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Relationships between soil biodiversity and multifunctionality in croplands depend on salinity and organic matter

Jiyu Jia [a,b,1], Jiangzhou Zhang [c,a,1], Yizan Li [a,b], Liz Koziol [d], Laura Podzikowski [e], Manuel Delgado-Baquerizo [f], Guangzhou Wang [a,*], Junling Zhang [a]

[a] College of Resources and Environmental Sciences, National Academy of Agriculture Green Development; Key Laboratory of Plant-Soil Interactions, Ministry of Education, China Agricultural University, Beijing 100193, China
[b] Department of Soil Quality, Wageningen University & Research, P.O. Box 47, 6700 AA Wageningen, The Netherlands
[c] College of Resources and Environment/International Magnesium Institute, Fujian Agriculture and Forestry University, Fuzhou 350002, China
[d] Kansas Biological Survey, University of Kansas, Lawrence, KS 66045, USA
[e] Department of Ecology and Evolutionary Biology, University of Kansas, Lawrence, KS 66045, USA
[f] Departamento de Sistemas Físicos, Químicos y Naturales, Universidad Pablo de Olavide, 41013 Sevilla, Spain

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ABSTRACT

Soil salinization is a widespread environmental problem adversely impacting global food production. Increasing soil organic matter (SOM) could alleviate salt stress, but soil salinity and SOM have differing effects on microbial diversity and activities. We explored how the relationships between soil biodiversity and multifunctionality were altered by soil salinity and SOM. We collected soils from the wheat-maize cropping system in the North China Plain and categorized soils according to salinity and SOM. Soil functions related to carbon, nitrogen, phosphorus, and micronutrient processing were measured as metrics of soil multifunctionality (SMF) characterization. We found significant positive relationships between SMF and bacterial diversity but not fungal diversity in soils with high SOM (>15 mg/kg) and low EC (<4 ds/m). The diversity and abundance of sensitive bacteria were more strongly correlated with SMF than those of non-sensitive bacteria. SOM directly and indirectly impacted SMF through changes in sensitive bacterial abundance, while soil EC impacted SMF via altered sensitive bacterial diversity. With respective to individual soil function, carbon and micronutrient cycling were predominantly determined by bacterial diversity. Our findings suggest coupling decreased salinization with the increase of SOM could increase soil multifunctionality by increasing diversity and abundance of sensitive soil microbes. These findings highlight the importance of sensitive microbial taxa to sustaining soil ecosystem functioning in croplands.

1. Introduction

Soil microorganisms play a key role in maintaining multiple soil functions such as litter decomposition, pathogen control, pollutant degradation, and nutrient cycling, which is defined as soil multifunctionality (SMF) (Wagg et al., 2019). Soil microbial diversity is positively correlated with SMF in both natural and agricultural ecosystems (Jing et al. 2015; Mori et al., 2016; Delgado-Baquerizo et al., 2017; Chen et al., 2020a; Li et al., 2021a,b; Luo et al., 2018). However, the biodiversity-multifunctionality relationship might be vulnerable to changes in soil health. This is of particular concern in agroecosystems, where anthropogenic activities are more likely to alter soil conditions, for example increasing soil salinization (Yang et al., 2020), which could adversely affect soil microbial functions (Zhou et al., 2020; Hu et al., 2021). Understanding how the soil biodiversity-multifunctionality relationship is modified by salinization is important for maintaining soil health in cultivated lands.

Soil salinization is a global environmental problem effecting about one tenth of dry lands (Pan et al., 2022; Wan et al., 2021b; Zhang et al., 2019). Soil salinity can increase ion toxicity and reduce water availability by lowering osmotic potential. Lowered water availability and increased ion toxicity can negatively affect soil microbial diversity (Chen et al., 2021), metabolic activities (Yuan et al., 2007), and functioning (Rath and Rousk, 2015; Rath et al., 2019a,b). Increased soil

* Corresponding author.
E-mail address: wanggz@cau.edu.cn (G. Wang).
[1] These authors contributed equally to this work.

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salinity is correlated with lowered soil organic matter (SOM), which could be a result of suppressed plant growth, which lowers organic matter inputs to soils (Setia et al. 2013; Wong et al. 2010). Improving SOM is an effective approach to alleviate stress caused by increased soil salinity (Wong et al., 2008). SOM can increase organic and inorganic substrates released to soil, diluting salt ions, such as Na^+, Cl^-, offsetting adverse effects from salt stress (Pathak and Rao 1998; Wong et al. 2010). SOM could also stimulate microbial production of organic compounds, such as amino acids and carbohydrates, which alleviate osmotic stress caused by salinity (Wong et al., 2009). Increased SOM can improve soil aggregate stability, provide a range of microhabitats in soils and increase microbial diversity and activity (Gupta and Germida, 2015). However, the positive effect of SOM on microbial diversity and activity in saline soils could be dependent on the degree of salinization of the soils (Dong et al. 2022). Addition of SOM improves microbial activities in soils with low electrical conductivity (EC < 2.05 ds/m), but has no effect when salinity is high (>2.05 ds/m). How the interaction between soil salinity and SOM affects the soil biodiversity and SMF relationship remains underexplored.

