most prevalent phylum, is recognized for its ability to break down lignin and facilitate nutrient absorption through ectomycorrhizal associations (Jung et al. 2024).

Influence of agriculture on the soil bacterial and fungal community

The sequencing data indicated sufficient sampling effort to characterize prokaryotic and fungal populations, ensuring representative taxonomic diversity (Supplementary Fig. S2). This was supported by the rarefaction curves approaching saturation (Rodriguez-R and Konstantinidis 2014). The alpha diversity indices did not show significant differences between agricultural systems ($p > 0.05$), indicating similarity among samples (Table 1). This trend was biologically relevant without showing it to be statistically significant ($p > 0.05$) mainly due to sample size. Interestingly, these results suggested that the microbiome diversity of coffee planted under different agricultural strategies behaved similarly across sites. Beta diversity index and multivariate permutational analysis of variance (PERMANOVA) revealed no significant compositional differences between treatments, indicating that the two management systems did not explain the observed heterogeneity (Fig. 3). These results suggest that the effects of agricultural management are restricted to specific microbial taxa, rather than influencing overall diversity of the microbial community (Bill et al. 2021). Comparing sustainably and conventionally managed soils, the most notable differences were a lower abundance of bacterial communities associated with conventional management. Previous studies have shown that the use of organic and inorganic fertilizers alters soil physicochemical properties, indirectly affecting microbial community composition (Jung et al. 2024).

Relation between soil in coffee´s microbiomes with soil properties

Sustainably managed soils were less acidic than conventionally managed fields, likely due to the greater density and diversity of shade trees and the absence of chemical fertilizer inputs. Nitrogen fertilizers are known to contribute to soil acidification. In contrast, the presence of shade trees is associated with lower rates of nitrification and reduced soil acidity compared to coffee grown in full sun (Babbar and Zak 1995). Our findings revealed a decrease in soil pH and organic matter under conventional management, consistent with previous studies (Sauvadet et al. 2019). In this study, redundancy analysis identified pH, K, Mg, Ca, and extractable acidity as key soil factors influencing the community composition of soil bacteria, fungi, and nematodes in coffee agroecosystems. These results align with previous research, which demonstrated that different bacteria and fungi thrive under specific pH conditions, with even minor fluctuations significantly affecting community structure (Fan et al. 2022). A study conducted in Costa Rica found that increased soil acidity and higher levels of Ca, Mg, and K were associated with significant shifts in the composition of fungal communities associated with coffee roots (Sternhagen et al. 2020). The observed changes are likely due to the extensive use of chemical fertilizers and lack of organic inputs, both major contributors to soil acidification in coffee plantations (Zhao et al. 2018; Ge et al. 2023).

Bacteria, the most diverse microbial group in coffee soil (Veloso et al. 2020), along with nematodes, exhibits a high sensitivity to environmental fluctuations demonstrated that both the species and functional diversity of bacteria increased with lower pH and extractable acidity. In contrast, the composition of fungal communities was more significantly influenced by pH, suggesting that fungi tend to be more abundant in soils with high pH levels. This adaptability may arise from the propensity of fungi to form stable associations with coffee plants (Jurburg et al. 2020; Zhao et al. 2024).

Relations between the relative soil bacterial and fungal phyla with nematode communities

The 10 most abundant taxa are critical for maintaining the structure and function of their ecological functions through greater connectivity within the community (Banerjee et al. 2018). Agricultural management practices determine the distribution of keystone taxa in coffee agroecosystems (Jurburg et al. 2020; Veloso et al. 2023; Kutos et al. 2024). The absence of correlation among certain taxa can significantly alter the structure and functioning of the entire microbial community (Trivedi et al. 2016, 2020). Previous studies have demonstrated that bacterial and fungal keystone taxa are essential for organic matter decomposition and transformation in agricultural soils, aligning with the findings of this research (Banerjee et al. 2019; Wu et al. 2022).

