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Original article

Microbial diversity and abundance in different acidified soils from mature pomelo planting orchard

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Summary

Soil acidification poses significant threats to the ecological environment and agricultural productivity in southern China. However, the variations in soil microbial communities along the acidic gradient profile remain poorly understood. In this study, we investigated soil microorganisms across normal, acidic, and strongly acidic soil samples using high-throughput sequencing technology. We described their distribution characteristics under different acidification backgrounds and depicted their responses to ambient environment factors. Our findings indicated that the Actinobacteriota (41.84%), Proteobacteria (27.91%), Chlorofexi (13.86%), Ascomycota (75.69%) and Basidiomycota (19.00%) comprised the core microbial populations among the samples. Meanwhile, Xanthobacteraceae (3.13%), Acidothermus (2.16%), Sordariomycetes (10.05%) and Thysanophora (8.71%) were more abundant in acidified soils, suggesting a higher probability of soil-borne diseases. Furthermore, soil acidification exerted more negative effects on the bacterial community, as revealed by PICRUSt predictions showing significant decreases in the pathways of carbohydrate, lipid and protein metabolism. In contrast, the fungal community demonstrated relatively stronger resistance to acid stress, as evidenced by the increased abundance of pathways related to signal transition and cell proliferation. Overall, our study sheds light on the responses of soil microbial communities to acidification stress and underscores the differential impacts on bacterial and fungal populations.

Keywords
bacteria, composition, fungi, pomelo, PICRUSt, soil acidification

Significance of this study

What is already known on this subject?

- Soil acidification has increasingly worsened in the red soil areas of China. In recent years, the causes and current status of soil acidification in agricultural soils have been preliminarily understood, and relevant control policies have been proposed. However, progress in understanding the soil micro-ecosystem in the context of acidification remains limited. Notably, soils from orchards in southern China are significantly acidified, yet research progress in this area is insufficient.

What are the new findings?

- This study summarized the differences and characteristics of microbial diversity and composition across varying levels of soil acidification and their different responses to soil acidity within bacterial and fungal communities, while also identifying the negative impacts on soil property and microorganism brought by soil acidification.

What is the expected impact on horticulture?

- Our study could be of interest for all researchers dealing with soil remediation and contamination. The core populations identified in our study may serve as potential components for bacterial manure in future agricultural practices.

Introduction

Soil acidification is an important manifestation of soil degradation, affecting over 40% of global land area. In China, acidified soils are predominantly found in the southern regions of the Yangtze River, where they constitute approximately 22.7% of the national soil area (Li et al., 2020). Notably, orchard planting areas in the southern areas of China are the most severely affected, with up to 80% of orchards classified as slightly acidic, necessitating remediation. Soil acidification critically affects the normal growth of fruits, thereby jeopardizing both food safety and the sustainable development of the fruit industry (Cai et al., 2011; Zhang et al., 2022). Relevant studies have showed that the optimal soil pH for pomelo growth is around 6.0, and lower pH levels are recognized as vital limiting factors for pomelo production, particularly in mature orchards (>10 years). Soil acidification disrupts nutrient cycling and enhances the leaching of essential elements such as potassium, calcium, and magnesium, while also diminishing phosphorus availability (Guo et al., 2022). This situation leads to nutritional deficiencies in pomelo trees. Furthermore, acidic soils can compromise soil structure and root activity, resulting in physiological disorders such as bitter pit, watercore, and fruit cracking during pomelo cultivation (Dong et al., 2022; Muneer et al., 2022). It is estimated that pomelo production faces a yield deficit of approximately 20%, which is not sustainable; however, po-

tential yields could double if acidified conditions are ameliorated (Yan et al., 2024).

Soil microorganisms – including bacteria, fungi, actinomycetes, and algae – are crucial for soil fertility, nutrient cycling, and overall plant health. Extensive research has highlighted geographical variations in the contributions of these microorganisms to nutrient cycling. Moreover, ecological niche differentiation among fungi and bacteria has been associated with soil pH levels. Interestingly, environmental variations tend to exert a more significant influence on microbial distribution than geographical distance. (Tedersoo et al., 2014; Du et al., 2023). The distribution of soil microorganisms is closely related to environmental factors. Most studies have shown that soil pH is correlated with soil organic matter (SOM), as well as the diversity and community composition of bacteria and fungi (Van Rijssel et al., 2022). Optimal microbial activity typically occurs at a soil pH of approximately 5.5, where core microbial populations consist mainly of Actinobacteria and Proteobacteria for bacteria, and Ascomycota for fungi (Debeljak and Baltar, 2023). These co-occurrence patterns can be influenced by soil pH (Shi et al., 2021). Soil characteristics subsequently affect the composition and activity of microbial communities, potentially impacting their evolutionary trajectories (Kumar et al., 2019). Sui et al. (2021) demonstrated that moisture content, total nitrogen, and available nitrogen concentrations significantly influence the community structures of soil bacteria and fungi in freshwater wetlands. Lin et al. (2021) revealed close correlations between microbial community differentiation and carbon and nitrogen contents. Shifts in microbial diversity and composition can directly influence soil fertility and plant pathogens, eliciting varied responses from microbial communities (Song et al., 2022).

Pinghe County, known as the "Pomelo Town of the World", is the major producing area of pomelo of China with a long history. With a total planting area of 46,667 ha, over 80% of these orchards are situated on mountainous terrain. Concurrently, local fertilizer application rates have been increasing annually. Soil acidification, driven by inappropriate and excessive fertilizer use, poses significant challenges for these mature pomelo orchards (Ding et al., 2024). As statistics indicated, the average pH of Guanxi pomelo soils is only 4.5, with many soils lacking adequate exchangeable magnesium, calcium, and phosphorus (Zhan et al., 2021). Furthermore, microbial diversity has been observed to decline with prolonged cultivation periods (Zheng et al., 2022). In this study, we hypothesize that soil acidification elicits differential responses from microbial communities, with distinct shifts observed between bacterial and fungal communities. To investigate this hypothesis soil chemical properties, bacterial diversity and fungal diversity from the Guanxi pomelo planting soils were studied and compared under varying acidity conditions to understand the divergence between bacterial and fungal communities in response to soil acidification. Additionally, correlation analyses were conducted between dominant microbial groups and soil properties to assess the impact of soil environment on microbial composition. Furthermore, functional predictions were conducted for both of the bacterial and fungal communities. Functional predictions for both bacterial and fungal communities were performed. Through this research, we aim to provide a comprehensive overview of soil microecology across the pH gradient in the acidified soils of Guanxi's pomelo orchards.