Soil microbes have different responses to changes in soil salinity and SOM, resulting in the relationship between soil biodiversity and SMF is context-dependent (Chen et al., 2020b,a; Wan et al., 2021b). In saline soils, microbial communities shift towards bacterial dominance, a pattern perhaps resulting from high phylogenetic and taxonomic turnover rates, which give bacteria the ability to quickly adapt to salt stress (Sardinha et al., 2003; Han et al., 2022). It is generally acknowledged that fungi tend to use recalcitrant organic matter, while bacteria are associated with the turnover of easily degradable substrates (Rousk et al., 2016). In agroecosystems, bacteria may be more sensitive to changes in salinity and SOM, because SOM in cultivated soils tends to contain more easily degradable rather than recalcitrant organic matter (Cheng et al., 2007), thus bacteria rather than fungi, may play a more important role in driving SMF (van Der Heijden et al., 2008; De Vries and Bardgett, 2012). Rare, rather than abundant taxa may be more sensitive to environmental changes, as rare taxa are thought to be less well adapted to disturbance (Chase et al., 2017; Liang et al., 2020), including changes in soil salinity and SOM (Jiao and Lu, 2020; Wan et al., 2021b). Exploring which groups of microbial taxa mediate the soil biodiversity-SMF relationships is critical for understanding how to best maintain soil health and improve agricultural ecosystem services.

The North China Plain is one of the most important granaries in China with about 140,000 km^2 of land in cultivation producing about 50 % of national wheat and 33 % of maize (Zhang et al., 2021). This area is characterized by low SOM and is currently facing high rates of soil salination from poor irrigation planning and high evapotranspiration (Yang et al., 2016). Soil salinization and SOM can have opposing effects on soil microbial communities and SMF making it essential to understand how the relationship between the soil microbes and SMF changes under differing SOM and EC statuses; and the role microbial community composition plays in determining biodiversity-multifunctionality relationships. We collected soil samples with categorically high and low salinity and SOM levels from wheat-maize cropping system in the North China Plain. We sequenced the bacterial and fungal communities and determined SMF to evaluate the relationship between soil biodiversity and ecosystem functioning. We hypothesized that (1) the relationship between microbial diversity and multifunctionality could be positively improved by SOM but negatively decreased by soil salinity; (2) sensitive bacteria, and specifically rare species, play a more crucial role in driving these relationships.

2. Materials and methods

2.1. Study sites and sample collection

We sampled soil in March of 2018 around Quzhou Experiment Station of China Agricultural University (114◦50′22.3″-115◦13′27.4″ E, 36◦35′43″-36◦57′ N) (Fig. 1). This area has a northern warm temperate zone continental monsoon climate, with an average annual temperature of 13.1 ℃ and a mean annual precipitation of 500 mm. Approximately 60 % of precipitation occurs from July to September. The soils are calcareous with light loam, medium loam, sandy loam, and clay textures (Zhang et al., 2021). Historically in this region soils were saline. Though a large amount of the land was remediated, some soils are still saline due to the influence of shallow, salty groundwater (Ma et al., 2008). Wheat-maize rotation is the typical cropping system in this region.

Fifty-five sites were selected for soil sampling after a region-wide survey was conducted (Fig. 1). Sites were selected if a wheat-maize cropping system was the dominant planting pattern over 1 km^2 area and had been maintained for at least 5 years. At each sampling site, four 3 × 3 m plots that were evenly distributed on the field were established within a field belonging to the same farming stakeholder. After removing any crop residues, five soil cores were collected to a depth of 20 cm using an auger (5 cm diameter) from each plot. Soils were pooled generating one sample per site. Soil samples were transported on ice to the laboratory immediately after collection, passed through a 2.0-mm mesh sieve, and divided into two subsamples. One subsample was stored at 4 °C for determination of soil physicochemical properties, while the second subsample was stored at −20 °C for DNA analysis.

