



OPEN ACCESS

EDITED BY

Hongchen Jiang,
China University of Geosciences Wuhan,
China

REVIEWED BY

Xiaojing Hu,
Northeast Institute of Geography and
Agroecology (CAS), China
Xiubing Gao,
Guizhou Tea Research Institute, China

*CORRESPONDENCE

Xiuming Liu
liuxiuming@vip.skleg.cn
Bin Lian
bin2368@vip.163.com

[†]These authors have contributed equally to
this work and share first authorship

SPECIALTY SECTION

This article was submitted to
Terrestrial Microbiology,
a section of the journal
Frontiers in Microbiology

RECEIVED 30 September 2022

ACCEPTED 08 November 2022

PUBLISHED 24 November 2022

CITATION

Li Y, Shen Q, An X, Xie Y, Liu X and
Lian B (2022) Organomineral fertilizer
application enhances *Perilla frutescens*
nutritional quality and rhizosphere
microbial community stability in karst
mountain soils.
Front. Microbiol. 13:1058067.
doi: 10.3389/fmicb.2022.1058067

COPYRIGHT

© 2022 Li, Shen, An, Xie, Liu and Lian. This
is an open-access article distributed under
the terms of the [Creative Commons
Attribution License \(CC BY\)](https://creativecommons.org/licenses/by/4.0/). The use,
distribution or reproduction in other
forums is permitted, provided the original
author(s) and the copyright owner(s) are
credited and that the original publication in
this journal is cited, in accordance with
accepted academic practice. No use,
distribution or reproduction is permitted
which does not comply with these terms.

Organomineral fertilizer application enhances *Perilla frutescens* nutritional quality and rhizosphere microbial community stability in karst mountain soils

Ying Li^{1,2†}, Qi Shen^{3†}, Xiaochi An², Yuanhuan Xie¹, Xiuming Liu^{1*} and Bin Lian^{2*}

¹State Key Laboratory of Environmental Geochemistry, Institute of Geochemistry, Chinese Academy of Sciences, Guiyang, China, ²College of Life Sciences, College of Marine Science and Engineering, Nanjing Normal University, Nanjing, China, ³Institute of Medical Plant Physiology and Ecology, School of Pharmaceutical Sciences, Guangzhou University of Chinese Medicine, Guangzhou, China

Introduction: Applications of organomineral fertilizer (OMF) are important measures for developing organic agriculture in karst mountain areas. However, the influence of OMF on the structure and function of soil microbial diversity and their relationship with crop yield and quality are still unclear.

Methods: Based on soil science, crop science, and high-throughput sequencing methods, we investigated the changes of rhizosphere soil microbial communities of *Perilla frutescens* under different fertilization measures. Then, the relationship between *P. frutescens* yield and quality with soil quality was analyzed.

Results: The results showed that the addition of OMF increased the amount of total carbon and total potassium in soil. OF, especially OMF, improved *P. frutescens* yield and quality (e.g., panicle number per plant, main panicle length, and unsaturated fatty acid contents). Both OF and OMF treatments significantly increased the enrichment of beneficial microorganism (e.g., *Bacillus*, *Actinomadura*, *Candidatus_Solibacter*, *Iamia*, *Pseudallescheria*, and *Cladorrhinum*). The symbiotic network analysis demonstrated that OMF strengthened the connection among the soil microbial communities, and the community composition became more stable. Redundancy analysis and structural equation modeling showed that the soil pH, available phosphorus, and available potassium were significantly correlated with soil microbial community diversity and *P. frutescens* yield and quality.

Discussion: Our study confirmed that OMF could replace CF or common OF to improve soil fertility, crop yield and quality in karst mountain soils.

KEYWORDS

karst soil, organomineral fertilizer, *Perilla frutescens*, nutritional quality, rhizosphere microbial community

Introduction

Application of chemical fertilizers (CFs) can significantly increase soil fertility and crop yield in a short time. However, long-term excessive application of CFs damages soil microbial communities and biological activities, which results in decreased soil quality, increased dependence of crop growth on fertilizer nutrients, and aggravated agricultural surface source pollution (Gomiero et al., 2011; Kour et al., 2020; Ren et al., 2020). To reduce the negative effects caused by excessive application of CFs, organic fertilizers (OFs) are usually used to replace or partially replace CFs to protect soil biodiversity and maintain soil ecological balance (Megali et al., 2013; Steffen et al., 2015). Increased OFs application can increase soil carbon storage and plant nutrients, and improve soil biological activity, which are of great significance for mitigating climate warming and developing sustainable agricultural production (Gattinger et al., 2012; Seufert et al., 2012). Many studies have shown that OFs application is an effective way to improve crop yield and quality (Liu et al., 2020, 2021; Du et al., 2022), and increase soil microbial richness and diversity (Zhou et al., 2015; Cui et al., 2018; Li et al., 2020). However, the contents of mineral nutrients such as nitrogen, phosphorus, and potassium in OFs are low, and the increased amount of fertilizer needed increases the cost and application difficulty. Therefore, it is very necessary to improve the contents of mineral elements in traditional OFs.

As a new fertilizer combining the advantages of organic fertilizer and inorganic fertilizer, the nutrient release effect of OMFs occurs simultaneously with the crop growth process, making the agronomic efficiency higher when compared with the inorganic fertilizer (Kiehl, 2008). Compared with CFs, OMFs can reduce the loss of some nutrients, such as nitrogen volatilization, phosphorus fixation and potassium leaching (Aguilar et al., 2019). Compared with common OFs, OMFs are rich in mineral elements necessary for crop growth. OMFs are usually composed of natural organic matter sources and inorganic element sources. Organomineral fertilizer ingredients are mostly agricultural wastes such as chicken manure, coffee shell, wood waste, sewage sludge and sugarcane cake, combined with urea, calcium superphosphate, potassium chloride, magnesium silicate, calcium sulfate and other inorganic chemical fertilizers (Efanov et al., 2001; Carvalho et al., 2014; Grohskopf et al., 2019; Gonçalves et al., 2021; Hawrot-Paw et al., 2022; Ngo et al., 2022). According to the published articles, the research on the application effect of organic mineral fertilizer mainly focuses on the agronomic efficiency of crops. Compared with the crop response to inorganic fertilizers, the response to organomineral fertilizers is quite variable. The reported results are gains (Efanov et al., 2001; Deeks et al., 2013; Carvalho et al., 2014; Sakurada et al., 2016; Vollú et al., 2018; Ngo et al., 2022), losses (Antille et al., 2017; Frazão et al., 2019), or equivalent efficiency (Corrêa et al., 2018; Dias et al., 2020; Mumbach et al., 2020). Those varied results may be related to the different ingredients of OMFs, the amount of fertilizer applied and the environment of the study sites. Limited research literature showed that OMF, as a source of organic carbon and

mineral elements, had a positive effect on the quantity and activity of soil microorganisms (Hawrot-Paw et al., 2022), but had little effect on the rhizosphere bacterial diversity of crops (Vollú et al., 2018).

The staggering production of cuttings and quarry by-products from mining activities results in a huge environmental burden; however, the combined use of these cuttings and low-grade mineral rocks can help reduce this pollution (Basak et al., 2021; Syed et al., 2021). The OMF formed by the combination fermentation of low-grade mineral powder and agricultural waste can more fully reflect the production concept of energy saving and environmental protection, and reduce the cost in the production process of inorganic fertilizers such as urea and phosphate fertilizer. Previous studies have shown that OMF produced by mixing rock powder containing potassium and phosphate with OF or mixing rock powder during OF fermentation can provide beneficial mineral nutrients for crop growth without introducing toxic heavy metal pollution (Theodoro and Leonardos, 2006; Biswas et al., 2009; Lian et al., 2020; Basak et al., 2021; Syed et al., 2021). As an important support of soil quality, soil microorganisms are sensitive to fertilization managements (Wang et al., 2020; Bello et al., 2021). However, there have been no reports on the effects of OMFs application on soil microbial community diversity and composition in karst mountain soils.

P. frutescens is an annual herb in the Labiaceae family and is a widely cultivated cash crop in Asian countries (Hu et al., 2010; Yu et al., 2017). In China, it has traditionally been used in medicine and food, and has been cultivated for more than 2000 years (Lee and Kim, 2007). The oil-rich seeds of *P. frutescens* are used to make condiments in traditional Asian cuisines (Luitel et al., 2017). As the raw material of cooking oil, perilla grains are rich in unsaturated fatty acids and have a high content of α -linolenic acid, up to 50–70%; this is the highest α -linolenic acid content known in plants (Yu et al., 2017). In addition to value as a food item, *P. frutescens* is also used in traditional Chinese medicine, and as food decoration and a coloring agent (Tian et al., 2014). Moreover, *P. frutescens* is an important agricultural crop in karst areas of southwest China (Tian et al., 2017).

Potassium is one of the main elements necessary for plant growth. According to the standard of the Second Soil Survey of China (China Soil Science Database¹), the soil in karst areas is in a state of potassium deficiency (total $K < 10 \text{ g}\cdot\text{kg}^{-1}$ and available $K < 100 \text{ mg}\cdot\text{kg}^{-1}$). Therefore, potassium supplementation is necessary to improve soil fertility in karst areas of southwest China. For this reason, our OMF was fermented from potassium-containing rocks (potassium feldspar) together with agricultural wastes such as chicken manure and straw. We hypothesized that the application of potassium-containing OMF was beneficial to improving *P. frutescens* quality and yield, and had positive effects on the distribution and structure of soil microbial communities. To test this hypothesis, the yield, quality, and rhizosphere soil

¹ <http://vdb3.soil.csdb.cn/>

microbial community characteristics of *P. frutescens* were analyzed and studied based on soil science, crop science, and high-throughput sequencing technology methods. The aim of this study was to reveal: (1) differences in soil microbial diversity and community structure of the *P. frutescens* rhizosphere under different fertilization treatments; (2) the relationship among *P. frutescens* yield and quality, soil characteristics, and microbial community under different fertilization treatments; and (3) the effects of OMF on soil and crop quality. This study investigated for the first time the feasibility of using OMFs to improve the quality of *P. frutescens* and the abundance of soil beneficial microbial community in the potassium-deficient karst areas. The results will be conducive to the application of new OMFs in karst areas, and improve the yield and quality of *P. frutescens* which is widely cultivated in this area.

Materials and methods

Experimental design and sample collection

The experimental field site was located in Changzhai Village, Changshun County, Guizhou Province, China (26°01'25" N, 106°30'55" E; elevation, 1,004 m). The strata are mainly light-colored limestone of the Permian Qixia Formation and Maokou Formation. The soil type is yellow soil according to the Chinese soil classification system (Gong, 1999) and Orthic Acrisols according to the World Reference Base (WRB) soil classification system (USS Working Group WRB, 2015). The region has a subtropical monsoon humid climate. The annual average temperature is 15.1°C, the annual average precipitation is 1396.7 mm, the annual sunshine duration is 1202.1 h, and the annual frost-free period is 275 days.

Four treatments were set up in the field experiment: blank control group (CK), no fertilization; CF group, compound CF was applied; OF group, ordinary OF was applied; OMF group, potassium-containing OMF was applied. Four parallel plots (5 m × 5 m) were set for each treatment group (total, 16 plots). The randomized complete block design was used to divide the sample area blocks (Supplementary Figure S1). On 7 May 2019, *P. frutescens* was planted and fertilized. The *P. frutescens* seeds were the 1st generation hybrids cultivated by the Oil Materials Research Institute of Guizhou Academy of Agricultural Sciences (China).

The fertilizer specifications used were as follows:

The raw materials for OF fermentation were mushroom residue, distiller's grains, straw, and chicken manure, which were mixed according to a mass ratio of 1:1:1:2 and EM microbial agent was added for fermentation (1 kg bacterial agent was added for every 10 T substrate). The mixture was then fermented in a fermentation tank for 30 days with periodic stirring. The total nutrient content (N + P₂O₅ + K₂O) was 7.2%, among which the content ratio of N:P₂O₅:K₂O was 0.9%:2.9%:3.4%, organic matter was 48.3%, and pH was 7.7.

Potassium-containing OMF was made by mixing the raw fermentation materials of the OF and potassium-containing rock powder, which contained 76% potassium feldspar, and passing the mixture through a 2-mm sieve. In accordance with a mass ratio of 3:1, the chemical composition was as follows: Al₂O₃, 17.11%; SiO₂, 54.06%; K₂O, 9.09%; CaO, 1.9%; Fe₂O₃, 6.15%; and MgO, 3.41% (Sun et al., 2019). Then, EM microbial agent was added for fermentation (1 kg bacterial agent per 10 T substrate). The raw materials were thoroughly mixed and fermented for 30 days with periodic stirring. The total nutrient content of OMF was 6.4%, with a content ratio of N: P₂O₅: K₂O of 1.6%:1.1%:3.7%, the content of organic matter was 56.4%, and the pH was 7.6. OF and OMF were produced by Guizhou Guifu Ecological Fertilizer Co., LTD. (China).

The compound CF was produced by Guizhou Xiyang Fertilizer Co., LTD. (China) and had a total nutrient content ≥45%, N:P₂O₅:K₂O content ratio was 15%:15%:15%. Urea was produced by Guizhou Chitianhua Tongzi Chemical Co., LTD. (China) with a total N ≥46.4%. Phosphate fertilizer was produced by Fuda Phosphorus Chemical Co., LTD. (China) with P₂O₅ ≥12%. The proportions of N, P, and K in OF and OMF groups were balanced by urea and phosphate fertilizer. All treatment groups had fertilizer applied with a content ratio of N:P₂O₅:K₂O of 15:15:15, and application amounts are shown in Table 1.

Rhizosphere soil sampling was conducted on 19 August 2019, which was the 105th day of *P. frutescens* growth. Rhizosphere soil samples were arbitrarily collected from eight *P. frutescens* plants in each plot and mixed into one sample. A total of 16 mixed soil samples were collected. When collecting rhizosphere soil, the whole plant was first dug up, and the scattered soil at the root was gently shaken off. The remaining soil attached to the root system was considered the rhizosphere soil (Sun et al., 2021). The soil samples were frozen and transported to the laboratory on dry ice, passed through a 2-mm sterile sieve, and the plant roots were removed. Each sample was divided into two parts: one part was naturally air-dried to determine physicochemical properties, and the other was stored in a -80°C freezer for DNA extraction.

Soil physicochemical analysis

Soil pH was analyzed by vibrating slurry with a water:soil ratio of 2.5:1 (v/w) and determined using a pH meter (Mettler-Toledo FE28, Switzerland; Marcos et al., 2019). Soil total organic carbon (TOC), total organic nitrogen (TON), total carbon (TC), and total nitrogen (TN) were determined using an elemental analyzer (Vario MACRO Cube, Germany; Liu et al., 2014). Total phosphorus (TP) and total potassium (TK) were determined by sodium hydroxide melting flame spectrophotometry (Ren et al., 2016). Available phosphorus (AP) was determined by the NaHCO₃ method, and available potassium (AK) was determined by ammonium acetate extraction-flame spectrophotometry (Lu, 1999).