Material and methods

Site depiction and soil sampling

Soil samples were collected from the Xiaoxi Town, Pinghe County, Fujian province, Southeast China (24°30'N~24°35'N, 117°21'E~116°40'E). The general characteristics of climate is mild climate (average 24.9°C) and abundant rainfall (1,821.1 mm year^{-1}). Totally, the pomelo trees in collecting areas have been planted for 20 years, and the total cultivation area is nearly 4 km^2. The sampling selection of acidified soils was initially referenced from the research reports of Li et al. (2020) and Huang et al. (2015). An on-site investigation utilizing both a pH meter and the GB code method (NY/T 1121.2-2006) was conducted from 2021 to 2022 as part of the "Pinghe County Soil Acidification" project, sponsored by the Science and Technology Bureau of Zhangzhou. The acidity of soils could be influence by various factors such as fertilizing strategy, irrigating method and field management. Notably, several soil improvement measures, including remediated with oyster shell powders or quicklime, have been conducted in severely acidified Guanxi pomelo soils since 2019 (Li et al., 2020; Chen et al., 2023). Consequently, soils with differing acidity levels were observed during the field examinations. The soil sampling method was adapted from Keiblinger et al. (2018) and was executed as follows: Based on the distribution of soil pH, three 25 × 25 m sampling plots were established, each representing distinct acidity levels. Within each plot, five topsoil (5–10 cm) samples were taken from each of the plot through soil diagonal sampling method and then mixed together. All samples were sealed in sterilized centrifuge tubes, then placed in an ice box and brought back to the laboratory. Part of the fresh soil samples were used for measuring the diversity of soil microbial communities. The remaining part is air-dried and finely ground through a 0.25 mm sieve for the determination of soil physico-chemical properties. Three biological replicates were conducted in each detection.

Determination of soil physicochemical properties

The soil pH was measured by Mettler Toledo pH meter; the organic matter content of soil was calculated via potassium dichromate oxidation colorimetry (Bao et al., 2011); the total nitrogen content of soil was determined by Kjeldahl method (Lynch et al., 1999); the available phosphorus (AP) content was detected by molybdenum antimony spectrophotometric method; the available potassium (AK) content were detected by flame photometry. The enzymatic activities of soil dehydrogenase (sDHA), soil acid phosphatase (sACP), soil urease (sUR) and soil sucrase (sSC) were assayed through Enzyme Activity kits provided by Suzhou Keming Co., Ltd., China.

DNA extraction and high-through sequencing analysis

The total DNA of soil were extracted by the FastDNA®SPIN Kit (MP. Bio., U.S.A.). Then, the extracted genomic DNA was detected by 1% agarose gel electrophoresis. According to the bacterial 16S rRNA and the fungal 18S rRNA genes, the primers 338F (5'-ACTCCTACGGGGGGCAG-3') and 806R (5'-GACTACHVGGGTWTCTAAT-3') (Bahram et al., 2018) and the SSU0817F (5'-TTAGCATGGAAATATATRRAATAGGGA-3') and 1196R (5'-TCTGGACCTGGTGAGTTTCC-3') (Song et al., 2008) respectively, were synthesized with barcodes, and then performed PCR reaction according to the TransGen AP221-02 Kit (China). Use the TruSeq™ DNA Sample Prep Kit to build a library: (1) Add the barcodes to the outer end of the

primer sequences; (2) Recycled PCR products; (3) Washed off by Tris-HCl and detected through agarose gel electrophoresis; (4) Denatured by NaOH and accumulated single stranded DNA fragments. The Illumina's Miseq PE300 platform was used for sequencing (Shanghai Meiji Biomedical Technology Co., Ltd.). The raw data could be obtained with the accession number of PRJNA1025347 from the NCBI Sequence Read Archive (SRA) database.

Bioinformatics analysis

The PE reads obtained through high-sequencing were quality-controlled by the fastp (v. 0.19.6) software and then spliced based on the overlap relationship between reads via the FLASH (v. 1.2.7) software. Noise reduction method for sequences were performed via DADA2 software, thus producing the representative OTUs and their abundances. Utilizing the Silva 132 database to annotate the bacterial sequences and utilizing the UNITE database to annotate the fungal sequences at 97% similarity. The α diversity index of microbial diversity, including Ace, Chao, Simpson and Shannon, were estimated by the Mothur (v. 1.30) software. The PICRUSt2 (Phylogenetic Investigation of Communities by Reconstruction of Unobserved States) software was used to predict the functional abundances of microbial community. The T-test method was used to check the significances between groups.

Statistical analysis

The IBM SPSS Statistics (v. 26) was used to perform significant difference test and correlation analysis. The Duncan's ($\alpha = 0.05$) test were adopted to contrast the soil physic-chemical properties and microbial level and diversity. R packages "ggcorrplot" and "ggthemes" were used to make heat maps. The on-line tool ClustVis was used to create cluster analysis.

Results

Soil physicochemical properties

The soil physicochemical properties at varying acidity levels are summarized in Table 1. The soils we collected have significant difference in pH among normal, acid and strongly acidic soils. Notably, the contents of AK (64.94 mg kg^{-1}) and SOM (14.40 g kg^{-1}) were significantly lower in strongly acidic soils ($P<0.05$), while no significant differences were observed between normal and acidic soils. The concentration of AP decreased with declining pH ($P<0.05$), with the average AP content in the normal soils being 2.6 times higher than that in strongly acidic soils, indicating that acidic conditions hinder the storage of available phosphorus. The TN content exhibited stability across the different soil types. The activities of four key enzymes involved in the degradation of soil organic matter – sDHA, sACP, sUR, and sSC – were measured, with results presented in Table 1. The sUR activity was highest (239.21 μg d^{-1} g^{-1}) in acid soils and lowest (65.72 μg d^{-1} g^{-1}) in strongly acidic soils ($P<0.05$). Furthermore, the sSC activity was significantly decreased with decreasing pH, indicating fewer soluble organic substances in acidic soils. The activities of sDHA and sACP remained stable across different soil types.