We then categorized soil samples into four groups based on the EC (range: 2.17–6.8 ds/m; mean: 4.04 ds/m) and SOM (range: 7.51–25.30 g/kg; mean: 14.62 g/kg) contents. An EC of 4 dS/m is considered the critical threshold below which conditions are too stressful to sustain crops (Hassani et al., 2020). We classified samples with an EC greater than 4 dS/m as high EC (HEC) and lower than 4 as low EC (LEC). Soils were categorized by SOM from data obtained from the Second National Soil Survey of China (Soil Survey Office of China, 1992). Sites with SOM content greater than 15 g/kg were classified as high SOM (HS) and below that as low SOM (LS). The four groups (HS-HEC, HS-LEC, LS-HEC and LS-LEC) consisted of 12, 13, 12, and 18 sites, respectively.

2.2. Soil parameter measurements and quantification of soil multifunctionality

To quantify soil multifunctionality, we selected soil properties that represent key supporting and regulating roles in carbon, nitrogen, phosphorus, and micronutrient cycling (Delgado-Baquerizo et al., 2017; Maestre et al., 2012; Zechmeister-Boltenstern et al., 2015; Chen et al., 2020; Zhang et al., 2021; Hu et al., 2021). To quantify carbon cycling, we measured soil organic carbon storage (SOC content × bulk density × sampling depth), dissolved organic carbon (DOC), recalcitrant organic carbon (ROC) content, β-1,4-Glucosidase (BG, starch degradation) activity, and soil respiration (SR) (see Table S1 for details on the methodology). We calculated SOC by dividing SOM content by a coefficient of 1.724 (Post et al., 1982). Nitrogen cycling was quantified by measuring enzyme activities, β-1,4-*N*-acetyl-glucosaminidase (NAG, chitin degradation), and gaseous emissions of N_2O (negative value of N_2O emission). Phosphorus cycling was quantified by measuring acid and alkaline phosphatase activities (ACP, ALP). We determined micronutrient cycling by measuring the available Fe, Mn, Cu, and Zn concentration. We also measured soil pH, electric conductivity (EC), available phosphorus (AP), available potassium (AK), bulk density, and soil texture.

We adopted three distinct approaches (single functions, the averaging approach and single threshold approach) to quantify SMF (Byrnes et al., 2014; Delgado-Baquerizo et al., 2017). All soil measurements were standardized with Z-score transformations (Maestre et al., 2012). Standardized ecosystem functions were averaged to obtain an overall multifunctionality index and single-function index (i.e., carbon, nitrogen, phosphorus and micronutrient cycling processes) (Byrnes et al., 2014; Delgado-Baquerizo et al., 2017). This approach is broadly employed and provides a straightforward measure of the multifunctionality of differing microbial communities (Wagg et al., 2019). The single-threshold approach was conducted to assess if multiple soil

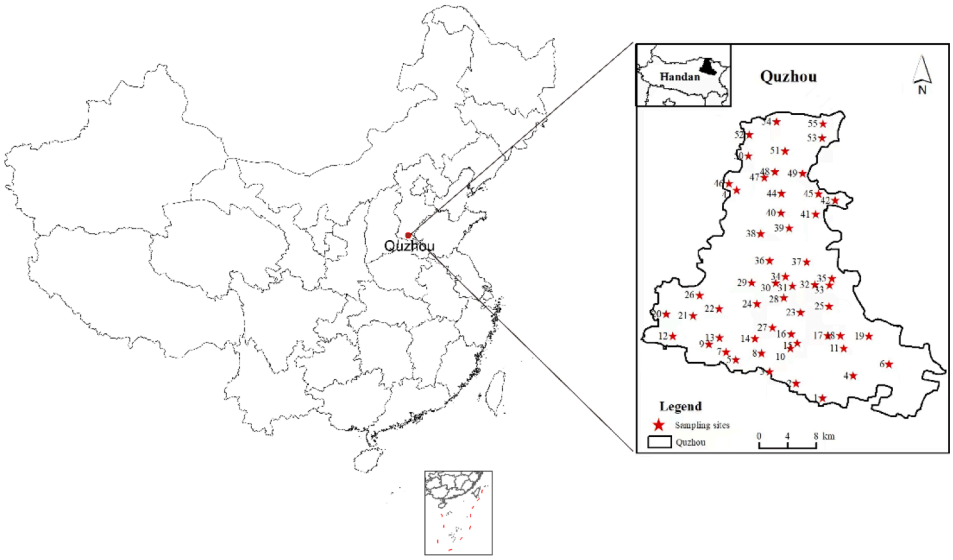


Fig. 1. The distribution of 55 sampling sites across Quzhou experimental station in North China Plain.

functions are concurrently performing at high levels and determined whether they exceed a specified threshold percentage of maximum functioning. Single-thresholds of 20 %, 40 %, 60 % and 80 % were defined and then a generalized linear model was fitted to estimate a linear relationship predicting the number of soil functions performing at or above their threshold as a function of soil microbial diversity (Byrnes et al., 2014).