TABLE 1 Fertilization doses of different treatment groups.

Treatments	Base fertilizer				
	Inorganic compound fertilizer kg.hm ⁻¹	Conventional organic fertilizer kg.hm ⁻¹	Organomineral fertilizer kg.hm ⁻¹	Urea (N) kg.hm ⁻¹	Calcium superphosphate (P ₂ O ₅) kg.hm ⁻¹
CK	0	0	0	0	0
CF	225.00	0	0	0	0
OF	0	993.35	0	53.48	40.37
OMF	0	0	912.47	41.28	197.55

CK is the control blank group; CF is conventional inorganic compound fertilizer group; OF is conventional organic fertilizer group; OMF is organomineral fertilizer group.

P. frutescens yield and quality analysis

On 21 September 2019, *P. frutescens* were harvested on the 137th day of growth. The *P. frutescens* yield was measured after harvest. The main indicators were plant height, biomass per plant, number of stem nodes, number of effective branches at one time, length of effective branches at one time, number of branch angles, number of panicles per plant, length of the main panicle, number of fruits in a single row of the main panicle, number of fruits on the main ear, and number of grains in the 10 main ears. After the perilla seeds were harvested, seed quality was inferred by determining fatty acid content (e.g., palmitic acid content, stearic acid content, oleic acid content, linoleic acid content, and linolenic acid content), total lipid content, and crude protein content. The fatty acid content was determined by gas chromatography–mass spectrometry (GCMS-QP2010, Shimadzu, Japan; Javier et al., 2018; Ko et al., 2018). Fat content was determined by sequential Soxhlet extraction according to ISO 659:2009 (Kourimska et al., 2018). The crude protein content was determined by the Kjeldahl method, the nitrogen concentration of the sample was calculated with a conversion factor (6.25), and the total nitrogen and protein mass were determined to obtain the crude protein content (Yaldiz and Camlica, 2020).

DNA extraction and high-throughput sequencing

Total soil DNA was extracted from 0.5 g soil according to the manufacturer's instructions for the E.Z.N.A.[®] Soil DNA Kit (Omega Bio-Tek, USA). The DNA extraction quality was detected using 1% agarose gel electrophoresis, and the DNA concentration and purity were determined using a NanoDrop2000 spectrophotometer (Thermo Fisher Scientific Co., LTD., USA). Using the extracted DNA as a template, the V3–V4 region of the bacterial 16s rRNA gene was amplified using the primers 338F (5'-ACTCCTACGGGAGGCAGCAG-3') and 806R (5'-GGACTACHVGGGTWTCTAAT-3'; Xu et al., 2016). The fungal ITS region was amplified using the primers ITS1F (5'-CTTGGTCATTTAGAGGAAGTAA-3') and ITS2R

(5'-GCTGCGTTCTTCATCGATGC-3'; Adams et al., 2013). PCR amplification conditions and high-throughput sequencing were conducted as described in Li et al. (2021). Sequencing was performed on Illumina's MiSeq PE300 platform (Shanghai Majorbio Bio-pharm Technology Co., LTD., China). The raw sequence data reported in this paper were deposited in the NCBI SRA database (serial numbers: bacteria, PRJNA836163; fungi, PRJNA836186).

Trimmomatic (version 0.33²) was used for quality control of the original sequences (Bolger et al., 2014), and FLASH (version 1.2.11³) was used for splicing (Magoc and Salzberg, 2011). The splicing sequence data were analyzed using UPARSE (version 7.1;⁴ Edgar, 2013), and sequences with a similarity of ≥97% were assigned to the same operational taxonomic unit (OTU). After quality control and concatenation of the original sequences of all samples, 1,088,672 and 976,526 high-quality sequences of bacteria and fungi were obtained, respectively. At the 97% sequence similarity level, the sequences clustered into 5,685 and 2,585 OTUs, respectively. For each representative sequence, the SILVA (bacteria⁵) and UNITE (fungi⁶) databases were used to annotate taxonomic information (Fan et al., 2020; Kang et al., 2022).

Statistical analysis

Mean value, standard deviation, and variance analysis of soil physicochemical properties and *Perilla* yield and quality were analyzed using Microsoft Excel 2010 and SPSS Statistics (version 20.0, IBM, USA). Differences between mean values were determined by one-way ANOVA and LSD post-hoc test ($p < 0.05$). All bioinformatic analyses were performed using R (version 3.6.1; <https://cran.r-project.org/bin/windows/base/old/3.6.1/>).

² <http://www.usadellab.org/cms/?page=trimmomatic>

³ <https://ccb.jhu.edu/software/FLASH/>

⁴ <http://drive5.com/uparse/>

⁵ <http://www.arb-silva.de>

⁶ <http://unite.ut.ee>

The alpha diversity (Sobs, Chao, and Shannon indices) of *Perilla* rhizosphere soil microbial communities was estimated based on OTUs. All indices were calculated by the “vegan” (Dixon, 2003) and “picante” (Kembel et al., 2010) packages in R (version 3.6.3). The linear discriminant analysis (LDA) effect size (LEfSe) method was used to assess potential bacterial and fungal biomarkers (from phylum to genus) within soil microbiomes that were specifically enriched under different fertilization management types based on $p < 0.05$ and an LDS score > 4.0 (Segata et al., 2011). Principal coordinates analysis (PCoA) was performed to calculate the gradient of compositional changes for bacterial and fungal microbial communities (based on Weighted-Unifrac distance matrix) using the ggplot2 package (Lozupone and Knight, 2005). Differences in bacterial and fungal communities between different samples were analyzed by Adonis test.

After variance inflation factor (VIF) analysis, pH, TC, TOC, TN, TK, AP, and AK with a VIF threshold less than 10 were selected for redundancy analysis (RDA) between environmental factors and soil microbial communities. Variance partitioning analysis (VPA) was used to quantitatively evaluate the individual and common explainability of environmental factor variables for microbial community differences. In addition, FAPROTAX (Louca et al., 2016) and FUNGuild (Nguyen et al., 2016) were used to analyze the ecological functions of soil bacteria and fungi, respectively. Kruskal–Wallis H test was used to test the significance of differences between groups.

Co-occurrence network analysis

To study the effect of different fertilization management techniques on the relationship of soil microbial communities, soil bacterial and fungal communities were combined based on fertilization management technique, and a soil microbial co-occurrence network based on genus classification was constructed. The co-occurrence network was constructed with genera that had a relative abundance greater than 0.1% based on random matrix theory (Deng et al., 2012). To simplify the networks for better visualization, a Spearman’s correlation between the two genera was considered statistically significant if the Spearman’s correlation coefficient (r) was > 0.6 and the p value was < 0.05 . Moreover, p values were adjusted using the Benjamini–Hochberg FDR method (Benjamini and Hochberg, 1995). Spearman’s correlation and network attributes were calculated using the WGCNA, Psych, Igraph, and fdrci packages in R (version 3.6.3) (Csardi and Nepusz, 2006). The network attributes included the number of edges, average clustering coefficient, average degree, modularity, average path length, graph density, and betweenness centrality. Higher numbers of nodes and edges, graph density, average degree, and lower average path length indicate a more complex and connected network (Ma et al., 2016; Jiao et al., 2021). The higher the betweenness centrality value of microbial species, the greater the critical role of the species in the

network. The Fruchterman–Reingold layout algorithm was used in the interactive platform Gephi (version 0.9.2⁷) for network visualization and network topology parameter calculation (Bastian et al., 2009). The network stability was evaluated by removing the nodes in the static network to estimate the speed of robustness decline, and the network robustness was evaluated by the natural connectivity of the nodes (Yuan et al., 2021; Zhu et al., 2022).

Structural equation model analysis

A structural equation model (SEM) was used to identify the direct and indirect effects of soil physicochemical properties (such as pH, TC, AK, and AP) on bacterial and fungal diversity (Shannon index), and *P. frutescens* yield (biomass per plant) and quality (linoleic acid content). To reduce SEM complexity, the representative indices of soil physicochemical properties were calculated by PCoA (Sun et al., 2021). All variables were standardized using Z-transformation (mean = 0, standard deviation = 1; Du et al., 2022).

The theoretical model assumed that: (1) soil pH has a direct impact on soil nutrient content, microbial community diversity, and *P. frutescens* quality or yield, (2) the soil available phosphorus, potassium, and total carbon had direct or indirect effects on the *P. frutescens* quality and yield and the soil microbial community, and (3) the *P. frutescens* yield has a direct effect on the soil microbial community. Model fitting was performed using root mean square error of approximation (RMSEA), probability level p value, Bentler comparative fit index (CFI), maximum likelihood goodness of fit (χ^2), and degrees of freedom (df) tests (Du et al., 2022). The SEM was constructed using Amos Graphics (version 24.0, IBM Corp., USA; Liu, L. et al., 2019).

Results

Soil physicochemical properties

Compared with the CK group, the OMF group significantly increased soil TC and TK contents ($p < 0.05$; Table 2). Fertilization also significantly increased soil AK content ($p < 0.05$; Table 2). In addition, there were no significant differences in the physicochemical properties between the different fertilization treatment groups. The measurement results of different fertilization treatment groups indicated that short-term fertilization treatments may not significantly improve soil physicochemical properties. However, numerical analysis demonstrated that OF and OMF treatments tended to produce better results than no fertilization and CF treatment.

⁷ <https://gephi.org/>

TABLE 2 Soil chemical properties under different fertilization treatments.

Chemical factor	CK	CF	OF	OMF
pH	5.98 ± 0.19a	5.91 ± 0.07a	6.04 ± 0.10a	6.00 ± 0.13a
TOC	15.73 ± 0.79a	16.12 ± 0.72a	16.31 ± 0.78a	16.49 ± 1.14a
TON	0.14 ± 0.01a	0.15 ± 0.01a	0.15 ± 0.01a	0.15 ± 0.01a
TC	20.43 ± 0.50b	20.78 ± 0.66ab	20.86 ± 0.29ab	21.16 ± 0.34a
TN	1.92 ± 0.06a	1.97 ± 0.05a	1.95 ± 0.04a	1.93 ± 0.03a
TP	0.80 ± 0.05a	0.81 ± 0.04a	0.82 ± 0.04a	0.81 ± 0.04a
TK	5.59 ± 0.14b	5.68 ± 0.20ab	5.70 ± 0.19ab	5.84 ± 0.09a
AP	28.51 ± 6.65a	35.24 ± 5.88a	30.89 ± 5.73a	30.42 ± 5.61a
AK	92.75 ± 20.35b	99.5 ± 44.44a	98.50 ± 31.29a	109.75 ± 30.83a

pH stands for soil pH; TOC represents soil total organic carbon content, g·kg⁻¹; TON stands for soil total organic nitrogen content, g·kg⁻¹; TC stands for soil total carbon content, g·kg⁻¹; TN stands for soil total nitrogen content, g·kg⁻¹; TP represents soil total phosphorus content, g·kg⁻¹; TK represents soil total potassium content, g·kg⁻¹; AP stands for soil available phosphorus content, mg·kg⁻¹; AK stands for soil available potassium content, mg·kg⁻¹. Different letters (a, b) on the same row indicate values that are significantly different (p < 0.05) based on one-way ANOVA and LSD post-hoc test.

P. frutescens yield and quality

The analysis of *P. frutescens* yield during the harvest period showed that, compared with the CK group, the CF, OF, and OMF groups all significantly improved the yield indicators, including the number of stem nodes, number of effective branches at one time, and number of branch angles. However, there were no significant differences among the three fertilization treatments (Table 3). In addition, the number of panicles per plant and length of the main panicle in the OMF group were significantly greater than those in the other treatment groups.

Analysis of *P. frutescens* seed quality showed that the contents of oleic acid, linoleic acid, α-linolenic acid, and fat in the OF and OMF groups were significantly higher than those in the CK and CF groups. Additionally, the OMF group had the highest contents of oleic acid, α-linolenic acid, and fat (Figure 1). The crude protein content of the OMF group was significantly higher than that of the other treatment groups (p < 0.05). This indicated that the application of OFs, especially OMF, helped improve *P. frutescens* quality.

Effects of fertilization treatments on soil microbial community composition

Alpha diversity analysis showed that different fertilization treatments did not significantly affect soil bacterial community richness and diversity, whereas OMF significantly increased soil fungal community richness (Figure 2). PCoA showed that there was no clear distinction between samples from different treatment groups on the PC1 and PC2 axes (Figures 3A,B); this indicated that there was no significant difference in soil bacterial community and fungal community composition among different fertilizer treatment groups in the short term.

TABLE 3 *Perilla frutescens* yield indexes under different fertilization treatments.

Fertilizer regimes	Individual plant biomass (g)	Plant height (cm)	Nodes on main stem	Number of once effective branches	Once effective branch length	Number of pod angles on branches	Spike number per plant	Length of main spike (cm)	Number of main spike per row	Number of pod horns in main ear	Grain number of 10 main spike
CK	365.56 ± 77.36a	130.81 ± 8.80a	10.06 ± 1.00b	18.81 ± 2.34b	109.06 ± 11.39a	26.25 ± 4.28b	51.31 ± 10.93c	27.56 ± 2.63b	32.13 ± 2.80a	128.50 ± 11.21a	35.94 ± 3.38ab
CF	383.31 ± 64.18a	130.88 ± 9.14a	10.69 ± 0.60ab	20.94 ± 1.24a	110.13 ± 11.63a	28.44 ± 3.52ab	55.25 ± 11.53bc	27.13 ± 2.19b	31.88 ± 1.59a	127.50 ± 6.35a	35.56 ± 2.85b
OF	433.31 ± 163.47a	134.25 ± 12.08a	10.63 ± 1.02ab	20.94 ± 1.65a	115.63 ± 15.13a	29.69 ± 2.87ab	59.63 ± 9.53ab	28.06 ± 2.52b	33.25 ± 1.84a	133.00 ± 7.38a	38.44 ± 1.09a
OMF	426.31 ± 68.00a	133.31 ± 5.58a	10.88 ± 1.02a	20.81 ± 2.26a	114.06 ± 8.98a	30.31 ± 2.87a	64.94 ± 11.33a	30.50 ± 2.50a	32.94 ± 2.49a	131.75 ± 9.96a	37.88 ± 1.71ab

Different letters (a, b) on the same column indicate values that are significantly different (P < 0.05) based on one-way ANOVA and LSD post-hoc test.