Soil microbial community diversity

A total of 361,023 valid microbial sequences were obtained after quality control from the raw reads. After removing single sequences, the remaining unique sequences were clustered based on 97% similarity, yielding 2,217 bacterial and 173 fungal operational taxonomic units (OTUs). By ran-

Table 1. Comparative analysis of soil physic-chemical properties of normal, acidic and strongly acidic soils.

Sample	pH	TN (g kg^{-1})	AK (mg kg^{-1})	AP (mg kg^{-1})	SOM (g kg^{-1})	sDHA (μg d^{-1} g^{-1})	sACP (μmol d^{-1} g^{-1})	sUR (μg d^{-1} g^{-1})	sSC (mg d^{-1} g^{-1})
Normal	6.50±0.01c	1.04±0.01a	94.05±3.32b	930.70±28.28c	17.35±1.20b	23.55±1.01a	23.07±2.87a	99.37±8.34a	9.70±1.04c
Acidic	5.61±0.00b	1.03±0.01a	86.09±0.88b	742.37±39.64b	18.30±0.28b	26.95±5.22a	24.45±3.21a	239.21±37.08b	7.09±0.38b
Strongly acidic	4.69±0.01a	1.05±0.02a	64.94±1.69a	357.59±15.57a	14.40±1.16a	25.69±2.68a	25.61±1.74a	65.72±16.69a	5.77±0.48a

Different letters indicate a significant difference at $P<0.05$ according to Duncan's new multiple range test.
TN: total nitrogen; AK: available potassium; AP: available phosphors; SOM: soil organic matter; sDHA: soil dehydrogenase; sACP: soil acid phosphatase; sUR: soil urease; sSC: soil sucrase.

dom sampling, the selected OTUs and their features were conducted to construct the Rank-abundance curves and Pan/Core curves, confirming that our sampling efforts were sufficient and the data reliable.

Figure 1 illustrated the distribution characteristics of OTUs across different soil samples. It was found that normal soils exhibited the highest variation in OTUs, comprising 1,827 bacterial OTUs and 143 fungal OTUs. Notably, the distribution of fungal OTUs differed from that of bacterial community, with the lowest number of fungal OTUs (124 OTUs) observed in strongly acidic soil samples. In contrast, normal and acidic soils showed only slight variations in fungal OTU numbers. The number of shared OTUs was accounted for 59.46% of the bacterial community and 56.07% of the fungal community, indicating that distinct microbial communities adapted to varying acidity levels.

Alpha diversity analysis, presented in Table 2, assessed species diversity within habitats. The Shannon index for bacterial and fungal communities was highest in normal soils, while the Ace and Chao indices were lowest in strongly acidic soils. Notably, the Chao index was highest in acid soils for bacterial communities. The Ace and Chao indices for fungal communities displayed slight variations between normal and acidic soils. These findings indicated that the diversity of bacterial and fungal communities was greater in normal soils than in acidic and strongly acidic soils, with no significant differences in diversity indices between normal and acid soils for fungal communities.