2.3. DNA extraction, high-throughput sequencing and bioinformatics

Soil DNA was extracted from 0.5 g of soil using MoBio PowerSoil DNA Isolation Kit (MoBio Laboratories, Carlsbad, CA, USA) according to the manufacturer's instructions. The DNA concentrations were measured on a NanoDrop ND-2000c UV–vis spectrophotometer (NanoDrop Technologies, Wilmington, DE, USA). The bacterial 16S rRNA gene and the fungal ITS1 gene were amplified for the V4-V5 hypervariable regions and ITS1 region using the primer pairs 515F/907R (Yusoff et al., 2013) and ITS1F/ITS2R (Adams et al., 2013). Each barcode unique sequence (8 mer) was added to the forward primer of each sample. For both bacteria and fungi, we conducted PCR amplification with 10-ng template DNA, 0.8 μl of each forward and reverse primer (both at 5 μM), 4 μl 5 × FastPfu Buffer, 2 μl 2.5-mM dNTPs, and 0.4 μl FastPfu polymerase (TransGen Biotech, Beijing, China), and adjusting the volume to 20 μl with PCR-grade water. Each sample was amplified in three technical replicates with the 20 μl reaction under the following conditions. For bacteria: 95 °C for 5 min, 37 cycles of 95 °C for 30 s, 55 °C for 30 s and 72 °C for 45 s of extension, followed by 72 °C for 10 min. For fungi, 94 °C for 4 min, 38 cycles of 94 °C for 45 s, 55 °C for 30 s and 72 °C for 45 s of extension, followed by 72 °C for 10 min. After amplification, the purified PCR products were mixed in equimolar ratios to obtain a quantitative sample DNA library for further sequencing. Sequencing was conducted using the Illumina MiSeq platform (Illumina, San Diego, CA, USA) at Major Biotechnology Co., ltd (Shanghai, China).

Raw sequences were demultiplexed and quality-filtered using the Quantitative Insights Into Microbial Ecology (QIIME) toolkit (version 1.8.0). Reads were end-trimmed to ensure the nucleotide quality score >30 before merging, and the maximum of expected error (ee) was set as 0.5 for merged reads filtering. After quality control, a total of 2,612,388 and 2,918,170 high-quality sequences were obtained for bacteria and fungi, respectively. These sequences were filtered for quality and split into operational taxonomic units (OTUs) at a 3 % dissimilarity level using the UPARSE pipeline (Edgar et al., 2011). The taxonomic assignment was performed using the SILVA (release 132) 16S rRNA database for bacteria and UNITE (release 7.2) fungal ITS database for fungi. Finally, A total of 6701 bacterial and 2320 fungal OTUs were obtained.

2.4. Statistical analysis

All statistical analyses were performed in R (version 4.0.1) unless otherwise noted. To determine the relationship between the soil microbial community and soil properties, we performed a redundancy analysis (RDA) using the 'Vegan' package (Oksanen et al., 2017). Only environmental variables that were significantly ($p < 0.05$, 999 permutations) correlated with the RDA model were selected. To test for differences in soil physicochemical parameters and extracellular enzyme activities between the four EC and SOM groups we performed a one-way ANOVA, and the least significant difference (LSD) was used to compare the means for each variable ($\alpha = 0.05$).

To visualize the variation in bacterial and fungal community structures with changing EC and SOM, we performed a principal co-ordinates analysis (PCoA) using Bray-Curtis dissimilarity. To determine the effect of EC and SOM on bacterial and fungal communities, a permutational multivariate analysis of variance (PERMANOVA) was conducted using the adonis in the 'Vegan' package (Oksanen et al., 2017). To determine the relationship between microbial biodiversity (Simpson's Diversity Index) and SMF for each of the four EC-SOM groups, we ran an ordinary least squares (OLS) linear regression model.