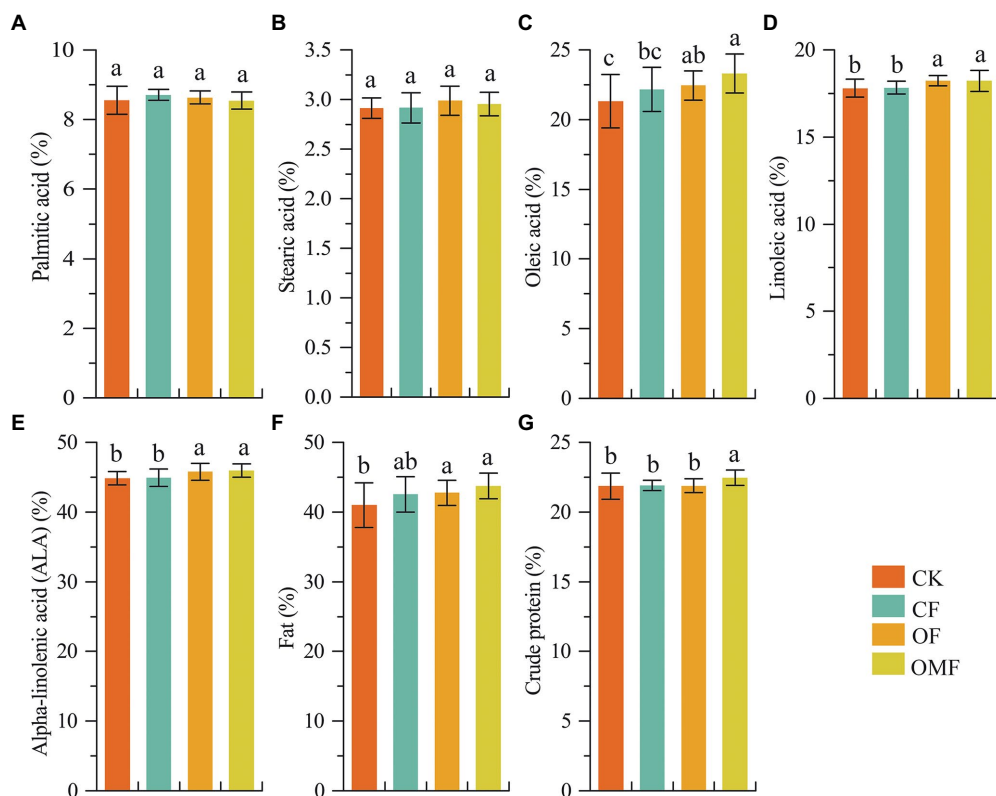


FIGURE 1

Perilla frutescens quality index under different fertilization treatments. Based on one-way ANOVA and LSD post hoc test, different letters (a,b) indicated significant differences among fertilization treatment groups ($P < 0.05$).

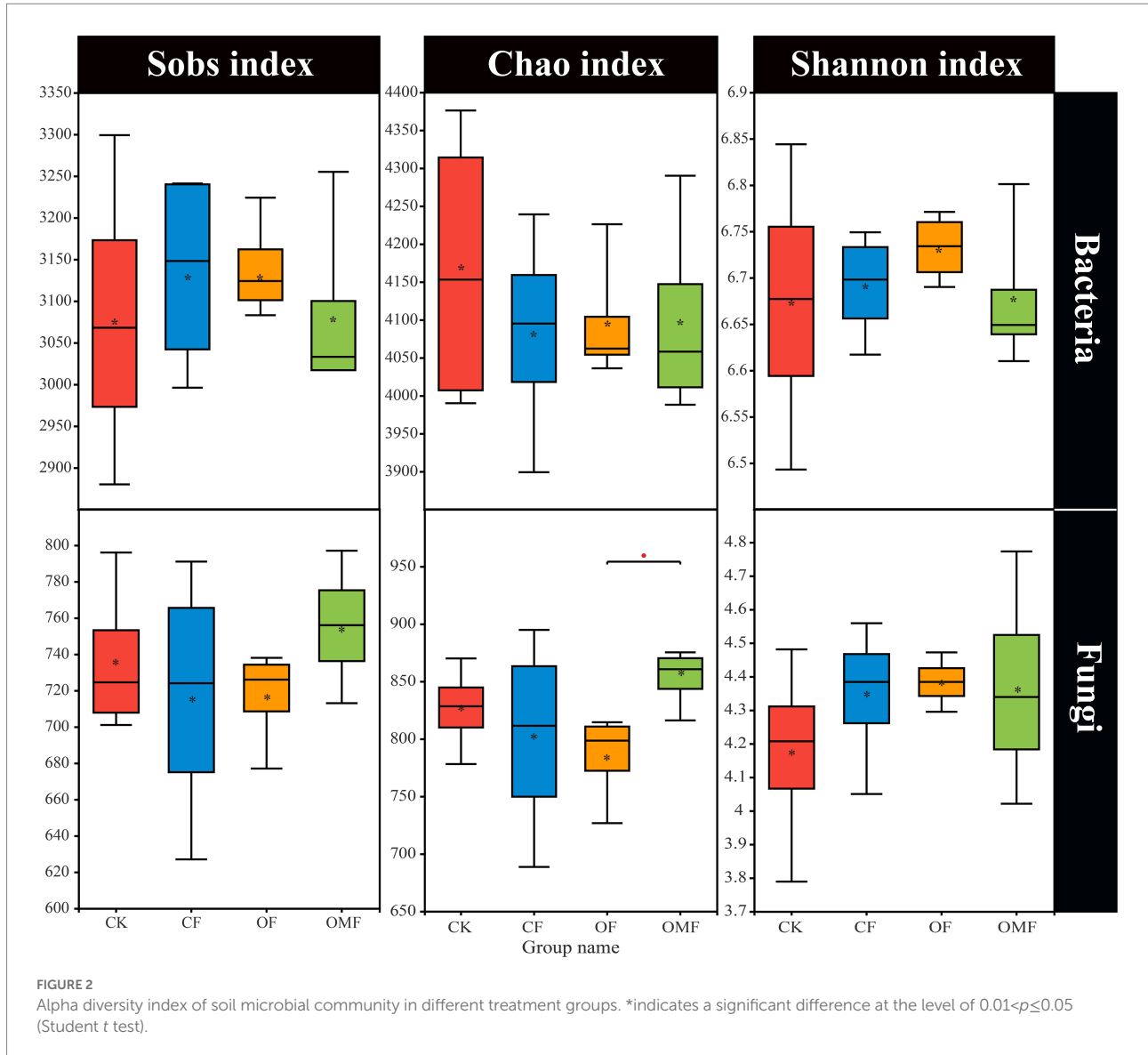
Fertilization management did not cause significant changes in phylum-level bacterial composition ($p > 0.05$, ANOVA analysis; Figure 3C). Proteobacteria, Actinobacteria, Acidobacteria, and Chloroflexi were the main dominant bacterial phyla in each fertilization treatment group. Fertilization management also did not significantly affect the fungal community composition at the phylum level ($p > 0.05$, ANOVA; Figure 3D). Ascomycota, Mortierellomycota, Basidiomycota, and Glomeromycota were the dominant fungal phyla in each treatment group. The taxonomic analysis of the dominant bacterial genera with relative abundance $> 1\%$ showed that different short-term fertilization treatments had no obvious effect on most dominant bacterial genera (Supplementary Table S1). However, the relative abundances of *Bacillus* and *Candidatus_Solibacter* significantly increased after fertilization, especially in the OF and OMF groups; the relative abundance of *Bryobacter* significantly decreased in the OF and OMF groups. The relative abundances of *Clonostachys* and *Gonytrichum* in the OMF group were significantly lower than those in the other groups, and the relative abundance of *Penicillium* in the OF group was significantly lower than that in the other treatment groups. In addition, there were no significant differences in other dominant fungal genera among the treatment groups (Supplementary Table S2).

The LEFSe results showed that *Bryobacter* was significantly enriched in the CK group; the nitrogen-fixing bacteria

Saccharimonadia and iron-reducing bacteria *Desulfobacca* were significantly enriched in the CF group; *Actinomadura*, *Nakamurellaceae* and *Nakamurella* were significantly enriched in the OF group; and *Iamia* and *Iamiaceae* was significantly enriched in the OMF group (Figure 4A). The LEFSe analysis of the fungal community showed (Figure 4B) that *Cyphellaceae*, *Piskurozymaceae*, *Filobasidiales*, *Solicocozyma*, and *Funneliformis* were mainly enriched in the CK group, and *Mycosphaerellaceae*, *Didymosphaeriaceae*, *Paraphaeosphaeria*, and *Pseudopithomyces* were mainly enriched in the CF group. *Helotiales*, *Glomerales*, *Cladorrhinum*, and *Pseudallescheria* in the OF group, and *Phaeosphaeriaceae*, *Bulleribasidiaceae*, and *Sodiomyces* were mainly enriched in the OMF group.

Co-occurrence network analysis of soil microbial communities under different fertilization management techniques

Analysis of the topological indicators of the bacterial community co-occurrence network revealed that the OMF group had the highest increase in the number of network edges and average degree (Table 4). The OF group had the highest modularity index, followed by the OMF group. This finding indicated that the application of OF and OMF could enhance the association of soil



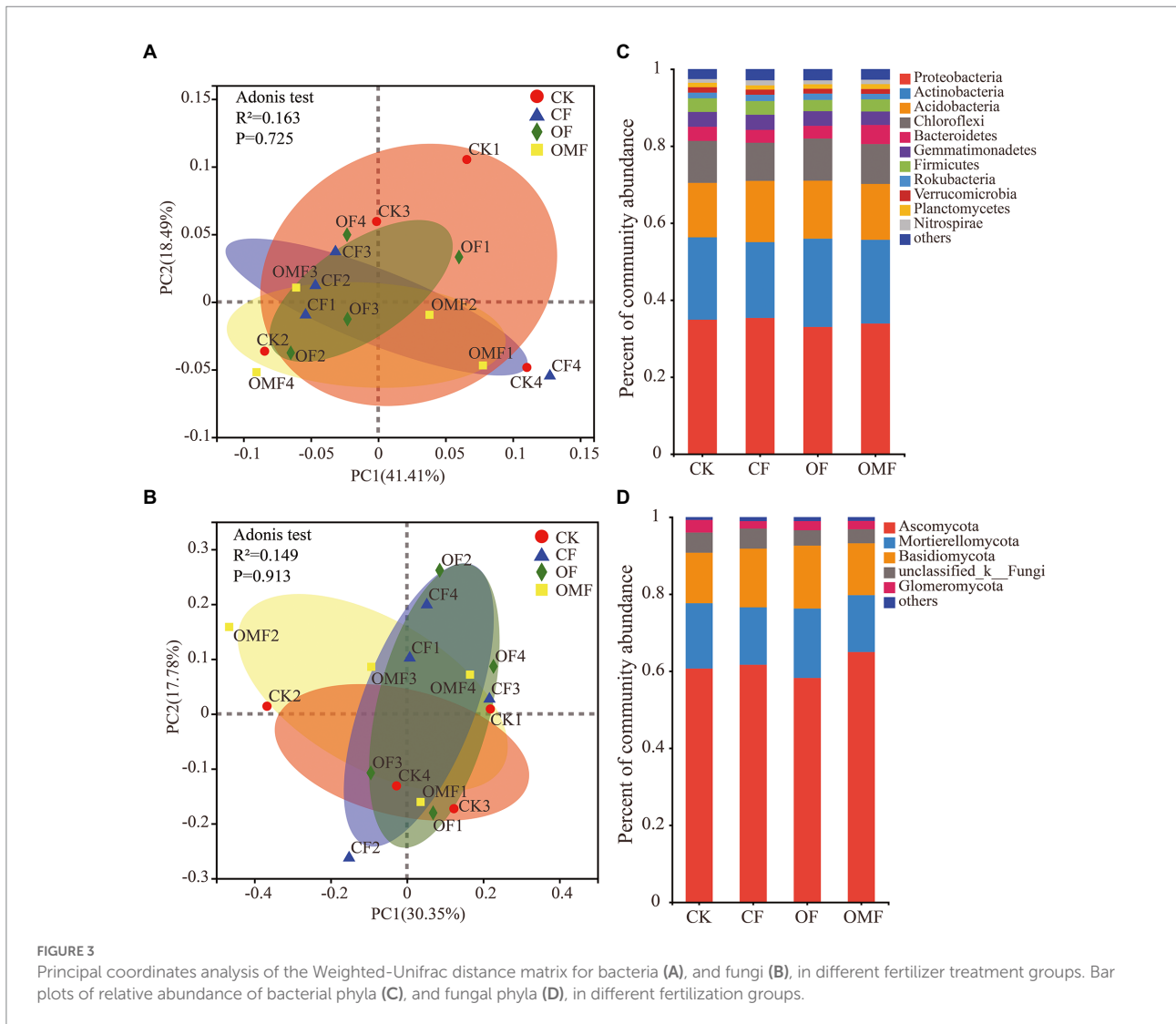
bacterial communities because the degree of modularity was higher. The robustness analysis results showed that the robustness of OF and OMF treatment groups were higher than that of CK and OF groups, and OMF groups was highest (Figure 5C).

Analysis of the network topology indicators of the fungal community showed that, compared with other treatment groups, the OMF group significantly increased the total number of edges in the network, number of positive correlation edges, number of nodes, graph density, and average degree (Table 4). The OMF group had the highest modularity index; this demonstrated that OMF can improve the association of fungal communities, and OMF can make the fungal community structure more modular and more stable. The robustness analysis results showed that the robustness of OMF and CF groups had little difference, but was higher than that of CK and OF groups (Figure 5D).

Analysis of the scale proportions of the top three modules in each group revealed that the proportion of the top three modules

of bacterial and fungal communities was greatest in the OF group followed by the OMF group (Supplementary Figure S2). This indicated that the bacterial communities and the fungal communities of the OF and OMF groups were more closely related.

The main nodes in the bacterial community network of each treatment group belonged to Proteobacteria, Actinobacteria, Acidobacteria, Chlorobacteria, Bacteroidetes, and Firmicutes; the main nodes in the fungal community network belonged to Ascomycota, Basidiomycota, and Glomeromycota. This finding indicated that these bacterial and fungal phyla were keystone microbiota in all treatment groups (Figure 5). According to the analysis of the betweenness centrality values (Supplementary Table S3), the top 10 genus-level species were different in each treatment group, which indicated that the genus-level microbiota that played a key role in the co-occurrence network differed among treatment groups.



Effects of different fertilizer treatments on the ecological function of soil microbial communities

According to FAPROTAX functional analysis, chemoheterotrophy, aerobic chemoheterotrophy, nitrification, aerobic ammonia oxidation, and nitrogen fixation were the top five bacterial community functions in each treatment group (Figure 6A). Among the top 50 functions, only human pathogens all significantly differed among different treatments, and the OF and OMF treatments reduced the proportion of human pathogenic bacteria in soil compared with CK and CF treatments. There were no significant differences in other bacterial community functions among different treatment groups.