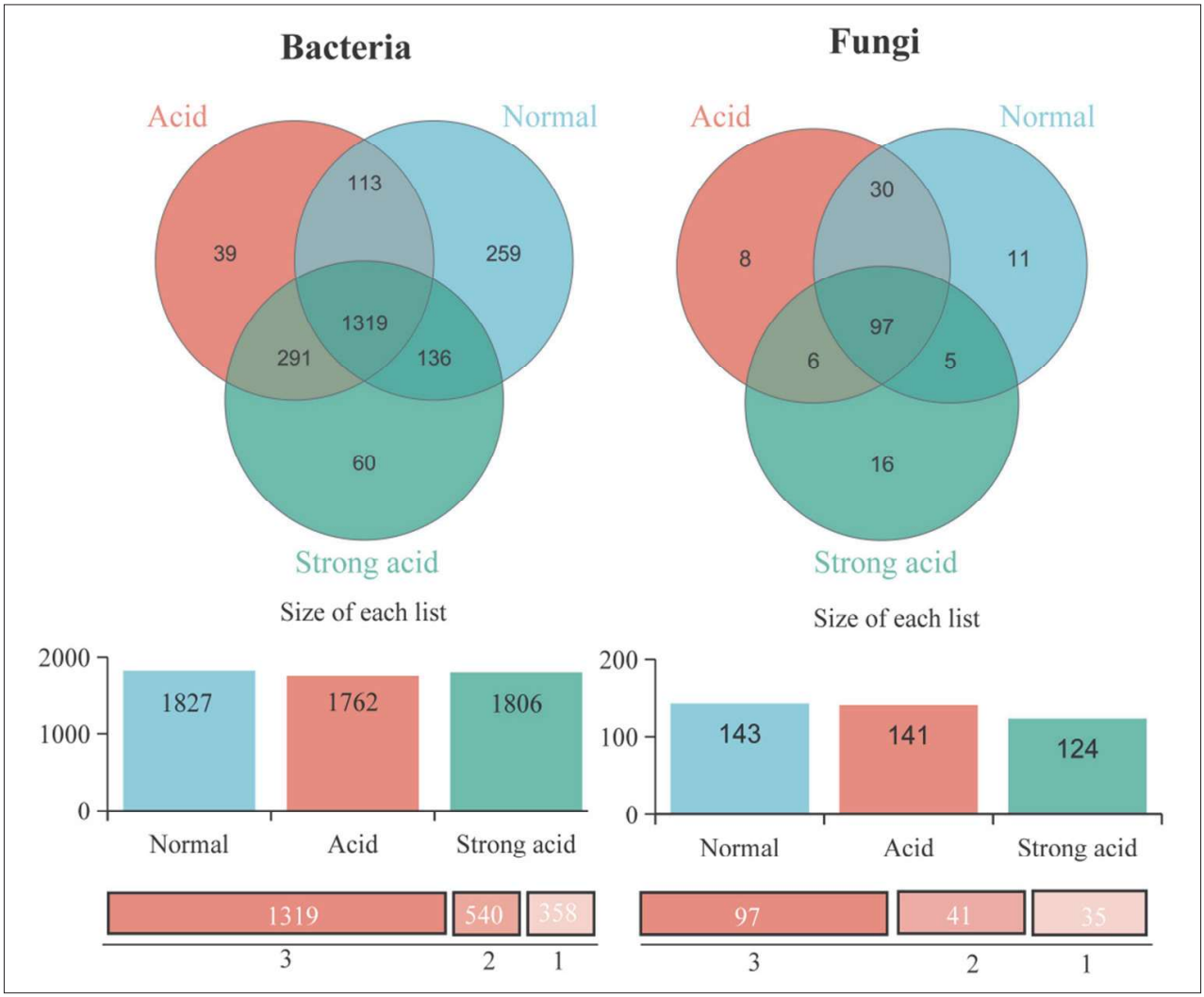


Figure 1. Venn diagram showing the shared operational taxonomic units (OTUs) of normal, acidic and strongly acidic soils. The column chart shows the size of each list and the bar chart shows the number of single or multiple elements.

Table 2. Soil α diversity index of fungal and bacterial communities in normal, acidic and strongly acidic soils.

	Sample	Shannon	Simpson	Ace	Chao	Coverage
Bacteria	Normal	6.1749	0.0059	1,979.58	1,958.51	0.9935
	Acidic	6.1398	0.0063	1,954.79	1,978.64	0.9917
	Strongly acidic	6.1394	0.0075	1,942.31	1,933.12	0.9939
Fungi	Normal	2.6708	0.1374	148.95	148.50	0.9999
	Acidic	2.6136	0.1635	145.16	148.25	0.9997
	Strongly acidic	2.5401	0.1793	130.78	128.40	0.9996

Soil microbial community structure and composition

The microbial distribution characteristics at both phylum and general levels were compared and showed in Figures 2 and 3. In total, 2,217 bacterial OTUs were clustered into 29 phyla, 77 classes, 178 orders, 271 families, and 472 genera. The dominant bacterial phyla included Actinobacteriota (41.84%), Proteobacteria (27.91%), Chlorofexi (13.86%), Firmaicutes (3.59%), Gemmatimonadota (3.22%) and Myxococcota (1.71%) (Figure 2). Actinobacteriota was the most abundant across all samples. The relative abundances of Chloroflexi and Planctomycetota increased with decreasing soil acidity, whereas Firmicutes and Gemmatimonadota were most abundant in acid soils. Additionally, 173 fungal OTUs were clustered into 21 phyla, 32 classes, 50 orders, 54 families, and 57 genera. The predominate fungal phyla included Ascomycota (75.69%), Basidiomycota (13.31%), Mucoromycota (5.65%), SAR (2.13%) and Platyhelminthes (1.23%) (Figure 2). Ascomycota was prevalent across all samples, particularly in acid and strongly acidic soils, with respective abundances of 82% and 81%. The relative abundance of Basidiomycota decreased markedly with declining pH, while Mucoromycota and SAR exhibited slight differences across soil types.

The top 15 genera from both bacterial and fungal samples were compared and illustrated in Figure 3. The bacterial community revealed that *Caballeronia paraburkholderia*, *Bryobacter*, *Vicinamibacterales*, *Bradyrhizobium*, *Xanthobacteraceae* and *Acidothermus* represented higher abundances (totaling 60%). In comparison to normal samples, The abundances of *Xanthobacteraceae*, *Acidothermus*, *Conexibacter* and *Ktedonobacteraceae* obviously increased in acidic samples. Conversely, *Bryobacter*, *Vicinamibacterales*, *RB41*, *Candidatus koribacter* and *Luedemannella* showed the highest abundance in normal samples. In the fungal community, *Tremellales*, *Pleosporales*, *Sordariomycetes*, *Thysanophora*, *Trichoderma*, and *Agaricomycetes* accounted for higher abundance (totaling 88%), with *Trichoderma* exhibiting the highest abundance (36%) (Figure 3). *Sordariomycetes* and *Thysanophora* were most abundant in strongly acidic samples, while *Agaricomycetes*, *Agaricales* and *Tremellales* showed the highest abundances in normal samples. Furthermore, the highest abundance of *Pleosporales* was observed in acidic samples.

Correlation analysis of soil parameters and soil microbial community

Table 3 indicated that AK was significantly negatively correlated with the Simpson and Ace indices in the bacterial community ($P < 0.05$). Both TN and SOM were significantly positively correlated with the Chao index, while sSC was significantly positively correlated with the Ace index in the bacterial community ($P < 0.01$). In the fungal community, pH was significantly positively correlated with the Shannon index, suggesting that the pH has a substantial impact on the diversity and structure of fungal communities ($P < 0.05$).

Correlation analyses between microbial abundances and environmental factors were conducted (Figure 4). In bacterial genera, *Acidibacter* was significantly positively correlated with AK, but negatively correlated with sSC ($P < 0.01$). *Conexibacter* and *Ktedonobacteraceae* were significantly positively correlated with sACP, while *Conexibacter* was significantly negatively correlated with pH ($P < 0.05$). Moreover, *Acidothermus* was significantly positively correlated AK ($P < 0.05$). In fungal genera, *Trichoderma* exhibited a significant positive correlation with TN and SOM ($P < 0.001$), whereas *Thysanophora* was significantly positively correlated with