Two complementary approaches were employed to identify microbes that were sensitive to changes in EC and SOM (Hartman et al. 2018). First, a correlation-based indicator species analysis was performed in 'indicspecies'. This estimates the point-biserial correlation coefficient (r) of an OTU's positive association to EC and SOM (De Cáceres et al., 2010), with significance at $p < 0.05$ using 104 permutations. Second, we identified differential OTU abundance of both kingdoms in the soil microbial community using likelihood ratio tests (LRT) for all EC-SOM groups with the package 'edgeR' (Robinson et al., 2010). OTUs whose abundances were identified as differing between groups were considered responsive at a false discovery rate (FDR) corrected threshold of $p < 0.05$. We classified sensitive OTUs (sOTUs) as OTUs that showed significant relationships in both the indicator species selection analysis methods and in the LRT. The Simpson's diversity index of sOTUs in each site was calculated with the 'Vegan' package. Spearman correlation was used to assess the relationship between soil functions and the sum of the abundances of sOTUs on the phylum level. We also identified abundant taxa and rare taxa among sOTUs. Abundant taxa were defined as OTUs with a relative abundance of at least 1 % in any site (i.e., relative

abundance within a sample) and an overall relative abundance of at least 0.1 % (i.e., abundance across all 55 samples) (Xiong et al., 2020). Rare taxa were defined as OTUs having local relative abundance less than 0.01 % and regional relative abundance less than 0.001 % (Xiong et al., 2020). OTU taxa defined as neither rare nor abundant were classified as intermediate taxa (Xiong et al., 2020).

To explore the effect of EC and SOM content on the microbial interactions, in particular between sOTUs in the soil bacterial and fungi community, we constructed co-occurrence networks. We normalized OTU sequence counts for each microbial kingdom separately using the "trimmed means of M" (TMM) method with the BioConductor package 'edgeR' (Hobbs et al., 2008) and expressed the normalized counts as relative abundance counts per million (CPM) (Hartman et al., 2018). Next, we conducted Spearman rank correlations between OTUs and visualized the positive, significant correlations ($R > 0.6$ and $p < 0.01$). Co-occurrence networks were visualized with the Fruchterman-Reingold layout with 10^4 permutations. Topological network properties were calculated with 'igraph', including the total number of network nodes (OTUs), total number of edges (connections between nodes), and degrees of co-occurrence (number of direct correlations to a node) (CsardI and Nepusz, 2016). Network modules were identified and implemented in 'igraph' utilizing the greedy optimization of modularity algorithm. To analyze differences in relative abundance of sOTUs between the EC and SOM groups in the different network modules we performed a two-way ANOVA and visualized the data using 'ggplot2' (Wickham, 2009). And LDA Effect Size (LEfSe) analysis were conducted to identify taxonomic biomarkers between different treatments across each module in the network.

To test the strength of the relationship between soil biodiversity and SMF accounting for multiple abiotic drivers simultaneously across all soil samples and in the HS-LEC group, we developed a structural equation model (SEM) using AMOS 17.0 (SPSS, Chicago, IL, USA). In this study, we try to evaluate the direct link between diversity and relative abundance of sOTU and multifunctionality (averaging) after controlling for soil parameters (EC and SOM). Bacterial and fungal sOTU diversity, relative abundance of bacterial and fungal sOTUs were used to predict soil multifunctionality directly. As soil properties can have direct effects and indirect effects on SMF by affecting soil microbial communities (Jiao et al. 2022), the direct and indirect effects of EC and SOM on SMF were also explored. The conceptual model and framework of the priori SEM were provided in Fig. S1. Maximum likelihood estimation was used to fit the covariance matrix to the model. The *a priori* theoretical model was adjusted according to the principle of the low Chi-square ($\chi 2$), nonsignificant probability ($p > 0.05$), high goodness-of-fit-index (GFI > 0.90), and root mean square error of approximation (RMSEA < 0.05) to ensure that the final model was adequately fitted.

3. Results

3.1. Effects of EC and SOM on bacterial and fungi community

There was no significant difference in microbial α-diversity (Simpson's diversity index) among four EC-SOM groups (Fig. S2). However, bacterial and fungal community structure differed significantly based on the PCoA (Fig. 2; Fig. S3). Both soil bacterial and fungal communities were distinctly grouped by EC and SOM, and the clustering of the bacterial community was more distinct. This was further supported through permutational multivariate analysis of variance (PERMANOVA). SOM and EC were the major drivers of bacterial community composition and EC was the major driver of fungal community composition (Fig. S2).

Among four groups, the most abundant bacterial phyla were *Proteobacteria* and *Acidobacteriota*, and the most abundant fungal phyla were *Ascomycota* and *Mortierellomycota* (Fig. S4). A total of 290 and 38 bacterial and fungal sOTUs were identified, respectively (Fig. S5). Compared to fungal sOTUs, bacterial sOTUs were more sensitive to EC ($F_{1,51} = 7.88$, $p < 0.01$) and SOM ($F_{1,51} = 17.87$, $p < 0.001$) (Fig. S6; Table S2). The sOTUs were assigned to 22 bacterial phyla and 5 fungal phyla. For each group, the most abundant phyla of bacteria were *Proteobacteria* and *Acidobacteriota* and the most abundant fungal phylum was *Ascomycota* (Fig. S7; S8). Based on the relative abundance of sOTUs, 223 and 67 bacterial sOTUs were identified as rare and intermediate taxa, respectively. All fungal sOTUs were intermediate taxa. However, there was no abundant taxa across all sOTUs (Table S3).