FUNGuild functional analysis indicated that Saprotroph, Saprotroph–Symbiotroph, Pathotroph–Saprotroph–Symbiotroph, Pathotroph, and Symbiotroph were the top five trophic modes of the fungal community (Figure 6B). Analysis of the relative abundance of arbuscular mycorrhizal fungi (AMF) in symbiotic

trophic fungi showed that the AMF abundance was significantly reduced in the CF group (Supplementary Figure S3A); this indicated that CFs inhibited AMF growth. *F_unclassified_o_Paraglomerales*, *Glomeraceae*, *Diversisporales_fam_Incertae_sedis*, *f_unclassified_o_GS24*, and *Paraglomeraceae* were the dominant families in AMF, but there were significant differences in their relative abundances among different fertilization treatments groups (Supplementary Figure S3B).

Effects of soil environmental factors on microbial community composition and diversity, and *P. frutescens* yield and quality

RDA indicated that the selected environmental factors explained 38.20% of the total change in bacterial communities (Figure 7A) and 31.32% of total changes in fungal communities (Figure 7B). The results of RDA showed that pH (ANOVA,

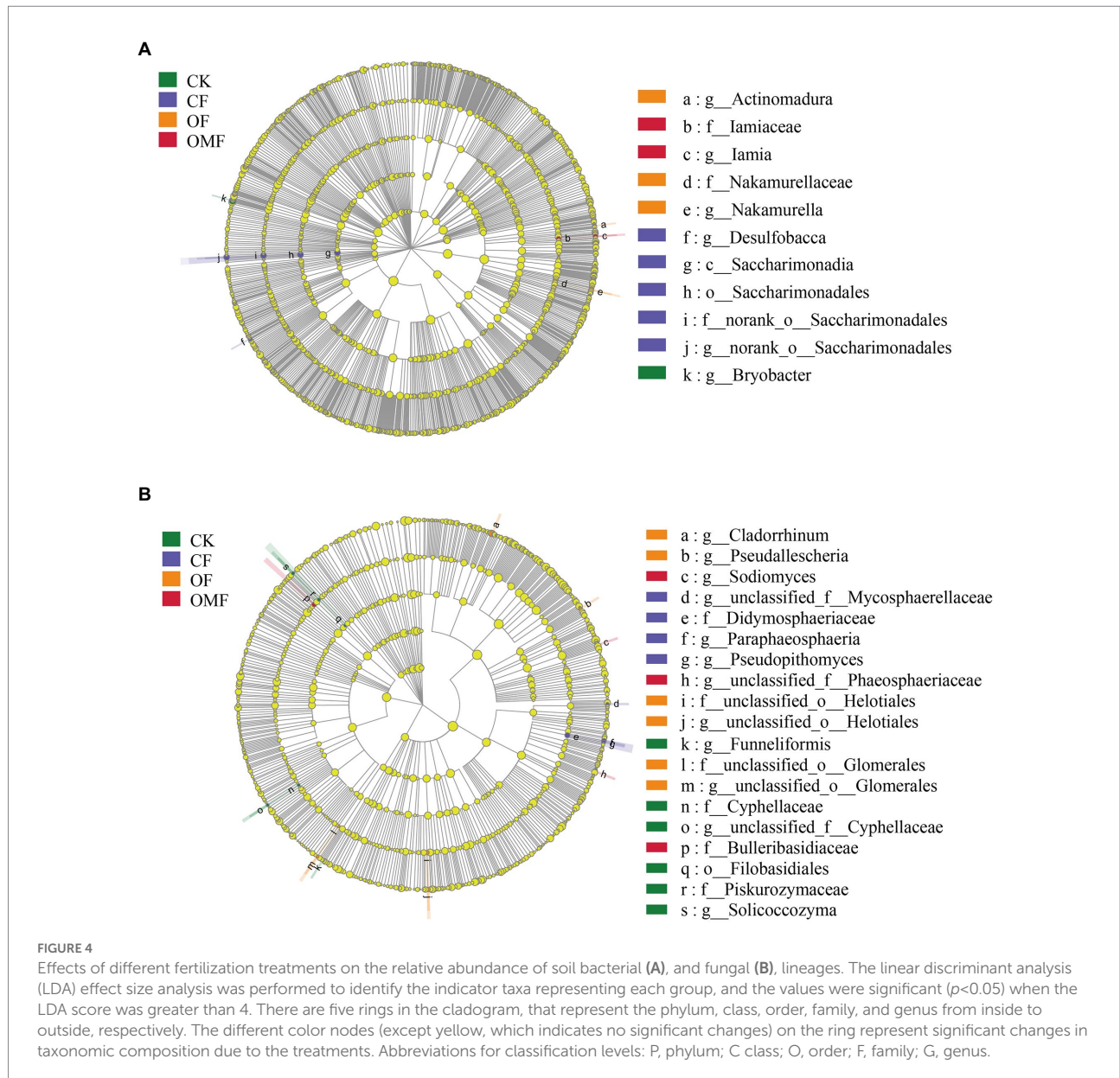


TABLE 4 Topological indices of each co-occurrence network in Figure 5.

	Bacteria				Fungi			
	CK	CF	OF	OMF	CK	CF	OF	OMF
No. of edges ¹	1,629	1,915	1,833	1,985	411	473	420	659
Modularity ²	3.702	5.209	7.045	5.807	1.154	1.190	1.584	1.808
Graph density ³	0.065	0.077	0.070	0.076	0.075	0.080	0.071	0.097
Average degree ⁴	14.480	17.175	15.939	17.336	7.829	8.679	7.706	11.265
Average path length ⁵	4.508	4.306	4.274	4.390	7.941	7.498	5.829	3.252
Average clustering coefficient ⁶	0.660	0.666	0.648	0.659	0.752	0.760	0.703	0.778

¹Number of connections/correlations obtained by Gephi software.

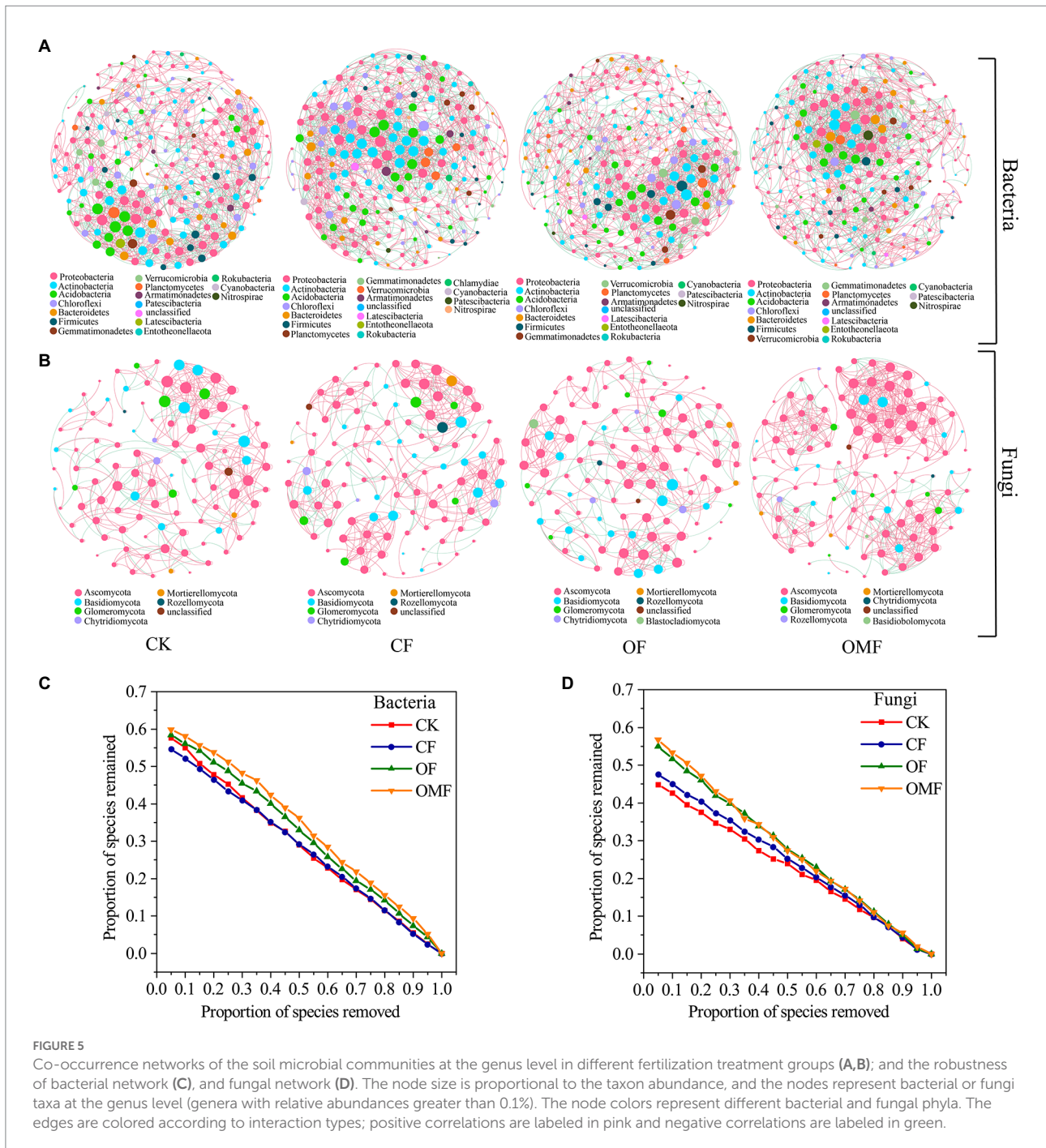
²Capability of the nodes to form highly connected communities, that is, a structure with high density of between nodes connections.

³Measure network integrity. A complete graph with all possible edges, that is, any two nodes with edge connections, has a density of 1.

⁴Average number of connections per node in the network, that is, the node connectivity.

⁵Average network distance between all pair of nodes or the average length off all edges in the network.

⁶How nodes are embedded in their neighborhood and the degree to which they tend to cluster together.



$p=0.021$) and AP (ANOVA, $p=0.024$) were the main factors affecting the soil bacterial community composition, and pH (ANOVA, $p=0.034$) and AK (ANOVA, $p=0.011$) were the main factors affecting the soil fungal community composition (Figure 7).

The SEM fit the measured data well (bacteria, $\chi^2/df=0.658$, $p=0.764$, CFI=1.000, RMSEA=0.000; fungi, $\chi^2/df=1.493$, $p=0.135$, CFI=0.920, RMSEA=0.181); this indicated high consistency between the hypothesized model and the observed data (Figure 8). The SEM showed that soil physicochemical properties accounted for 68% of *P. frutescens* quality, among

which AK and TC were significantly positively correlated with *P. frutescens* quality, and pH and AP were significantly negatively correlated with *P. frutescens* quality (Figure 8). AK and AP were significantly positively correlated with bacterial diversity, and *P. frutescens* yield was significantly negatively correlated with bacterial diversity; these factors accounted for 68% of bacterial diversity (Figure 8A). AP was significantly positively correlated with and explained 61% of *P. frutescens* yield. TC and *P. frutescens* yield were directly and significantly positively correlated with fungal community diversity, whereas AK was directly and

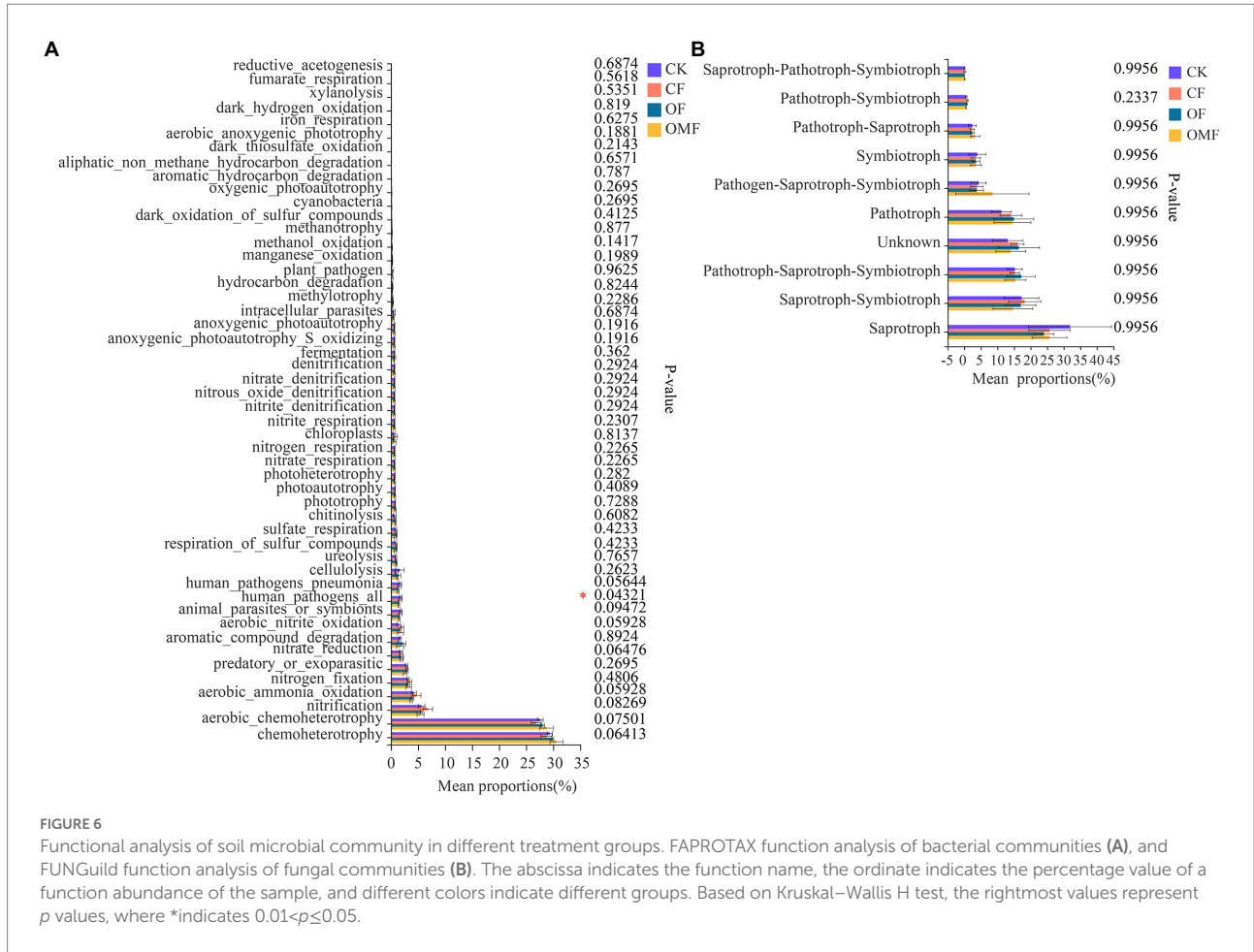


FIGURE 6

Functional analysis of soil microbial community in different treatment groups. FAPROTAX function analysis of bacterial communities (A), and FUNGuild function analysis of fungal communities (B). The abscissa indicates the function name, the ordinate indicates the percentage value of a function abundance of the sample, and different colors indicate different groups. Based on Kruskal–Wallis H test, the rightmost values represent p values, where * indicates $0.01 < p < 0.05$.