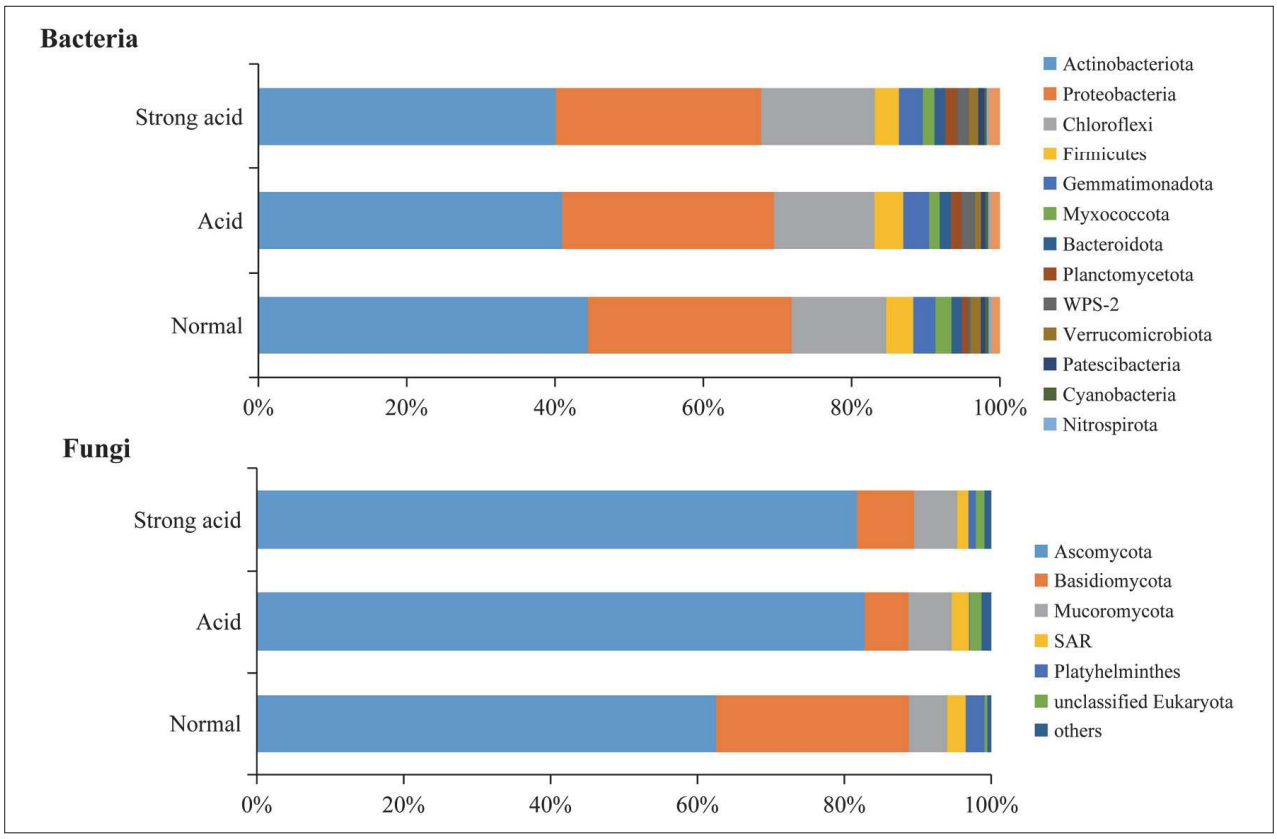


Figure 2. Relative abundances of the main bacterial and fungal phyla of the soils in normal, acidic and strongly acidic. The 'Others' and 'Unclassified Eukaryota' comprised the unclassified and low-abundance phyla (RA < 0.1%).

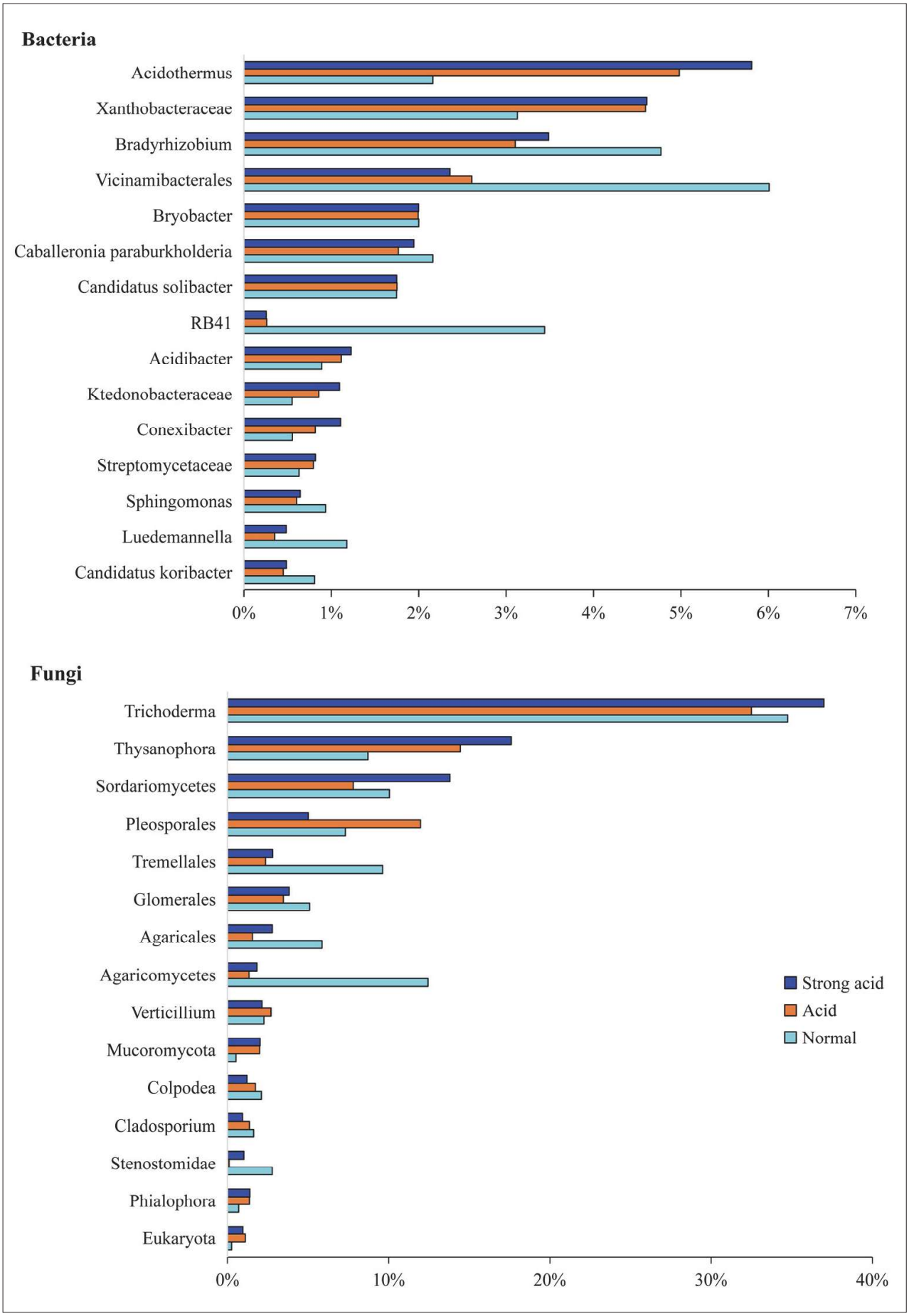


Figure 3. Relative abundances of the top seven fungal genera and top 16 bacterial and fungi genera of the soil in normal, acidic and strongly acidic in the pomelo garden.