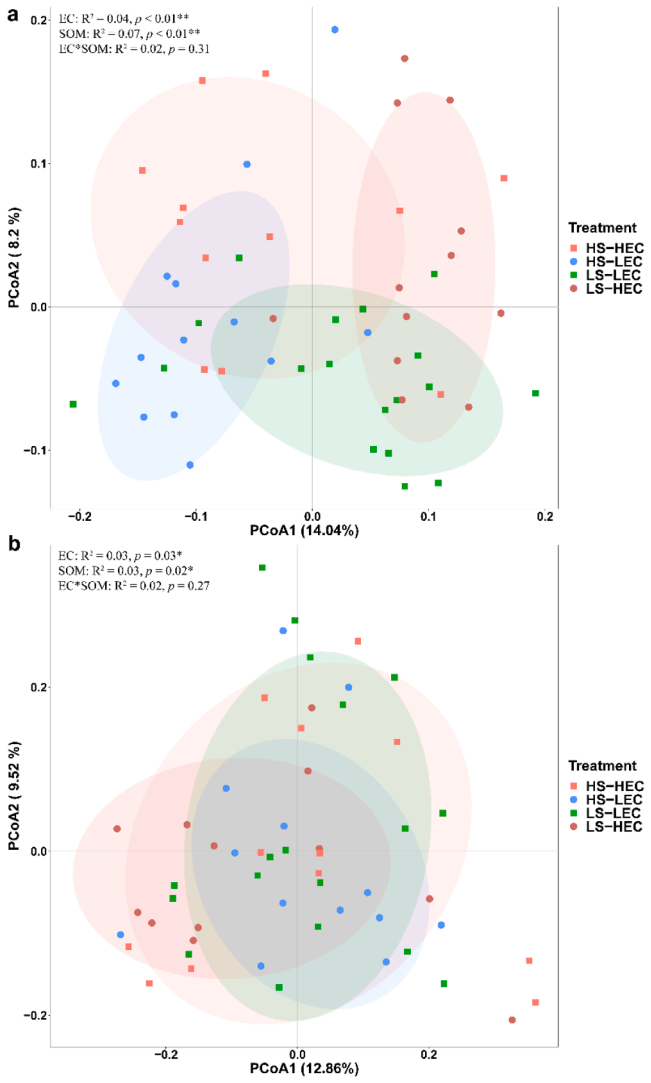


Fig. 2. Principal coordinates analysis (PCoA) of soil bacterial (a) and fungal (b) community based on the Bray-Curtis dissimilarities across four groups: HS-HEC (light red), HS-LEC (light blue), LS-HEC (green), LS-LEC (dark red). "HS", "LS", "HEC", "LEC" represent high and low organic matter, high and low electronic conductivity respectively.

3.2. Microbial co-occurrence networks

The bacterial network comprised a higher number of significantly co-occurring OTUs than the fungal network (Fig. 3a; Fig. 3b). Network connectivity, the average number of connections per OTU, was also higher in the soil bacterial network (Table 1). We found 177 bacterial and 13 fungal sOTUs in the networks, accounting for 44.47 % and 14.61 % of total 398 bacterial and 82 fungal network nodes (Table 1). Five modules contained sOTUs in the bacterial networks and three modules in the fungal network contained sOTUs (Fig. 3), and sOTU showed different responses to EC and SOM across modules (Fig. 3c; Fig. 3d; Table S4). For bacteria, M1 changed with EC ($F_{1,51} = 8.98$, $p < 0.01$), and in particular, species in genera of *Chloroflexi, Steroidobacterale,*