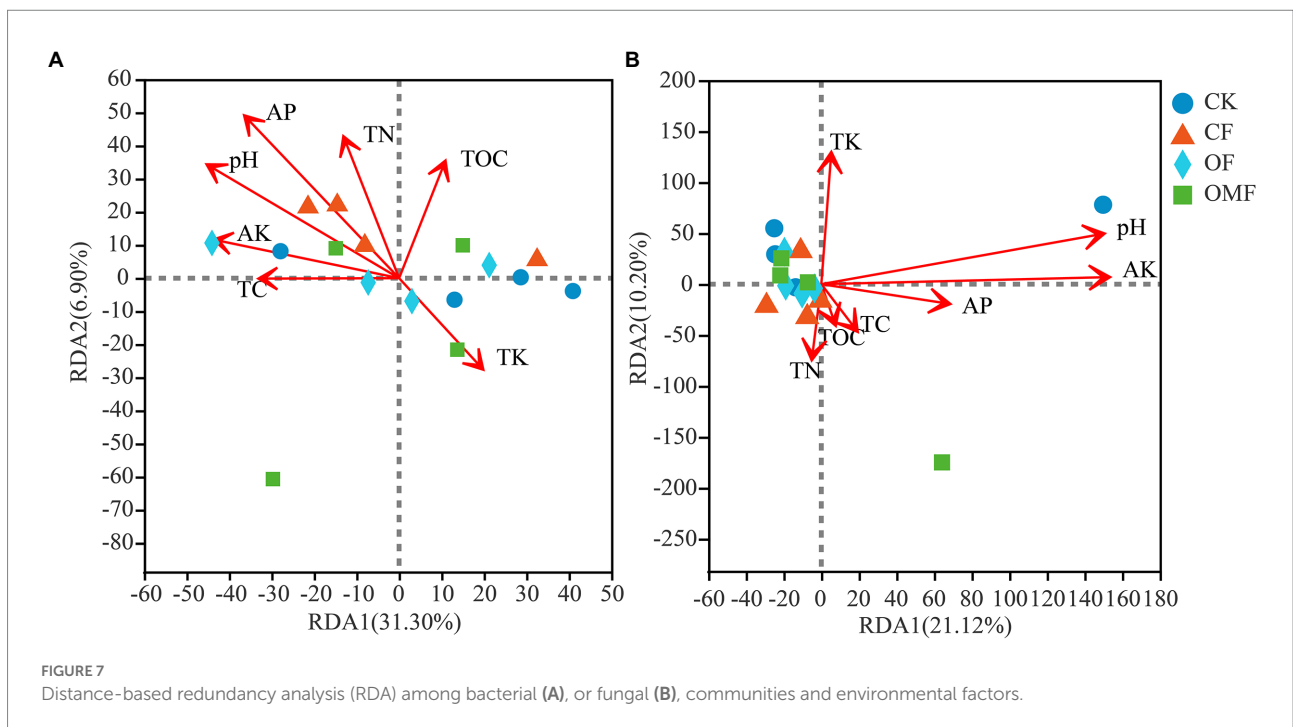


FIGURE 7

Distance-based redundancy analysis (RDA) among bacterial (A), or fungal (B), communities and environmental factors.

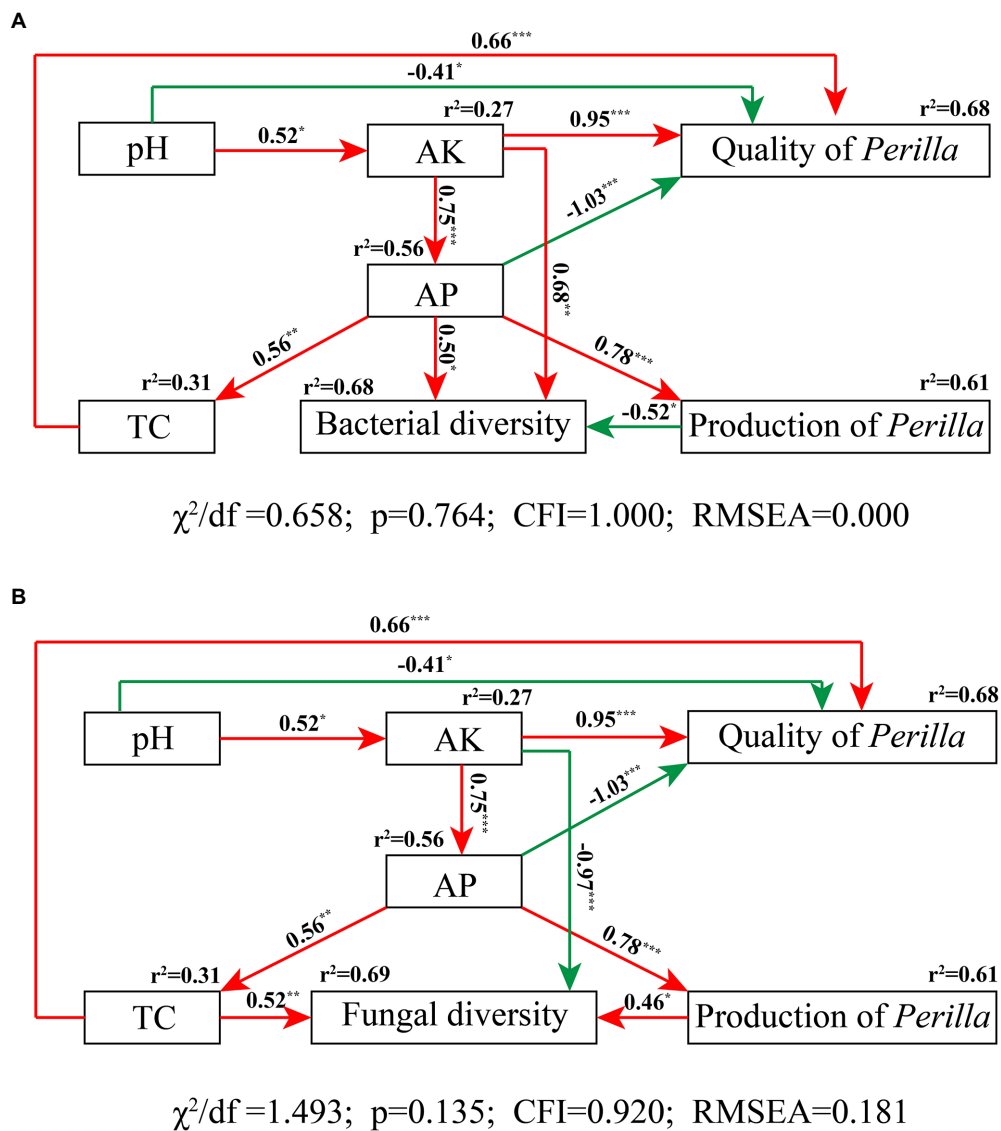


FIGURE 8
Structural equation modeling results describing the relationship among soil nutrients, microbial diversity, and *P. frutescens* yield and quality. The relationship among soil pH value, total soil carbon content (TC), available potassium (AK), available phosphorus (AP), *P. frutescens* production, and *P. frutescens* quality with bacterial diversity (A), and fungal diversity (B). Red lines: positive correlation; green lines: negative correlation. The numbers above the arrows indicate correlation strength. r^2 values indicate the proportion of variance explained for each variable. χ^2 , Chi-square; df, degrees of freedom; p, probability level; RMSEA, goodness-of-fit statistics for each model. Significance levels of each predictor are shown as *for $p < 0.05$, **for $p < 0.01$, and ***for $p < 0.001$.

significantly negatively correlated with fungal community diversity (Figure 8B).

Discussion

Effects of organomineral fertilizer on soil properties and *P. frutescens* yield and quality

Compared with the CK group, OMF application significantly increased the TC and TK contents of the soil (Table 2). The

experiment proved that although short-term application of OMF could not significantly improve most of the soil physicochemical properties, it could guarantee the same effect as the same amount of inorganic fertilizer. Numerical analysis showed that OMF especially OMF application had a trend of improving soil fertility compared with no fertilization and CF application, which was consistent with previous continuous fertilization results (Zhao et al., 2016; Du et al., 2022).

The yield test results of *P. frutescens* at harvest showed that the number of panicles per plant and length of the main panicle were significantly greater in the OMF group compared with the other treatment groups (Table 3); this indicated that OMF

increased *P. frutescens* yield to a certain extent. The quality inspection results of *P. frutescens* showed that OF and OMF treatments significantly increased the contents of unsaturated fatty acids, total fat, and total protein in *P. frutescens*, and the OMF treatment values were higher (Figure 1). These results were similar to those of a previous study that investigated the effect of OMF on *Purslane* growth, which also showed that OMF treatment increased unsaturated fatty acid content (Yang et al., 2020). The SEM results also demonstrated that soil AK content was significantly positively correlated with *P. frutescens* quality (Figure 8). Therefore, OMF application was beneficial for improving *P. frutescens* quality.

Effects of different fertilization treatments on soil microbial communities

Microorganisms are the driver of soil fertility changes; they can directly indicate soil quality and play an important role in plant growth and crop yield (Fan et al., 2020; Finkel et al., 2020). In this study, short-term fertilization treatments did not significantly affect alpha diversity (Figure 2). Similar studies also showed that soil microbial alpha diversity was stable and not easily affected by agricultural management practices (Coller et al., 2019; Gui et al., 2021; Kang et al., 2022). How fertilization management affects soil microbial diversity depends on soil properties (Mendes et al., 2015), such as soil pH, which is generally considered a decisive factor underlying microbial diversity (Bissett et al., 2011).

Actinobacteria and Firmicutes are generally considered to be beneficial microorganisms for plants (Yang et al., 2017). Actinobacteria can control plant bacterial diseases by producing various antibiotics, secreting cell wall-degrading enzymes, and inducing host resistance (Conn et al., 2008; Chater et al., 2010; Liu et al., 2012). LEFSe analysis showed that the treatment of OF and OMF promoted the enrichment of some bacteria belong to Actinobacteria, including *Actinomadura*, *Nakamurellaceae*, *Nakamurella*, *Iamiaceae*, and *Iamia* (Figure 4). *Actinomadura* can produce several antibiotics that inhibit the growth of soil pathogens and reduce the occurrence of crop diseases and insect pests (Li et al., 2022). *Bacillus* and *Candidatus_Solibacter* were also significantly increased in OF and OMF groups (Supplementary Table S1). *Bacillus* is commonly formulated as biocontrol agents because they secrete antibiotics or antimicrobial proteins (Ahimou et al., 2000; Weller et al., 2002; Moyne et al., 2004), and improve soil fertility by increasing soil mineral nutrient availability (Chen et al., 2016). Additionally, *Candidatus_Solibacter* is a bacterium that decomposes organic matter (Rime et al., 2015).

LEFSe analysis showed that the main enriched fungal species (e.g., Glomerales, *Cladorrhinum*, and *Pseudallescheria*) in the OF groups belonged to the phyla Ascomycota and Glomeromycota (Figure 4B). Among them, *Pseudallescheria* is a biocontrol fungus; it is an important natural enemy of some plant parasitic nematodes

that can parasitize eggs and infect larvae and females, and can significantly reduce the damage of plant nematode diseases such as those caused by root-knot, cyst, and stem nematodes of various crops (Wang et al., 1997; Ko et al., 2010; Zhu et al., 2020). *Cladorrhinum* is an effective biocontrol fungus for controlling the soil-borne *Rhizoctonia solani* pathogen (Liu, H. et al., 2019). Ascomycota is a key driver of the degradation of organic residues in soil (Richardson, 2009; Ma et al., 2013); therefore, the Ascomycota abundance may increase with increasing organic matter content (Du et al., 2022). Glomeromycota can undergo symbiosis with terrestrial plants to form arbuscular mycorrhizae, and this symbiosis can help plants absorb inorganic salts in soil, especially phosphorus (Smith and Read, 2008; Calaca and Bustamante, 2022). Our results showed that, OF treatments promoted increase in the number of beneficial fungi in the karst soil.

In conclusion, short-term fertilization treatments affected soil microbial communities, and OF and OMF had advantages over CF. However, compared with previous long-term experimental results, some differences in this study were not significant. Therefore, extending the fertilization period and intensifying fertilization may produce significant fertilization effects (Kox et al., 2020).

OMF treatment increased connectivity and structural stability of soil microbial communities

There is a complex association network among soil microbial communities, and they do not exist alone. When soil microbial community composition changes because of fertilization management, the microbial co-occurrence network also changes (Kang et al., 2022). The OF and OMF groups had higher modularity indices, which indicated that OF and OMF improved the soil microbial community connectivity and made the community connected more closely (Figure 5; Supplementary Figure S2; Table 4). This result is generally consistent with those of other studies on OF application (Ling et al., 2016; Wang et al., 2017; Liu et al., 2020; Kang et al., 2022).

Complex networks with higher connectivity are more tolerant of environmental disturbances than simple networks with lower connectivity (Santolini and Barabási, 2018). In this study, the network connectivity of both bacterial and fungal communities was highest in the OMF group (Table 4); this indicated that OMF treatment resulted in higher anti-interference ability of soil microorganisms. As the core components of soil organic matter degradation, bacteria and fungi usually form different functional groups and change the interaction between their ecological networks because of the decomposition or utilization of organic and inorganic nutrients (Wang et al., 2017; Dai et al., 2018; Samaddar et al., 2019), and they tend to maintain a complex network structure (Kang et al., 2022). The robustness analysis

showed that the application of OF, especially OMF, could improve the stability of bacterial and fungal network structures (Figures 5C,D).