Proteobacteria and Actinobacteria, as eutrophic bacteria, are well-adapted to thrive in environments rich in carbon (Ge et al. 2023). Proteobacteria play a key role in

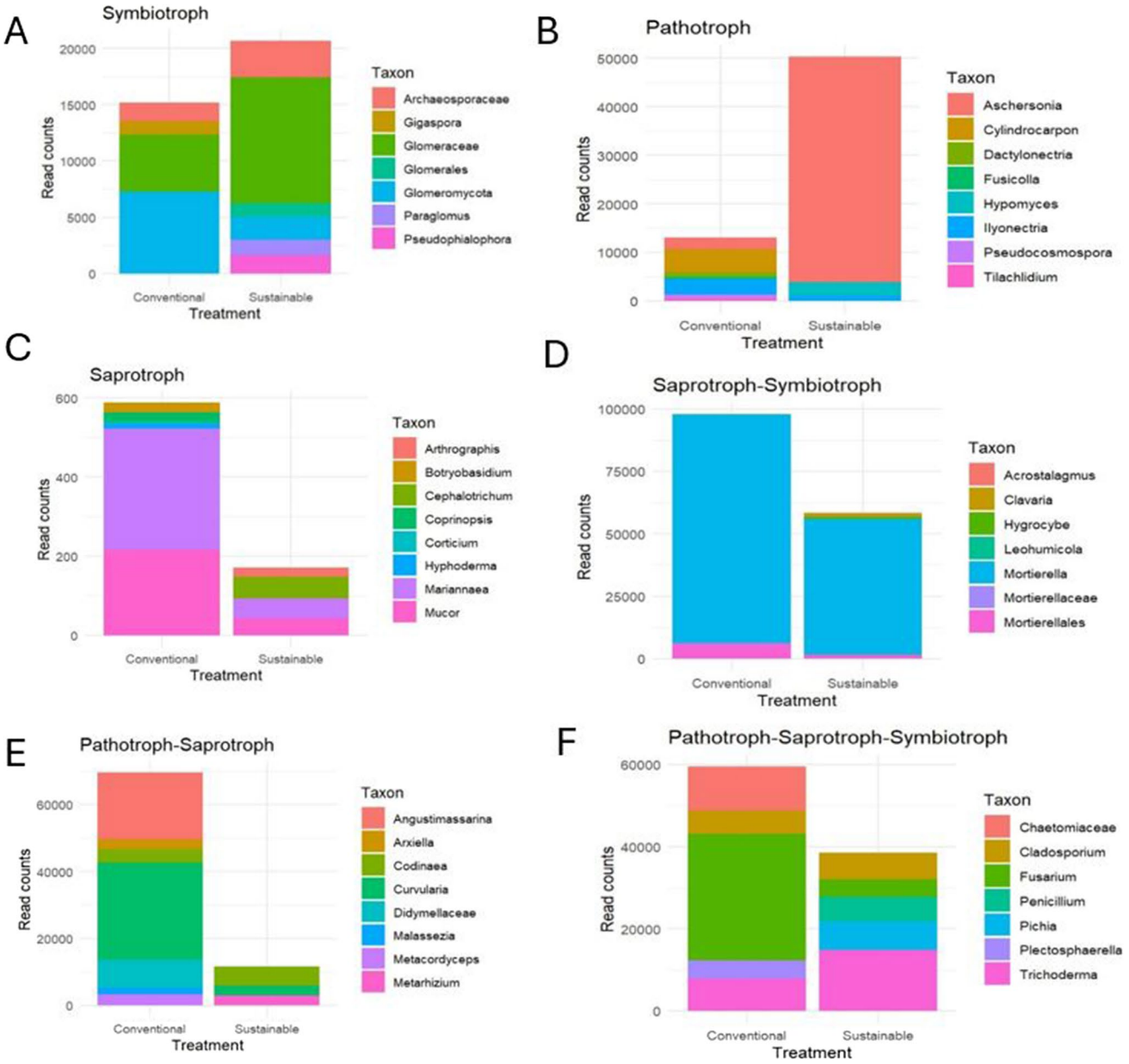


Fig. 9 Abundances are represented as read counts per farm for fungal taxa categorized by trophic modes. Symbiotroph (**A**), Pathotroph (**B**), Saprotroph (**C**), Saprotroph-Symbiotroph (**D**), Pathotroph-Saprotroph (**E**), and Pathotroph-Saprotroph-Symbiotroph (**F**)."Taxon"refers to the highest taxonomic level identified through the FUNGuild functional prediction database