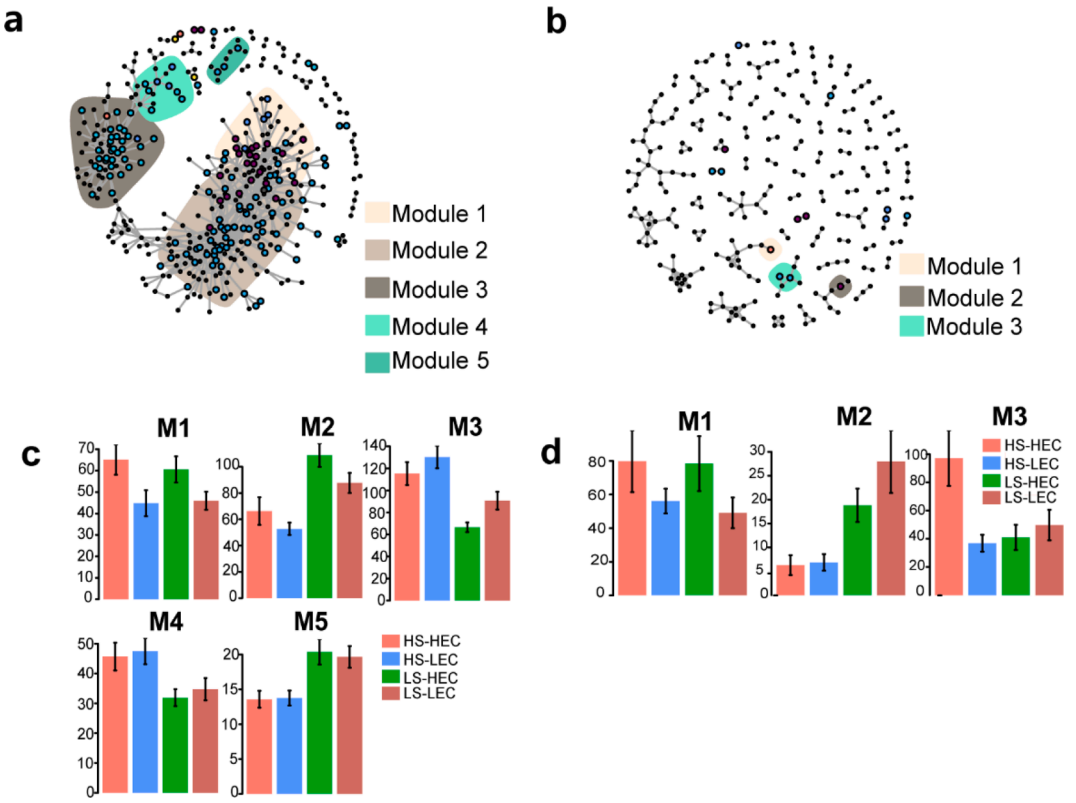


Fig. 3. Co-occurrence patterns of sensitive OTUs. Co-occurrence networks visualizing significant correlations ($R > 0.6$, $p < 0.01$; indicated with gray lines) between OTUs in bacterial (a) and fungal (b) communities. Shaded areas represent the network modules containing sOTUs. Cumulative relative abundance (as counts per million, CPM; y-axis in ×1000) of all bacteria (c) and fungi (d) of the sensitive modules (M) in the bacterial and fungi networks. The cumulative relative abundance in samples of HS-HEC (light red), HS-LEC (light blue), LS-HEC (green), LS-LEC (dark red) groups indicates the overall response of sensitive modules to the change of EC content and SOM content.

Table 1
Properties of soil bacterial and fungal co-occurrence networks.

	Node	Edge	Network connectivity	sOTU
Bacteria	398	947	4.76	177
Fungi	82	53	1.29	13

Gammaproteobacteria, Acidobacteriota and *Woeseia* were significantly enriched in high salinity treatment (Table S5). M4 and M5 were dramatically responsive to SOM ($F_{1,51} = 10.58$, $p < 0.01$; $F_{1,51} = 17.74$, $p < 0.01$). M2 ($F_{1,51} = 4.60$, $p = 0.03$; $F_{1,51} = 20.42$, $p < 0.001$) and M3 ($F_{1,51} = 5.16$, $p = 0.02$; $F_{1,51} = 23.24$, $p < 0.001$) were significantly influenced by both EC and SOM (Fig. 3c; Table S4). For species in M3 and M4, the abundance of *Rubrobacter, Microlunatus, Thermoleophilia, SBR1031, Latescibacteria, Myxococcota, Tepidisphaerales, Nitrosococcus and Nocardioidacea* were enriched in high SOM treatment (Table S5). For