sSC ($P < 0.05$). *Verticillium* was significantly positively correlated with sUR ($P < 0.05$), and *Pleosporales* was significantly negatively correlated with AP ($P < 0.05$). *Stenostonmidae* was significantly negatively correlated with sDHA ($P < 0.05$).

Microbial community function predictions

To investigate the functional activities of microbial community across different acidity backgrounds, the Phylogenetic Investigation of Communities by Reconstruction of Unobserved States (PICRUSt) approach was employed (Langille et al., 2013) to predict potential microbial functional pathways. In the bacterial community, PICRUSt analyses revealed a significant decrease in the relative abundances of pathways related to the growth, biosynthesis and catabolism from normal to strongly acidic soils (Figure 5). Conversely, pathways related to signal transduction (e.g., Ras/Rap1 signaling pathways, calcium signaling pathway, cAMP signaling pathway) were more prevalent in acidic soils, with the lowest abundances observed in normal soils. Comparative analyses of different pathways in the fungal community were also conducted (Figure 5). In normal soils, the fungal community showed increased abundances of pathways associated with carbohydrate transport and metabolism, nucleotide transport and metabolism, RNA processing and modification, and secondary biosynthesis. In strongly acidic soils, the fungal community showed increased abundances of pathways associated with defense, signal transduction and intracellular secretion. Additionally, pathways related to extracellular were more enriched in acidic soils. Collectively, these alterations in microbial function suggest that strongly acidic conditions are detrimental to both bacterial and fungal survival; however, fungi exhibited greater tolerance to acidity stress.

Discussion

Bacteria and fungi play significant roles in soil formation, development, nutrient cycling, and fertility evolution. This study compared the physicochemical properties of fungal and bacterial communities in pomelo orchard soils subjected to varying degrees of acidification. The results proved the hypotheses and showed that the bacterial and fungal communities exhibit distinct responses to acidified soil conditions, with differences in microbial composition being the primary factor underlying the functional differentiation of soil microorganisms across different acidity levels.

The impact of soil pH on nutrient status is substantial, with significant declines observed in nitrogen, phosphorus, and potassium levels as pH decreased. These conditions created an environment characterized by low phosphorus efficiency and infertile soil, as demonstrated by Carrino-Kyker et al. (2019) and Zhang et al. (2021) in agricultural contexts. Microorganisms are highly sensitive to their environment. Previous studies have shown that microbial interactions are influenced by ecological factors, with soil pH playing a direct role in the distribution and activity of soil microbial communities (Naz et al., 2022; Muneer et al., 2022). Our findings revealed that the diversity of bacterial communities in pomelo orchard soils was significantly influenced by nutrient levels, including nitrogen, potassium and organic matter (Table 3). These results aligned with those reported by Cookson et al. (2007) and Chevrette et al. (2022). Furthermore, the diversity of bacterial communities was significantly declined in acidic and strongly acidic soils (Table 2), indicating that bacteria were particularly responsive to soil acidity. Nonetheless, no significant correlation was found between bacterial community diversity and pH (Table 3), which was not entirely

Table 3. Correlation analyses of α diversity index and soil parameters.

		pH	TN	AK	AP	SOM	sDHA	sACP	sUR	sSC
Bacteria	Shannon	-0.876	0.861	0.718	0.746	0.861	0.157	0.845	-0.642	-0.764
	Simpson	0.958	-0.240	**-1.000***	-0.047	-0.240	-0.815	-0.973	-0.097	0.996
	Ace	0.980	-0.329	**-0.998***	-1.139	-0.329	-0.758	-0.990	-0.005	**1.000****
	Chao	0.564	**-0.998***	-0.328	-0.966	**0.998***	0.304	-0.514	0.919	0.392
Fungi	Shannon	**0.998***	-0.561	-0.947	-0.390	-0.561	-0.565	-0.993	0.253	0.967
	Simpson	-0.989	0.373	0.993	0.186	0.373	0.726	0.996	-0.043	-0.999*
	Ace	-0.744	-0.198	0.893	-0.384	-0.198	0.985	0.782	0.513	-0.860
	Chao	-0.856	-0.011	0.961	-0.205	-0.011	0.934	0.885	0.343	-0.940

* and ** represent significance ($P < 0.05$ and $P < 0.01$) of soil samples by *t*-test.