Keystone microbial groups play an important role in maintaining ecosystem homeostasis (Banerjee et al., 2018; Fan et al., 2020). According to the degree values of the network nodes, it was found that the key bacterial and fungal phyla in the nodes were not significantly different among the treatment groups (Figure 5); this was consistent with the composition and distribution of dominant species in the community (Figures 3C,D). At the phylum level, microorganisms had strong stability and were not easily affected by fertilization management. The genera with the highest betweenness centrality scores are generally considered keystone taxa (González et al., 2010; Vick-Majors et al., 2014). In this study, the keystone genera differed among fertilization treatment groups. The keystone genus of the bacterial community in the OMF group was *Pseudomonas*, and the keystone genus of the fungal community was *Metarhizium* (Supplementary Table S3), both of which are recognized as biocontrol microorganisms. *Pseudomonas* can adsorb heavy metals in soil and promote plant growth (Costa-Gutierrez et al., 2020; Ghorbanzadeh et al., 2020; Wu et al., 2022), whereas *Metarhizium* can kill plant pests and mitigate plant diseases (Riguetti Zanardo Botelho et al., 2019; Gebremariam et al., 2021; González-Pérez et al., 2022). In conclusion, this study demonstrated that the application of organic fertilizer, especially OMF, can not only enhance the connectivity, cohesiveness and stability of microbial community network structure, but also increase the abundance of beneficial microorganisms.

Relationship among soil physicochemical properties, soil microbial community, and *P. frutescens* yield and quality

The RDA results showed that soil pH was the most important factor affecting bacterial and fungal communities (Figure 7). This result was consistent with the previous study (Cho et al., 2016; Gu et al., 2019). Changes in soil pH can alter soil structure, fertility, and vegetation communities, thereby directly or indirectly affecting soil microbial community composition (Laubert et al., 2009; Qi et al., 2018). In addition, in this study, AP was also the main factor affecting bacterial communities, and AK was the main factor affecting fungal communities (Figure 7). Fertilizers may be absorbed and used by plants after entering the soil, or they may remain in the soil, leading to changes in the composition of bacterial communities (Sun et al., 2016) and fungal communities (Zhou et al., 2016). Therefore, different fertilization treatments affected soil microbial community composition by mediating the effects of soil physicochemical properties, especially pH, and AP and AK.

SEM results showed that both soil TC and AK content was positively correlated to the quality (linoleic acid content) of

P. frutescens (Figure 8), indicated that improve soil carbon and available potassium content could improve the quality of *P. frutescens*. There was a direct and significant positive correlation between *P. frutescens* yield and AP (Figure 8); this indicated that *P. frutescens* yield was mainly affected by the AP content in soil, and increasing the AP content can improve *P. frutescens* yield. Soil bacterial diversity was significantly positively correlated with soil AK (Figure 8A), but fungal diversity was significantly negatively correlated with soil AK (Figure 8B). Some previous studies showed that soil bacteria and fungi exhibited different patterns in response to fertilization treatments (Álvarez-Martín et al., 2016; Ai et al., 2018), and our study also supported this conclusion. Fungi are generally considered more closely related to plants and they are able to provide nutrients to plants in a symbiotic relationship (Chen et al., 2017), whereas bacteria are more affected by soil properties and environmental factors (Singh et al., 2008; Delgado-Baquerizo et al., 2016, 2018); our study obtained similar results (Figures 7, 8). In this study, we found that soil bacterial diversity was significantly negatively correlated with *P. frutescens* yield, and fungal diversity was significantly positively correlated with *P. frutescens* yield. This result may be opposite to many previous long-term fertilization studies. Because, in this study, short-term application of OF and OMF significantly increased *P. frutescens* yield (biomass per plant), but there was no significant change in bacterial diversity (Shannon index), and the value of OMF group even showed a downward trend (Figure 2). The application of organic fertilizer may stimulate the rapid growth of some dominant bacteria and beneficial bacteria in soil in a short time, while the abundance of some oligotrophic microorganisms that are not adapted to the existence of organic fertilizer will decline, resulting in the decrease of bacterial diversity. Through the correlation analysis among soil physicochemical properties, microbial communities and *P. frutescens* agronomic efficiency, it can be concluded that the application of OF or OMFs can improve the physicochemical properties of soil, especially the contents of total carbon, available potassium and available phosphorus, which can promote the quality and yield of *P. frutescens*.

Conclusion

The results of this study demonstrated that, under short-term fertilization management, OMF increased the total carbon and total potassium contents of soil. OF, especially OMF, improved measures of *P. frutescens* yield and quality, including the number of panicles per plant, length of the main panicle, and contents of unsaturated fatty acids such as α -linolenic acid, total fat, and total protein, while significantly increasing the number of beneficial microbial communities in the soil. The co-occurrence network analysis also revealed that OF and OMF improved the connectivity and stability of soil microbial communities. In conclusion, application of OF,

especially OMF, is a good strategy to shape the composition of beneficial bacterial communities in the soil, and to improve soil fertility and crop yield and quality in karst areas.

Data availability statement

The datasets presented in this study can be found in online repositories. The names of the repository/repositories and accession number(s) can be found at: <https://www.ncbi.nlm.nih.gov/>, PRJNA836163; <https://www.ncbi.nlm.nih.gov/>, PRJNA836186.

Author contributions

BL and XL designed the study and modified the manuscript. YL and QS did the experimental work, carried out the data analysis, and wrote the manuscript. XA and YX contributed to the data analysis and original draft writing. All authors contributed to the article and approved the submitted version.

Funding

This work was supported by the Strategic Priority Research Program of the Chinese Academy of Science (XDA23060102), the Project on Social Development by Department of Science and Technology of Guizhou Province (SY-[2014]3041), the talents of Guizhou Science and Technology Cooperation Platform (2016-5648) and the Opening Fund of the State Key Laboratory of Environmental Geochemistry (SKLEG2021XXX).

References

- Adams, R. I., Miletto, M., Taylor, J. W., and Bruns, T. D. (2013). Dispersal in microbes: fungi in indoor air are dominated by outdoor air and show dispersal limitation at short distances. *ISME J.* 7, 1262–1273. doi: 10.1038/ismej.2013.28
- Aguilar, A. S., Cardoso, A. F., Lima, L. C., Luz, J. M. Q., Rodrigues, T., and Lana, R. M. Q. (2019). Influence of organomineral fertilization in the development of the potato crop CV. Cupid. *Biosci. J.* 35, 199–210. doi: 10.14393/BJ-v35n1a2019-41740
- Ahimou, F., Jacques, P., and Deleu, M. (2000). Surfactin and iturin A effects on *Bacillus subtilis* surface hydrophobicity. *Enzyme Microb. Technol.* 27, 749–754. doi: 10.1016/S0141-0229(00)00295-7
- Ai, C., Zhang, S., Zhang, X., Guo, D., Zhou, W., and Huang, S. (2018). Distinct responses of soil bacterial and fungal communities to changes in fertilization regime and crop rotation. *Geoderma* 319, 156–166. doi: 10.1016/j.geoderma.2018.01.010
- Álvarez-Martín, A., Hilton, S. L., Bending, G. D., Rodríguez-Cruz, M. S., and SanchezMartín, M. J. (2016). Changes in activity and structure of the soil microbial community after application of azoxystrobin or pirimicarb and an organic amendment to an agricultural soil. *Appl. Soil Ecol.* 106, 47–57. doi: 10.1016/j.apsoil.2016.05.005
- Antille, D. L., Godwin, J., Sakrabani, R., Seneweera, S., Tyrrel, S. F., and Johnstron, A. E. (2017). Field-scale evaluation of biosolids derived organomineral fertilizers applied to winter wheat in England. *Agron. J.* 109, 654–674. doi: 10.2134/agronj2016.09.0495
- Banerjee, S., Schlaeppi, K., and van der Heijden, M. G. A. (2018). Keystone taxa as drivers of microbiome structure and functioning. *Nat. Rev. Microbiol.* 16, 567–576. doi: 10.1038/s41579-018-0024-1
- Basak, B. B., Sarkar, B., and Naidu, R. (2021). Environmentally safe release of plant available potassium and micronutrients from organically amended rock mineral powder. *Environ. Geochem. Health* 43, 3273–3286. doi: 10.1007/s10653-020-00677-1

Acknowledgments

Thanks to the editors and reviewers for their professional revision suggestions, which greatly improved the quality of this manuscript. We thank Mallory Eckstut, PhD, from Liwen Bianji (Edanz) (www.liwenbianji.cn) for editing the English text of a draft of this manuscript.

Conflict of interest

The authors declare that the research was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

Publisher's note

All claims expressed in this article are solely those of the authors and do not necessarily represent those of their affiliated organizations, or those of the publisher, the editors and the reviewers. Any product that may be evaluated in this article, or claim that may be made by its manufacturer, is not guaranteed or endorsed by the publisher.

Supplementary material

The Supplementary material for this article can be found online at: <https://www.frontiersin.org/articles/10.3389/fmicb.2022.1058067/full#supplementary-material>

- Bastian, M., Heymann, S., and Jacomy, M. (2009). “Gephi: an open source software for exploring and manipulating networks.” In *The Third International AAAI Conference on Weblogs and Social Media LCWSM*, San Jose, 361–362.
- Bello, A., Wang, B., Zhao, Y., Yang, W., Ogundeyi, A., Deng, L., et al. (2021). Composted biochar affects structural dynamics, function and co-occurrence network patterns of fungi community. *Sci. Total Environ.* 775:145672. doi: 10.1016/j.scitotenv.2021.145672
- Benjamini, Y., and Hochberg, Y. (1995). Controlling the false discovery rate - a practical and powerful approach to multiple testing. *J. R. Stat. Soc. B* 57, 289–300. doi: 10.1111/j.2517-6161.1995.tb02031.x
- Bissett, A., Richardson, A. E., Baker, G., and Thrall, P. H. (2011). Long-term land use effects on soil microbial community structure and function. *Appl. Soil Ecol.* 51, 66–78. doi: 10.1016/j.apsoil.2011.08.010
- Biswas, D. R., Narayanasamy, G., Datta, S. C., Singh, G., Begum, M., Maiti, D., et al. (2009). Changes in nutrient status during preparation of enriched organomineral fertilizers using rice straw, low-grade rock phosphate, waste mica, and phosphate solubilizing microorganism. *Commun. Soil Sci. Plant Anal.* 40, 2285–2307. doi: 10.1080/00103620902961243
- Bolger, A. M., Lohse, M., and Usadel, B. (2014). Trimmomatic: a flexible trimmer for Illumina sequence data. *Bioinformatics* 30, 2114–2120. doi: 10.1093/bioinformatics/btu170
- Calaca, F. J. S., and Bustamante, M. M. C. (2022). Richness of arbuscular mycorrhizal fungi (*Glomeromycota*) along a vegetation gradient of Brazilian Cerrado: responses to seasonality, soil types, and plant communities. *Mycol. Prog.* 21:27. doi: 10.1007/s11557-022-01785-1