biogeochemical cycling of essential mineral nutrients in the soil and are notably abundant in coffee field soils (Chaudhry et al. 2012; Andrade et al. 2023; Kutos et al. 2024). In addition to being a keystone group, they are also commonly recognized as fast-growing copiotrophic organisms (Bez et al. 2023; Kutos et al. 2024). In this study, soils from sustainable farms demonstrated bacterial-driven decomposition, marked by a notable presence of bacterivorous nematodes, particularly from the *Rhabditidae* and *Cephalobidae* guilds. This nematode proliferation has been observed in coffee systems as an indicator of nutrient-rich conditions (Júnior et al. 2021). By using nematodes as bioindicators of soil health to infer the condition of the soil food web, coffee management practices were found to share similar traits, with agroecosystems characterized by moderately disturbed, nitrogen-enriched soils and a balanced but primarily bacterial decomposition process (Ferris et al. 2001).

Ascomycota and Mortierellomycota are typical saprophytic fungi known for their ability to adapt and thrive under various agricultural practices (Rao et al. 2020; Ochoa-Henriquez et al. 2024). This adaptability aligns with their capacity to degrade carbon sources rich in lignin found in the soil (Frąc et al. 2018).

Moreover, sustainable agricultural practices can enhance the abundance of frugivores, such as *Aphelenchus*, which belong to the cp-2 functional guild, highlighting a direct ecological connection between fungi and nematodes. These practices provide the necessary energy to support fungal activity (Maina et al. 2020). The work of supports this finding, stating that fungal-feeding nematodes contribute to the regulation of fungal biomass and are important in nutrient cycling in agroecosystems. Similarly, a higher abundance of *Aphelenchus* nematodes, which primarily feed on arbuscular mycorrhizal fungi (AMF) in soils with high organic matter content (Arias and Abarca 2014).

Predicted metabolic function of bacterial and fungal communities

Soil microbes affect soil nutrient cycling, decomposition processes, and soil health by modifying their metabolic functions (Banerjee and van der Heijden 2023). The KEGG orthologs (KOs) associated with carbon, nitrogen, phosphorus, and sulfur metabolisms were strongly linked to management practices. The abundance of these KOs, however, showed no significant variation across agricultural systems. While predicted KEGG metabolic profiles under different agricultural management systems suggest many shared functional traits, certain metabolic pathways were enriched across treatments. Management practices in agroecosystems induce spatial and temporal shifts in soil physicochemical properties, which may accelerate the degradation of C and N in these environments (Sternhagen et al. 2020). Such changes can enhance the presence of heterotrophic bacteria, like Proteobacteria, key microorganisms involved in the breakdown of carbohydrates and amino acids (Viruel et al. 2022). One possible explanation could be the higher input of synthetic fertilizers in conventional systems, which can increase the availability of nitrogen and carbon sources, thereby stimulating microbial activity in these pathways (Wu et al. 2022). This trend suggests that frequent disturbances caused by practices in conventional systems drive the adaptation of microbial communities, making them more durable. As a result, these communities are better equipped to maintain ecosystem functions compared to those in agroecosystems with less frequent disturbances.

FUNGuild is a database for comparing fungal functions and classifying fungi. As a result, it has been widely utilized in fungal community research (Nguyen et al. 2016). The FUNGuild predictions for coffee soil fungi under the agricultural management practices in this study aligned with the functional groups previously identified (Sternhagen et al. 2020; Ochoa-Henriquez et al. 2024). Plant pathogens were less abundant in conventionally managed fields compared to sustainable fields, where the genus *Aschersonia* was dominant. Direct impact on coffee was not observed; and, therefore, even when such species are present, they are not using coffee as a host, which can also be as part of other plant-pathogen interactions with weeds or surrounding plants. Interestingly, for the first time a high abundance of *Aschersonia* in coffee soil is reported. While information regarding their role in coffee soil is limited, these fungi are recognized as entomopathogenic species specifically targeting Aleyrodidae and Coccoidea (Nakai and Lacey 2017).