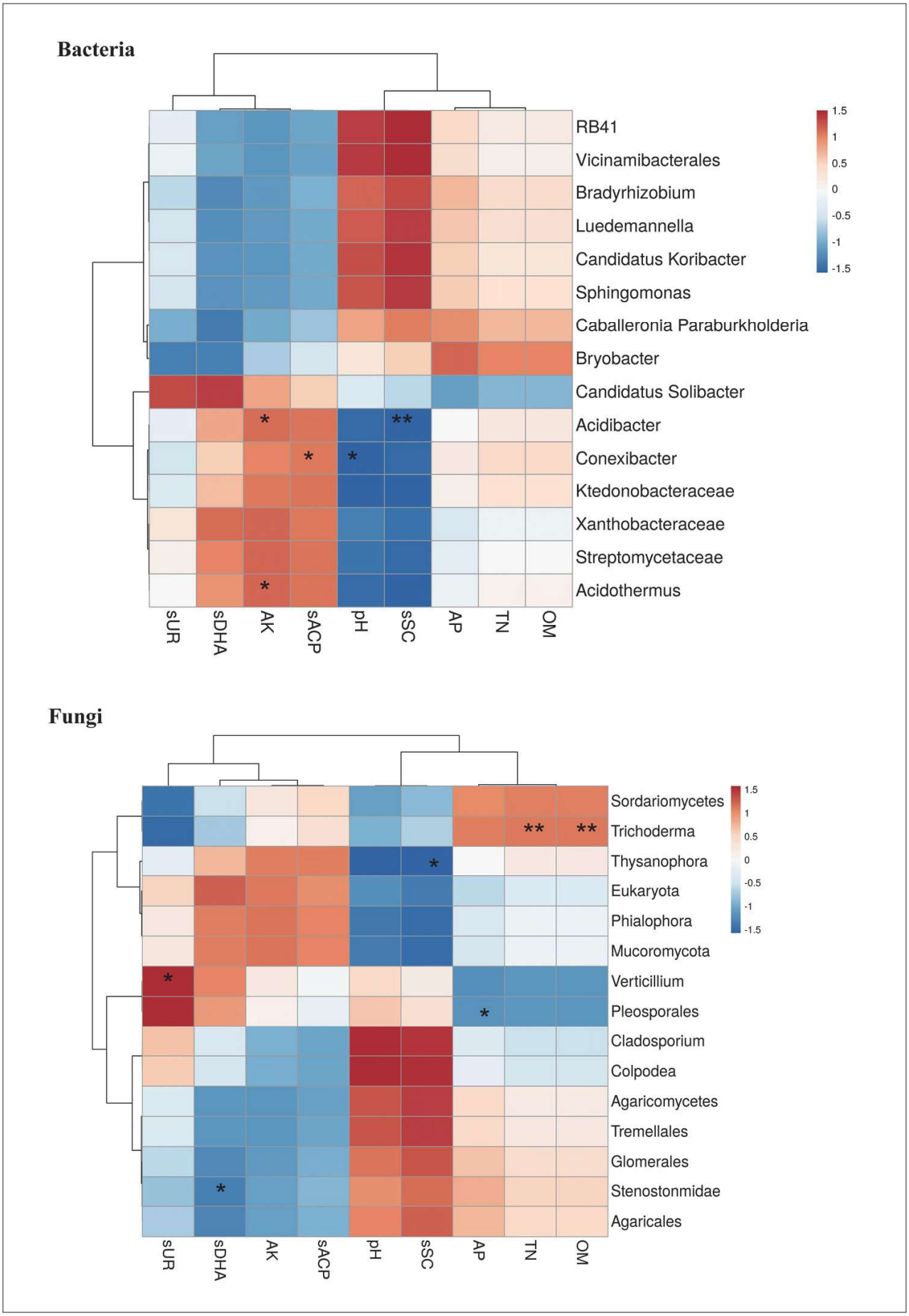


Figure 4. Correlation matrix for environmental parameters and species. Red signifies a positive correlation, while blue signifies a negative correlation. * 0.01≤p<0.05, ** 0.001≤p<0.01. The upper right inset bar indicates the value of correlation coefficient.