- Carvalho, R. P., Moreira, R. A., Cruz, M. C. M., Fernandes, D. R., and Oliveira, A. F. (2014). Organomineral fertilization on the chemical characteristics of Quartzarenic Neosol cultivated with olive tree. *Sci. Hortic.* 176, 120–126. doi: 10.1016/j.scienta.2014.07.006
- Chater, K. F., Biro, S., Lee, K. J., Palmer, T., and Schrempf, H. (2010). The complex extracellular biology of *Streptomyces*. *FEMS Microbiol. Rev.* 34, 171–198. doi: 10.1111/j.1574-6976.2009.00206.x
- Chen, L., Liu, Y., Wu, G., Veronican Njeri, K., Shen, Q., Zhang, N., et al. (2016). Induced maize salt tolerance by rhizosphere inoculation of *Bacillus amyloliquefaciens* SQR9. *Physiol. Plant.* 158, 34–44. doi: 10.1111/ppl.12441
- Chen, Y. L., Xu, T. L., Veresoglou, S. D., Hu, H. W., Hao, Z. P., Hu, Y. J., et al. (2017). Plant diversity represents the prevalent determinant of soil fungal community structure across temperate grasslands in northern China. *Soil Biol. Biochem.* 110, 12–21. doi: 10.1016/j.soilbio.2017.02.015
- Cho, S. J., Kim, M. H., and Lee, Y. O. (2016). Effect of pH on soil bacterial diversity. *J. Environ. Prot. Ecol.* 40, 75–83. doi: 10.1186/s41610-016-0004-1
- Coller, E., Cestaro, A., Zanzotti, R., Bertoldi, D., Pindo, M., Larger, S., et al. (2019). Microbiome of vineyard soils is shaped by geography and management. *Microbiome* 7:170. doi: 10.1186/s40168-019-0758-7
- Conn, V., Walker, A., and Franco, C. (2008). Endophytic actinobacteria induce defense pathways in *Arabidopsis thaliana*. *Mol. Plant-Microbe Interact.* 21, 208–218. doi: 10.1094/MPMI-21-2-0208
- Corrêa, J. C., Rebellatto, A., Grohskopf, M. A., Cassol, P. C., Hentz, P., and Rigo, A. Z. (2018). Soil fertility and agriculture yield with the application of organomineral or mineral fertilizers in solid and fluid forms. *Pesqui. Agropecu. Bras.* 53, 633–640. doi: 10.1590/S0100-204X2018000500012
- Costa-Gutiérrez, S. B., Raimondo, E. E., Lami, M. J., Vincent, P. A., Espinosa-Urgel, M., and de Cristóbal, R. E. (2020). Inoculation of *Pseudomonas* mutant strains can improve growth of soybean and corn plants in soils under salt stress. *Rhizosphere* 16:100255. doi: 10.1016/j.rhisph.2020.100255
- Csardi, G., and Nepusz, T. (2006). The igraph software package for complex network research. *Interf. Complex Syst.* 1695, 1–9.
- Cui, X., Zhang, Y., Gao, J., Peng, F., and Gao, P. (2018). Long-term combined application of manure and chemical fertilizer sustained higher nutrient status and rhizospheric bacterial diversity in reddish paddy soil of Central South China. *Sci. Rep.* 8:16554. doi: 10.1038/s41598-018-34685-0
- Dai, Z., Su, W., Chen, H., Barberán, A., Zhao, H., Yu, M., et al. (2018). Long-term nitrogen fertilization decreases bacterial diversity and favors the growth of *Actinobacteria* and *Proteobacteria* in agroecosystems across the globe. *Glob. Chang. Biol.* 24, 3452–3461. doi: 10.1111/gcb.14163
- Deeks, L., Chaney, K., Murray, C., Sakrabani, R., Gedara, S., Le, M., et al. (2013). A new sludge-derived organo-mineral fertilizer gives similar crop yields as conventional fertilizers. *Agron. Sustain. Dev.* 33, 539–549. doi: 10.1007/s13593-013-0135-z
- Delgado-Baquerizo, M., Oliverio, A. M., Brewer, T. E., Benavent-Gonzalez, A., Eldridge, D. J., Bardgett, R. D., et al. (2018). A global atlas of the dominant bacteria found in soil. *Science* 359, 320–325. doi: 10.1126/science.aap9516
- Delgado-Baquerizo, M., Reich, P. B., Khachane, A. N., Campbell, C. D., Thomas, N., Freitag, T. E., et al. (2016). It is elemental: soil nutrient stoichiometry drives bacterial diversity. *Environ. Microbiol.* 19, 1176–1188. doi: 10.1111/1462-2920.13642
- Deng, Y., Jiang, Y. H., Yang, Y. F., He, Z. L., Luo, F., and Zhou, J. Z. (2012). Molecular ecological network analyses. *BMC Bioinf.* 13:113. doi: 10.1186/1471-2105-13-113
- Dias, M. A. D., Lana, R. M. Q., Mageste, J. G., Marques, O. J., Silva, A. D., Lemes, E. M., et al. (2020). Mineral and organomineral sources of nitrogen to maize agronomic performance. *Biosci. J.* 36, 1528–1534. doi: 10.14393/BJ-v36n5a2020-45632
- Dixon, P. (2003). VEGAN, a package of R functions for community ecology. *J. Veg. Sci.* 14, 927–930. doi: 10.1111/j.1654-1103.2003.tb02228.x
- Du, T. Y., He, H. Y., Zhang, Q., Lu, L., Mao, W. J., and Zhai, M. Z. (2022). Positive effects of organic fertilizers and biofertilizers on soil microbial community composition and walnut yield. *Appl. Soil Ecol.* 175:104457. doi: 10.1016/j.apsoil.2022.104457
- Edgar, R. C. (2013). UPARSE: highly accurate OTU sequences from microbial amplicon reads. *Nat. Methods* 10, 996–998. doi: 10.1038/Nmeth.2604
- Efanov, M. V., Galochkin, A. I., Schott, P. R., Dudkin, D. V., and Klepikov, A. G. (2001). Nitrogen-containing organomineral fertilizer based on wood waste. *Russ. J. Appl. Chem.* 74, 1774–1776. doi: 10.1023/A:1014850528793
- Fan, K., Delgado-Baquerizo, M., Guo, X., Wang, D., Zhu, Y., and Chu, H. (2020). Biodiversity of key-stone phylotypes determines crop production in a 4-decade fertilization experiment. *ISME J.* 15, 550–561. doi: 10.1038/s41396-020-00796-8
- Finkel, O. M., Salas-Gonzalez, I., Castrillo, G., Conway, J. M., Law, T. F., Teixeira, P. J. P. L., et al. (2020). A single bacterial genus maintains root growth in a complex microbiome. *Nature* 587, 103–108. doi: 10.1038/s41586-020-2778-7
- Frazaõ, J. J., Benites, V. M., Ribeiro, J. V. S., Pierobon, V. M., and Lavres, J. (2019). Agronomic effectiveness of a granular poultry litter-derived organomineral phosphate fertilizer in tropical soils: soil phosphorus fractionation and plant responses. *Geoderma* 337, 582–593. doi: 10.1016/j.geoderma.2018.10.003
- Gattinger, A., Muller, A., Haeni, M., Skinner, C., Fliessbach, A., Buchmann, N., et al. (2012). Enhanced top soil carbon stocks under organic farming. *Proc. Natl. Acad. Sci. U. S. A.* 109, 18226–18231. doi: 10.1073/pnas.1209429109
- Gebremeriam, A., Chekol, Y., and Assefa, F. (2021). Phenotypic, molecular, and virulence characterization of entomopathogenic fungi, *Beauveria bassiana* (Balsam) Vuillemin, and *Metarhizium anisopliae* (Metschn.) Sorokin from soil samples of Ethiopia for the development of mycoinsecticide. *Heliyon* 7:e07091. doi: 10.1016/j.heliyon.2021.e07091
- Ghorbanzadeh, N., Mahsefat, M., Farhangi, M. B., Khalili Rad, M., and Proietti, P. (2020). Short-term impacts of pomace application and *Pseudomonas* bacteria on soil available phosphorus. *Biocatal. Agric. Biotechnol.* 28:101742. doi: 10.1016/j.cbab.2020.101742
- Gomiero, T., Pimentel, D., and Paoletti, M. G. (2011). Environmental impact of different agricultural management practices: conventional vs. organic agriculture. *Crit. Rev. Plant Sci.* 30, 95–124. doi: 10.1080/07352689.2011.554355
- Gonçalves, C. A., de Camargo, R., de Sousa, R. T. X., Soares, N. S., de Oliveira, R. C., Stanger, M. C., et al. (2021). Chemical and technological attributes of sugarcane as functions of organomineral fertilizer based on filter cake or sewage sludge as organic matter sources. *PLoS One* 16:e0236852. doi: 10.1371/journal.pone.0236852
- Gong, Z. T. (1999). Soil system classification in China-theory, method and practice *Beijing: Science press.*
- González, A. M. M., Dalsgaard, B., and Olesen, J. M. (2010). Centrality measures and the importance of generalist species in pollination networks. *Ecol. Complex.* 7, 36–43. doi: 10.1016/j.ecocom.2009.03.008
- González-Pérez, E., Ortega-Amaro, M. A., Bautista, E., Delgado-Sanchez, P., and Jimenez-Bremont, J. F. (2022). The entomopathogenic fungus *Metarhizium anisopliae* enhances *Arabidopsis*, tomato, and maize plant growth. *Plant Physiol. Biochem.* 176, 34–43. doi: 10.1016/j.plaphy.2022.02.008
- Grohskopf, M. A., Corrêa, J. C., Fernandes, D. M., Teixeira, P. C., and Mota, S. C. A. (2019). Mobility of nitrogen in the soil due to the use of organomineral fertilizers with different concentrations of phosphorus. *Commun. Soil Sci. Plant Anal.* 51, 208–220. doi: 10.1080/00103624.2019.1705321
- Gu, S., Hu, Q., Cheng, Y., Bai, L., Liu, Z., Xiao, W., et al. (2019). Application of organic fertilizer improves microbial community diversity and alters microbial network structure in tea (*Camellia sinensis*) plantation soils. *Soil Tillage Res.* 195:104356. doi: 10.1016/j.still.2019.104356
- Gui, H., Fan, L., Wang, D., Yan, P., Li, X., Zhang, L., et al. (2021). Organic management practices shape the structure and associations of soil bacterial communities in tea plantations. *Appl. Soil Ecol.* 163:103975. doi: 10.1016/j.apsoil.2021.103975
- Hawrot-Paw, M., Mikiciuk, M., Koniuszy, A., and Meller, E. (2022). Influence of organomineral fertiliser from sewage sludge on soil microbiome and physiological parameters of maize (*Zea mays* L.). *Agronomy* 12:1114. doi: 10.3390/agronomy12051114
- Hu, Y., Sun, L. W., Mokgolodi, N. C., Zhang, Y. X., Wen, C. X., Xie, X. L., et al. (2010). Primary identifications and palynological observations of *Perilla* in China. *J. Syst. Evol.* 48, 133–145. doi: 10.1111/j.1759-6831.2010.00067.x
- Javier, S., Canales, F., Tweed, J., and Lee, M. (2018). Fatty acid profile changes during gradual soil water depletion in oats suggests a role for jasmonates in coping with drought. *Front. Plant Sci.* 9:1007. doi: 10.3389/fpls.2018.0107
- Jiao, S., Lu, Y., and Wei, G. (2021). Soil multitrophic network complexity enhances the link between biodiversity and multifunctionality in agricultural systems. *Glob. Chang. Biol.* 28, 140–153. doi: 10.1111/gcb.15917
- Kang, Y., Ma, Y., Wu, W., Zeng, S., Jiang, S., Yang, H., et al. (2022). Bioorganic and silicon amendments alleviate early defoliation of pear trees by improving the soil nutrient bioavailability, microbial activity, and reshaping the soil microbiome network. *Appl. Soil Ecol.* 173:104383. doi: 10.1016/j.apsoil.2021.104383
- Kembel, S. W., Cowan, P. D., Helmus, M. R., Cornwell, W. K., Morlon, H., Ackerly, D. D., et al. (2010). Picante: R tools for integrating phylogenies and ecology. *Bioinformatics* 26, 1463–1464. doi: 10.1093/bioinformatics/btq166
- Kiehl, E. J. (2008). *Fertilizantes organominerais. 4. ed.* Piracicaba, SP: Degaspari, 160 p.
- Ko, O., Jn, O., and Hc, O. (2018). Pharmacological potentials, characterization and fatty acids profile of *Persea americana* mill. (*Avocado*) seed oil using gas

- chromatography-mass spectroscopy. *Biochem. Anal. Biochem.* 7, 1–3. doi: 10.4172/2161-1009.100036
- Ko, W. H., Tsou, Y. J., Ju, Y. M., Hsieh, H. M., and Ann, P. J. (2010). Production of a fungistatic substance by *Pseudallescheria boydii* isolated from soil amended with vegetable tissues and its significance. *Mycopathologia* 169, 125–131. doi: 10.1007/s11046-009-9237-1
- Kour, D., Rana, K. L., Yadav, A. N., Yadav, N., Kumar, M., Kumar, V., et al. (2020). Microbial biofertilizers: bioresources and ecofriendly technologies for agricultural and environmental sustainability. *Biocatal. Agric. Biotechnol.* 23:101487. doi: 10.1016/j.bcab.2019.101487
- Kourimska, L., Sabolova, M., Horcicka, P., Rys, S., and Bozik, M. (2018). Lipid content, fatty acid profile, and nutritional value of new oat cultivars. *J. Cereal Sci.* 84, 44–48. doi: 10.1016/j.jcs.2018.09.012
- Kox, M., Elzen, E., Lamers, L. P. M., Jetten, M. S. M., and Kessel, M. (2020). Microbial nitrogen fixation and methane oxidation are strongly enhanced by light in *Sphagnum* mosses. *AMB Expr.* 10:61. doi: 10.1186/s13568-020-00994-9
- Lauber, C. L., Hamady, M., Knight, R., and Fierer, N. (2009). Pyrosequencing-based assessment of soil pH as a predictor of soil bacterial community structure at the continental scale. *Appl. Environ. Microbiol.* 75, 5111–5120. doi: 10.1128/AEM.00335-09
- Lee, J. K., and Kim, N. S. (2007). Genetic diversity and relationships of cultivated and weedy types of *Perilla frutescens* collected from East Asia revealed by SSR markers. *Korean J. Breed. Sci.* 39:491–499.
- Li, Y., Liu, X. M., Yin, Z. Y., Chen, H., Cai, X. L., Xie, Y. H., et al. (2021). Changes in soil microbial communities from exposed rocks to arboreal rhizosphere during vegetation succession in a karst mountainous ecosystem. *J. Plant Interact.* 16, 550–563. doi: 10.1080/17429145.2021.2002955
- Li, Y., Liu, X. M., Zhang, L., Xie, Y. H., Cai, X. L., Wang, S. J., et al. (2020). Effects of short-term application of chemical and organic fertilizers on bacterial diversity of cornfield soil in a karst area. *J. Soil Sci. Plant Nut.* 20, 2048–2058. doi: 10.1007/s42729-020-00274-2
- Li, Q., Zhang, D., Song, Z., Ren, L., Jin, X., Fang, W., et al. (2022). Organic fertilizer activates soil beneficial microorganisms to promote strawberry growth and soil health after fumigation. *Environ. Pollut.* 295:118653. doi: 10.1016/j.envpol.2021.118653
- Lian, B., Xiao, B., Xiao, L. L., Wang, W. J., and Sun, Q. B. (2020). Molecular mechanism and carbon sink effects of microbial transformation in potassium-bearing rocks. *Earth Sci. Front.* 27, 238–246. doi: 10.13745/j.es.fsf.2020.5.38
- Ling, N., Zhu, C., Xue, C., Chen, H., Duan, Y., Peng, C., et al. (2016). Insight into how organic amendments can shape the soil microbiome in long-term field experiments as revealed by network analysis. *Soil Biol. Biochem.* 99, 137–149. doi: 10.1016/j.soilbio.2016.05.005
- Liu, X., Bolla, K., Ashforth, E. J., Zhou, Y., Gao, H., and Huang, P. (2012). Systematics-guided bioprospecting for bioactive microbial natural products. *Antonie Van Leeuwenhoek* 101, 55–66. doi: 10.1007/s10482-011-9671-1
- Liu, L., Chen, H., Liu, M., Yang, J. R., Xiao, P., Wilkinson, D. M., et al. (2019). Response of the eukaryotic plankton community to the cyanobacterial biomass cycle over 6 years in two subtropical reservoirs. *ISME J.* 13, 2196–2208. doi: 10.1038/s41396-019-0417-9
- Liu, Z., Guo, Q., Feng, Z. Y., Liu, Z. D., Li, H. Y., Sun, Y. F., et al. (2020). Long-term organic fertilization improves the productivity of kiwifruit (*Actinidia chinensis* Planch.) through increasing rhizosphere microbial diversity and network complexity. *Appl. Soil Ecol.* 147:103426. doi: 10.1016/j.apsoil.2019.103426
- Liu, H., Pan, F., Han, X., Song, F., Zhang, Z., Yan, J., et al. (2019). Response of soil fungal community structure to long-term continuous soybean cropping. *Front. Microbiol.* 9:3316. doi: 10.3389/fmicb.2018.03316
- Liu, J., Shu, A., Song, W., Shi, W., and Gao, Z. (2021). Long-term organic fertilizer substitution increases rice yield by improving soil properties and regulating soil bacteria. *Geoderma* 404:115287. doi: 10.1016/j.geoderma.2021.115287
- Liu, J., Sui, Y., Yu, Z., Shi, Y., Chu, H., Jin, J., et al. (2014). High throughput sequencing analysis of biogeographical distribution of bacterial communities in the black soils of Northeast China. *Soil Biol. Biochem.* 70, 113–122. doi: 10.1016/j.soilbio.2013.12.014
- Louca, S., Parfrey, L. W., and Doebeli, M. (2016). Decoupling function and taxonomy in the global ocean microbiome. *Science* 353, 1272–1277. doi: 10.1126/science.aaf4507
- Lozupone, C., and Knight, R. (2005). UniFrac: a new phylogenetic method for comparing microbial communities. *Appl. Environ. Microbiol.* 71, 8228–8235. doi: 10.1128/AEM.71.12.8228-8235.2005
- Lu, R. K. (1999). *Methods of agrochemical soil analysis vol China Agricultural Science Press, Beijing.*
- Luitel, B. P., Ko, H. C., Hur, O. S., Rhee, J. H., Baek, H. J., Ryu, K. Y., et al. (2017). Variation for morphological characters in cultivated and weedy types of *Perilla frutescens* Britt. germplasm. *Korean J. Plant Resour.* 30, 298–310. doi: 10.7732/kjpr.2017.30.3.298
- Ma, B., Wang, H. Z., Dsouza, M., Lou, J., He, Y., Dai, Z. M., et al. (2016). Geographic patterns of co-occurrence network topological features for soil microbiota at continental scale in eastern China. *ISME J.* 10, 1891–1901. doi: 10.1038/ismej.2015.261
- Ma, A., Zhuang, X., Wu, J., Cui, M., Lv, D., Liu, C., et al. (2013). *Ascomycota* members dominate fungal communities during straw residue decomposition in arable soil. *PLoS One* 8:e66146. doi: 10.1371/journal.pone.0066146
- Magoc, T., and Salzberg, S. L. (2011). FLASH: fast length adjustment of short reads to improve genome assemblies. *Bioinformatics* 27, 2957–2963. doi: 10.1093/bioinformatics/btr507
- Marcos, M. S., Bertiller, M. B., and Olivera, N. L. (2019). Microbial community composition and network analyses in arid soils of the Patagonian Monte under grazing disturbance reveal an important response of the community to soil particle size. *Appl. Soil Ecol.* 138, 223–232. doi: 10.1016/j.apsoil.2019.03.001
- Megali, L., Glauser, G., and Rasmann, S. (2013). Fertilization with beneficial microorganisms decreases tomato defenses against insect pests. *Agron. Sustain. Dev.* 34, 649–656. doi: 10.1007/s13593-013-0187-0
- Mendes, L. W., de Lima Brossi, M. J., Kuramae, E. E., and Tsai, S. M. (2015). Land-use system shapes soil bacterial communities in southeastern Amazon region. *Appl. Soil Ecol.* 95, 151–160. doi: 10.1016/j.apsoil.2015.06.005
- Moyno, A. L., Cleveland, T. E., and Tuzun, S. (2004). Molecular characterization and analysis of the operon encoding the antifungal lipopeptide bacillomycin D. *FEMS Microb. Lett.* 234, 43–49. doi: 10.1016/j.femsle.2004.03.011
- Mumbach, G. L., Gatiboni, L. C., Bona, F. D., Schmitt, D. E., Corrêa, J. C., Gabriel, C. A., et al. (2020). Agronomic efficiency of organomineral fertilizer in sequential grain crops in southern Brazil. *Agron. J.* 112, 3037–3049. doi: 10.1002/agj2.20238
- Ngo, H. T. T., Watts-Williams, S. J., Panagaris, A., Baird, R., McLaughlin, M. J., and Cavnar, T. R. (2022). Development of an organomineral fertiliser formulation that improves tomato growth and sustains arbuscular mycorrhizal colonisation. *Sci. Total Environ.* 815:151977. doi: 10.1016/j.scitotenv.2021.151977
- Nguyen, N. H., Song, Z. W., Bates, S. T., Branco, S., Tedersoo, L., Menke, J., et al. (2016). FUNGuild: an open annotation tool for parsing fungal community datasets by ecological guild. *Fungal Ecol.* 20, 241–248. doi: 10.1016/j.funeco.2015.06.006
- Qi, D., Wieneke, X., Tao, J., Zhou, X., and Desilva, U. (2018). Soil pH is the primary factor correlating with soil microbiome in karst rocky desertification regions in the Wushan County, Chongqing, China. *Front. Microbiol.* 9:1027. doi: 10.3389/fmicb.2018.01027
- Ren, H., Qin, X., Huang, B., Fernández-García, V., and Lv, C. (2020). Responses of soil enzyme activities and plant growth in a eucalyptus seedling plantation amended with bacterial fertilizers. *Arch. Microbiol.* 202, 1381–1396. doi: 10.1007/s00203-020-01849-4
- Ren, C. J., Zhao, F. Z., Kang, D., Yang, G. H., Han, X. H., Tong, X. G., et al. (2016). Linkages of C:N:P stoichiometry and bacterial community in soil following afforestation of former farmland. *Forest Ecol. Manag.* 376, 59–66. doi: 10.1016/j.foreco.2016.06.004
- Richardson, M. (2009). The ecology of the *zygomycetes* and its impact on environmental exposure. *Clin. Microbiol. Infect.* 15, 2–9. doi: 10.1111/j.1469-0691.2009.02972.x
- Riguetti Zanardo Botelho, A. B., Alves-Pereira, A., Colonhez Prado, R., Zucchi, M. I., and Delalibera Júnior, I. (2019). *Metarhizium* species in soil from Brazilian biomes: a study of diversity, distribution, and association with natural and agricultural environments. *Fungal Ecol.* 41, 289–300. doi: 10.1016/j.funeco.2019.07.004
- Rime, T., Hartmann, M., Brunner, I., Widmer, F., Zeyer, J., and Frey, B. (2015). Vertical distribution of the soil microbiota along a successional gradient in a glacier forefield. *Mol. Ecol.* 24, 1091–1108. doi: 10.1111/mec.13051
- Sakurada, L. R., Batista, M. A., Inoue, T. T., Muniz, A. S., and Pagliari, P. H. (2016). Organomineral phosphate fertilizers: agronomic efficiency and residual effect on initial corn development. *Agron. J.* 108, 2050–2059. doi: 10.2134/agronj2015.0543
- Samaddar, S., Truu, J., Chatterjee, P., Truu, M., Kim, K., Kim, S., et al. (2019). Long-term silicate fertilization increases the abundance of actinobacterial population in paddy soils. *Biol. Fertil. Soils* 55, 109–120. doi: 10.1007/s00374-018-01335-6
- Santolini, M., and Barabási, A. L. (2018). Predicting perturbation patterns from the topology of biological networks. *Proc. Natl. Acad. Sci. U. S. A.* 115, E6375–E6383. doi: 10.1073/pnas.1720589115
- Segata, N., Izard, J., Waldron, L., Gevers, D., Miropolsky, L., Garrett, W. S., et al. (2011). Metagenomic biomarker discovery and explanation. *Genome Biol.* 12:R60. doi: 10.1186/gb-2011-12-6-r60
- Seufert, V., Ramankutty, N., and Foley, J. A. (2012). Comparing the yields of organic and conventional agriculture. *Nature* 485, 229–232. doi: 10.1038/nature11069