Taxa within Mortierellomycota are common soil residents exhibiting saprotrophic-symbiotrophic functions, with their highest abundance observed in sustainable coffee farms, where they accelerate organic matter degradation. Recent reports have highlighted their beneficial role in this process within coffee farms (Kutos et al. 2024). Our findings are consistent with those of a previous study, which identified *Mortierella* as the predominant saprotrophic-symbiotrophic genus in five out of six coffee farms studied, designating it as an indicator species for organic agriculture (Ochoa-Henriquez et al. 2024).

Curvularia dominated the pathotroph-saprotroph group. Certain agricultural practices have been shown to reduce overall fungal diversity, potentially creating conditions that allow *Curvularia* to proliferate either as a saprophyte or, opportunistically, as a pathogen (Duong et al. 2020; Rao et al. 2020). In this same trophic group, insect-pathogenic species from the genus *Metarhizium* were characteristic of sustainable soils, as also reported in Colombian coffee plantations (Ochoa-Henriquez et al. 2024). In addition to their entomopathogenic role, *Metarhizium* species can colonize plant root tissues as endophytes, improving plant tolerance to pests and diseases through symbiotic interactions. This dual functionality makes them essential contributors to sustainable agricultural systems. In the pathotroph-saprotroph-symbiotroph mode, *Fusarium* was one of the dominant genera in conventional soil. This aligns with previous reports from coffee plantations and montane forests, where *Fusarium* has been described as devastating to coffee production (Arias and Abarca 2014). Within the same trophic group, it is important to highlight *Trichoderma*, which was abundant in sustainable soil. The antimicrobial properties of *Trichoderma* have been widely utilized as biocontrol agents against various phytopathogens in coffee agroecosystems (Mulaw et al. 2010; Mulatu et al. 2023). Consequently, further studies are needed to better understand how management regimes affect functional traits of bacterial and fungal communities in coffee agroecosystems.

Conclusions

This study highlights the influence of agricultural management on soil microbial communities and identifies keystone taxa as central players in bacterium-fungus-nematode networks. Their

association with specific management practices underscores their potential role in shaping soil ecosystem dynamics.

Sustainable coffee management promotes a more intricate and interconnected microbial network, facilitating enhanced species interactions and improving energy transfer efficiency. This finding suggests that sustainable practices contribute to greater ecosystem stability and resilience.

By fostering beneficial microbial communities, sustainable practices can improve plant health and maintain regional microbial biodiversity. These findings provide valuable insights for coffee growers seeking to optimize soil health and productivity through informed on-farm management decisions.

The observed differences in bacterivore and fungivore abundance, along with the metabolic processes related to organic matter decomposition, indicate that sustainable management enhances microbial nutrient cycling. Based on predicted metabolic functions, this could be particularly relevant in phosphorus and sulfur metabolism, which play critical roles in soil fertility and plant nutrition.

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Author contributions The authors were involved in different stages of the experiment. A.G. and F.E. designed, performed the field experiment, and project administration. J.J. and J.R. were responsible for processing and laboratory work of soil samples, DNA extraction, sequencing, and bioinformatics analysis. J.R. analyzed and interpretation the nematode community samples, and I.V. provided assistance and guidance for the identification of the nematode community samples. V.F. and D.B. helped perform the functional prediction analyses. J.R. contributed to writing and editing, with input from all authors. All authors provided critical feedback and shaped the research, analysis, and manuscript.

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Data availability No datasets were generated or analysed during the current study.

Declarations

Ethics approval This article does not contain any studies with human participants or animals performed by any of the authors.

Conflict of interest The authors declare no competing interests.

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