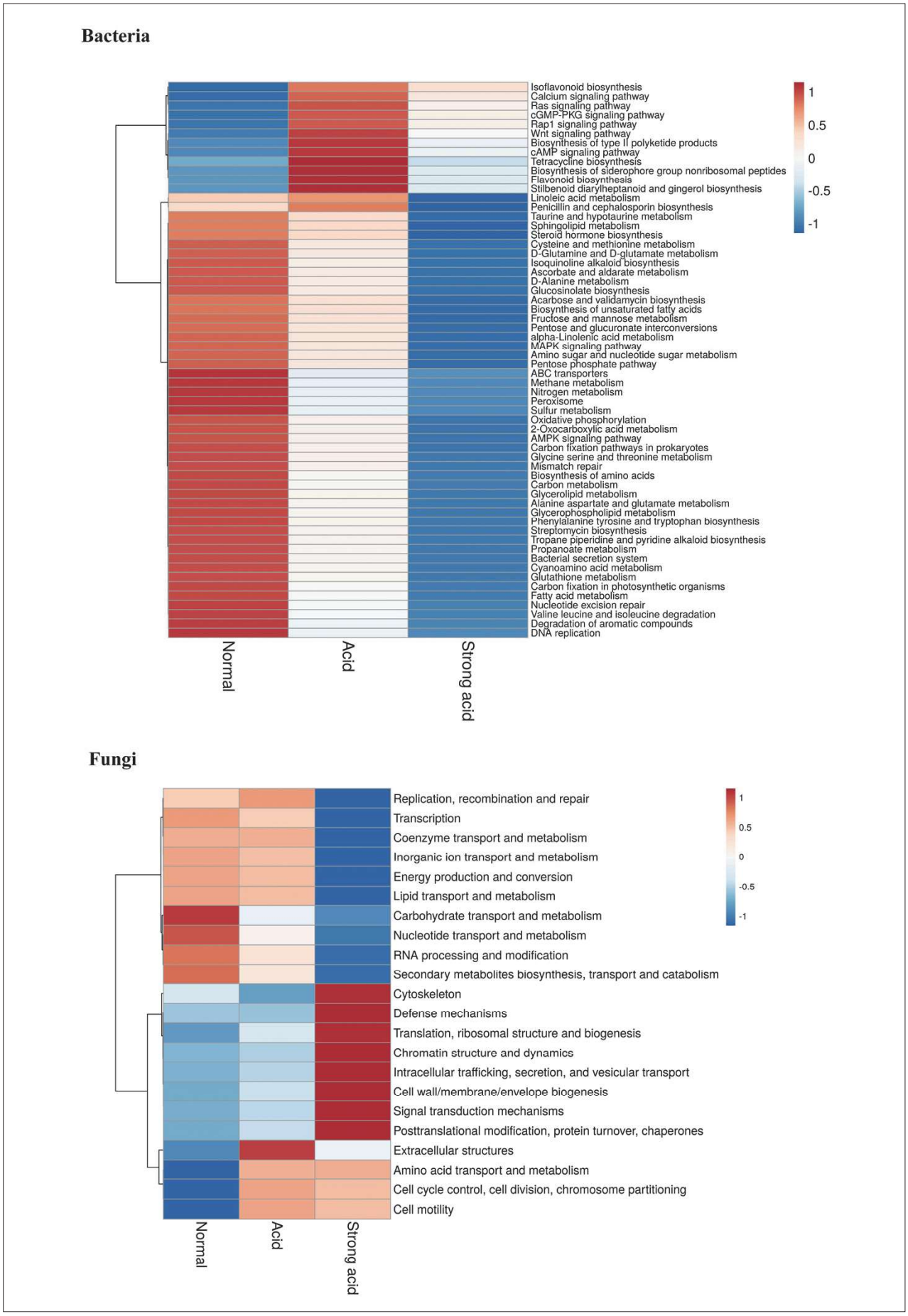


Figure 5. Most relatively abundant inferred pathways and functions employing PICRUSt2 analysis. The functions of bacterial and fungi communities were analysed based on PICRUSt by KEGG annotation at level 2.

inconsistent with Cho et al. (2016), who studied bacterial community diversity in mountain soils. This lack of correlation suggested that bacteria may exhibit a broad adaptability to both acidic and alkaline conditions, though they could be severely affected by nutrient fluctuations associated with variations in soil pH. In contrast, a significant correlation was observed between fungal community diversity and soil pH (Table 3), with lower fungal diversity linked to declined soil pH. Moreover, the diversity of fungal community remained stable between normal and acidic soils, but showed a significant decline in strongly acidic soils (Table 2). These results aligned with the findings of Liu et al. (2015) and Tedersoo et al. (2014), who proposed that pH serves as a crucial predictor of soil fungal diversity, with fungal diversity being more sensitive to soil acidity while exhibiting greater tolerance to varying nutrient levels.

Despite variations in soil properties across different pH levels, over 50% of OTUs in both bacterial and fungal communities were shared. This finding corroborates previous studies (Tedersoo et al., 2014; Delgado et al., 2021; Muneer et al., 2022; Jiao et al., 2022). In contrast, certain genera exhibited pronounced differences along the soil pH gradient. For instance, *Bradyrhizobium*, *Vicinamibacterales* and *RB41* – members of the Acidobacteriota – demonstrated significantly higher relative abundance in normal soils (Figure 3). These groups were widely distributed across various agricultural soils, with *Vicinamibacterales* thriving in phosphorus-rich environments and exhibiting significant phosphate solubilization capacity (Wu et al., 2022). This finding supports the notion that soil pH indirectly influences bacterial communities through changes in nutrient status. Furthermore, *RB41* was found prevalent in various soil types, and contributed to soil carbon flux, reportedly comprising 45–57% of carbon flow in soils when in association with *Bradyrhizobium* and *Streptomyces* (Stone et al., 2021). The low abundance of these groups in acidic and strongly acid soils observed in this study may impair the decomposition of organic matter, as suggested by Wang and Kuzyakov (2024), who identified soil acidity as one of the most significant factors influencing SOM decomposition. Additionally, an increase in the relative abundance of *Xanthobacteraceae* and *Acidothermus* was noted, which were recognized as potential disease-suppressive or disease-inducible bacteria (Li et al., 2020; Goh et al., 2020), with decreasing soil pH (Figure 3). In the fungal community, groups within *Basidiomycota*, such as *Agaricales*, *Agaricomycetes* and *Tremellales*, exhibited higher relative abundances in normal soils, reflecting their role as decomposers capable of mobilizing inorganic nutrients from plant residues (Stursová et al., 2012; Likar et al., 2022). Conversely, *Thysanophora* and *Sordariomycetes*, both belonging to the Ascomycota, were abundant in strongly acidic soils. These genera have been implicated in soil-borne diseases, such as black-foot disease in grapevines (Abeywickrama et al., 2021) and root rot in wheat (Scherm et al., 2013). Thus, these findings suggested that soil acidification may facilitate the proliferation of soil-borne pathogens, exacerbating the incidence of diseases and pests.

The differing responses of bacterial and fungal communities were further elucidated through PICRUSt analysis. Enriched metabolic pathways exhibited significant variation along the soil pH gradient as well as between bacterial and fungal communities (Figure 5). Generally, most bacteria are neutralophiles but can endure fluctuations in pH. Our study indicated significant bacterial cell damage attributable to acid stress, consistent with findings by Schwarz et al. (2022) and Li et al. (2021) which reported that soil acidification adversely affected bacterial metabolism and increased the production of pollutants under acidic conditions. Notably, the acid response of bacterial cells intensified in soils with a pH of approximately 5.6, with many signal transduction genes being enriched (Figure 5). This adaptation may facilitate bacterial survival in acidic environments (Xu et al., 2022; Liu et al., 2015). In contrast, the fungal community exhibited greater stability and resilience to acid stress in our study. For example, pathways involved in signaling, translation, cell wall biogenesis were significantly up-regulated in strongly acidic soils (Figure 5). These genes are critical for sustaining fungal community dynamics (de Menezes et al., 2017). Similar conclusions were drawn by Choma et al. (2020) and Peñalva and Arst (2002), who noted that fungi can modulate their metabolic activities in response to ambient pH levels.

Conclusions

Our findings suggested that declining soil pH negatively impacted soil properties and the microbial community. Specifically, an acidic environment decreased the availability of nutrients, reduced microbial diversity, weakened SOM decomposition, and promoted the prevalence of soil-borne diseases. Additionally, bacterial and fungal community exhibited different responses under normal, acidic and strongly acidic conditions. Firstly, soil pH indirectly affected bacterial composition by lowering nutrient levels, while it directly affected fungal composition. Second, bacteria communities were more sensitive to both acidic and strongly acidic conditions. In contrast, fungal communities, although influenced by soil acidity, tended to endure better and respond positively through metabolic regulation. Overall, maintaining balanced soil pH is essential for enhancing soil health and fruit production. Further research utilizing metagenomic or metatranscriptomic approaches could delve deeper into gene expression patterns within microbial communities in acidified soil environments.

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Authors' contributions

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