- Singh, B. K., Nunan, N., Ridgway, K. P., McNicol, J., Young, J. P. W., Daniell, T. J., et al. (2008). Relationship between assemblages of mycorrhizal fungi and bacteria on grass roots. *Environ. Microbiol.* 10, 534–541. doi: 10.1111/j.1462-2920.2007.01474.x
- Smith, S. E., and Read, D. J. (2008). “The symbionts forming arbuscular mycorrhizas,” in *Mycorrhizal Symbiosis*. eds. S. E. Smith and D. J. Read (San Diego: Academic Press), 13–41.
- Steffen, W., Richardson, K., Rockstrom, J., Cornell, S. E., Fetzer, I., Bennett, E. M., et al. (2015). Planetary boundaries: guiding human development on a changing planet. *Science* 347:1259855. doi: 10.1126/science.1259855
- Sun, R., Dsouza, M., Gilbert, J. A., Guo, X., Wang, D., Guo, Z., et al. (2016). Fungal community composition in crop phyllosphere and root endosphere are more resistant to long-term chemical fertilization is most influenced by the type of organic matter. *Environ. Microbiol.* 18, 5137–5150. doi: 10.1111/1462-2920.13512
- Sun, A., Jiao, X. Y., Chen, Q., Wu, A. L., Zheng, Y., Lin, Y. X., et al. (2021). Microbial communities in crop phyllosphere and root endosphere are more resistant than soil microbiota to fertilization. *Soil Biol. Biochem.* 153:108113. doi: 10.1016/j.soilbio.2020.108113
- Sun, Q. B., Ruan, Y. L., Chen, P., Wang, S. J., Liu, X. M., and Lian, B. (2019). Effects of mineral-organic fertilizer on the biomass of green Chinese cabbage and potential carbon sequestration ability in karst areas of Southwest China. *Acta Geochim.* 38, 430–439. doi: 10.1007/s11631-019-00320-6
- Syed, S., Wang, X., Prasad, T. N. V. K. V., and Lian, B. (2021). Bio-organic-mineral fertilizer for sustainable agriculture: current trends and future perspectives. *Fortschr. Mineral.* 11:1336. doi: 10.3390/min11121336
- Theodoro, S. H., and Leonardos, O. H. (2006). The use of rocks to improve family agriculture in Brazil. *An. Acad. Bras. Cienc.* 78, 721–730. doi: 10.1590/S0001-37652006000400008
- Tian, S. G., Guo, P., Shen, Q., Wang, X. P., Yang, S., Shang, Z. W., et al. (2017). Main traits and quality of seven *Perilla frutescens* varieties (lines) in Guizhou. *Guizhou Agric. Sci.* 45, 107–109.
- Tian, J., Zeng, X., Zhang, S., Wang, Y., Zhang, P., Lü, A., et al. (2014). Regional variation in components and antioxidant and antifungal activities of *Perilla frutescens* essential oils in China. *Ind. Crop. Prod.* 59, 69–79. doi: 10.1016/j.indcrop.2014.04.048
- USS Working Group WRB. (2015). *World reference base for soil resources 2014, update 2015 international soil classification system for naming soils and creating legends for soil maps*. World Soil Resources Reports No. 106. FAO, Rome.
- Vick-Majors, T. J., Priscu, J. C., and Amaral-Zettler, L. A. (2014). Modular community structure suggests metabolic plasticity during the transition to polar night in ice-covered Antarctic lakes. *ISME J.* 8, 778–789. doi: 10.1038/ismej.2013.190
- Vollú, R. E., Cotta, S. R., Jurelevicius, D., Leite, D. C. A., Parente, C. E. T., Malm, O., et al. (2018). Response of the bacterial communities associated with maize rhizosphere to poultry litter as an organomineral fertilizer. *Front. Environ. Sci.* 6:118. doi: 10.3389/fenvs.2018.00118
- Wang, Y., Chen, G. W., Sun, Y. F., Zhu, K., Jin, Y., Li, B. G., et al. (2020). Different agricultural practices specify bacterial community compositions in the soil rhizosphere and root zone. *Soil Ecol. Lett.* 4, 18–31. doi: 10.1007/s42832-020-0058-y
- Wang, L., Li, J., Yang, F., E, Y., Raza, W., Huang, Q., et al. (2017). Application of bioorganic fertilizer significantly increased apple yields and shaped bacterial community structure in orchard soil. *Microb. Ecol.* 73, 404–416. doi: 10.1007/s00248-016-0849-y
- Wang, C. J., Song, C. Y., Zhang, X. D., Xie, Y. Q., Liu, X. Z., and Wang, M. Z. (1997). Sustainable control efficacy of *Paecilomyces lilacinus* against *Heterodera glycines*. *Chin. J. Biol. Contr.* 13:26.
- Weller, D., Raaijmakers, J., Gardener, B., and Thomashow, L. (2002). Microbial populations responsible for specific soil suppressiveness to plant pathogens. *Annu. Rev. Phytopathol.* 40, 309–348. doi: 10.1146/annurev.phyto.40.030402.110010
- Wu, S., Zhou, Z., Zhu, L., Zhong, L., Dong, Y., Wang, G., et al. (2022). Cd immobilization mechanisms in a *Pseudomonas* strain and its application in soil Cd remediation. *J. Hazard. Mater.* 425:127919. doi: 10.1016/j.jhazmat.2021.127919
- Xu, N., Tan, G. C., Wang, H. Y., and Gai, X. P. (2016). Effect of biochar additions to soil on nitrogen leaching, microbial biomass and bacterial community structure. *Eur. J. Soil Biol.* 74, 1–8. doi: 10.1016/j.ejsobi.2016.02.004
- Yaldiz, G., and Camlica, M. (2020). Yield components and some quality properties of fenugreek cultivar and lines. *Banat's. J. Biotechnol.* XI, 40–47. doi: 10.7904/2068-4738-XI(22)-40
- Yang, H. W., Li, J., Xiao, Y. H., Gu, Y. B., Liu, H. W., and Liang, Y. L. (2017). An integrated insight into the relationship between soil microbial community and tobacco bacterial wilt disease. *Front. Microbiol.* 8:2179. doi: 10.3389/fmicb.2017.02179
- Yang, Y. R., Syed, S., Mao, S. X., Li, Q., Ge, F., Lian, B., et al. (2020). Bioorganic-mineral fertilizer can remediate chemical fertilizer-oversupplied soil: Purslane planting as an example. *J. Soil Sci. Plant Nutr.* 20, 892–900. doi: 10.1007/s42729-020-00175-4
- Yu, H., Qiu, J. F., Ma, L. J., Hu, Y. J., Li, P., and Wan, J. B. (2017). Phytochemical and phytopharmacological review of *Perilla frutescens* L. (Labiatae), a traditional edible-medicinal herb in China. *Food Chem. Toxicol.* 108, 375–391. doi: 10.1016/j.fct.2016.11.023
- Yuan, M. M., Guo, X., Wu, L., Zhang, Y., Xiao, N., Ning, D., et al. (2021). Climate warming enhances microbial network complexity and stability. *Nat. Clim. Chang.* 11, 343–348. doi: 10.1038/s41558-021-00989-9
- Zhao, J., Ni, T., Li, J., Lu, Q., Fang, Z., Huang, Q., et al. (2016). Effects of organic-inorganic compound fertilizer with reduced chemical fertilizer application on crop yields, soil biological activity and bacterial community structure in a rice-wheat cropping system. *Appl. Soil Ecol.* 99, 1–12. doi: 10.1016/j.apsoil.2015.11.006
- Zhou, J., Guan, D., Zhou, B., Zhao, B., Ma, M., Qin, J., et al. (2015). Influence of 34-years of fertilization on bacterial communities in an intensively cultivated black soil in Northeast China. *Soil Biol. Biochem.* 90, 42–51. doi: 10.1016/j.soilbio.2015.07.005
- Zhou, J., Jiang, X., Zhou, B. K., Zhao, B. S., Ma, M. C., Guan, D. W., et al. (2016). Thirty-four years of nitrogen fertilization decreases fungal diversity and alters fungal community composition in black soil in Northeast China. *Soil Biol. Biochem.* 95, 135–143. doi: 10.1016/j.soilbio.2015.12.012
- Zhu, J., Ren, Z., Huang, B., Cao, A., Wang, Q., Yan, D., et al. (2020). Effects of fumigation with allyl isothiocyanate on soil microbial diversity and community structure of tomato. *J. Agric. Food Chem.* 68, 1226–1236. doi: 10.1021/acs.jafc.9b07292
- Zhu, W., Zhu, M., Liu, X., Xia, J., Yin, H., and Li, X. (2022). Different responses of bacteria and microeukaryote to assembly processes and co-occurrence pattern in the coastal upwelling. *Microb. Ecol.* doi: 10.1007/s00248-022-02093-7. Epub ahead of print.