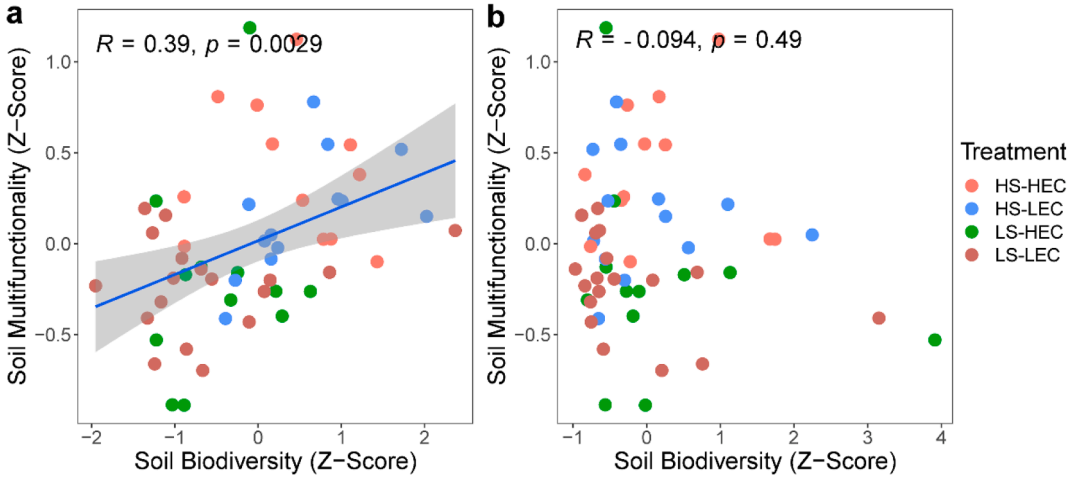


Fig. 4. Relationships between the bacterial (a) and fungal (b) diversity and soil multifunctionality for all 55 farms. Four colored circles represent different groups: HS-HEC (light red), HS-LEC (light blue), LS-HEC (green), LS-LEC (dark red). Solid blue line represents the fitted ordinary least squares (OLS) linear regressions. The gray shaded area shows the 95% confidence interval of the fit.

fungi, M1 contained sOTUs that were sensitive to EC ($F_{1,51} = 4.30$, $p = 0.04$) and M2 was affected by SOM content ($F_{1,51} = 13.83$, $p < 0.001$), whereas the sOTUs in M3 were sensitive to neither EC ($F_{1,51} = 1.75$, $p = 0.19$) nor SOM content. ($F_{1,51} = 0.57$, $p = 0.45$) (Fig. 3d; Table S4). However, we didn't find any taxonomic biomarkers of each module in the fungal network.

3.3. Relationships between microbial diversity and soil multifunctionality

We explored the relationship between soil microbial diversity and SMF using three metrics of multifunctionality: average, single function, and single-threshold approaches. For average approach, SMF was positively and significantly correlated with bacterial diversity (R = 0.39, $p < 0.01$) (Fig. 4a), and this was mainly associated with sensitive bacteria (R = 0.40, $p < 0.01$; R = 0.33, $p = 0.01$) across all four groups (Fig. 5a; Fig. 5c). For signal soil function, the total and sensitive bacterial diversity were positively correlated with carbon (R = 0.38, $p < 0.01$; R = 0.37, $p < 0.01$) and micronutrient cycling (R = 0.35, $p = 0.01$; R = 0.39, $p < 0.01$) (Table S6). A significantly positive relationship was observed between the relative abundance of sensitive bacteria and carbon cycling (R = 0.40, $p < 0.01$). However, no statistically significant relationships were found between fungal diversity (both total and sensitive community) and SMF (Fig. 4b; Fig. 5b; Fig. 5d) or any individual soil function (Table S6). For single-threshold approach, we also observed a positive relationship between bacterial diversity and soil multifunctionality at thresholds of 20 % (R = 0.39, $p < 0.01$) and 40 % (R = 0.30, $p = 0.03$) (Fig. S8).

At the phylum level, specific taxa of sOTUs affected SMF and soil single functions (Fig. 6). Carbon cycling and SMF were positively correlated with the abundance of *Armatimonadota*, *Entotheonellaeota* and *Myxococcota*, but negatively correlated with the abundance of *Methylomirabilota* and *MBNT15*. Carbon cycling was negatively correlated with the abundance of *Proteobacteria*, *Bdellovibrionoda*, *Firmicutes*, *Nitrospirota* and positively with *Planctomycetota* and *Verrucomicrobiota*. Phosphorus cycling was positively correlated with the abundance of *Bacteroidota*. Nitrogen cycling was positively correlated with *Firmicutes* and negatively with *Latescibacterota*, *Acidobacteriota* and *Cyanobacteria*. There were significantly positive relationships between micronutrient cycling and the abundance of *Cyanobacteria*, *Actinobacteriota*, *Myxococcota*, *Armatimonadota* and *Entotheonellaeota*, while negative relationships were observed with *MBN15* and *Desulfobacterota*. However, we didn't observe any significant relationship between soil multifunctionality, individual soil function and abundance of fungal sOTUs.

For individual group, we observed positive relationships only in the HS-LEC group, in particular between SMF and total bacterial diversity (R = 0.60, $p = 0.03$), and diversity (R = 0.66, $p = 0.01$) and relative

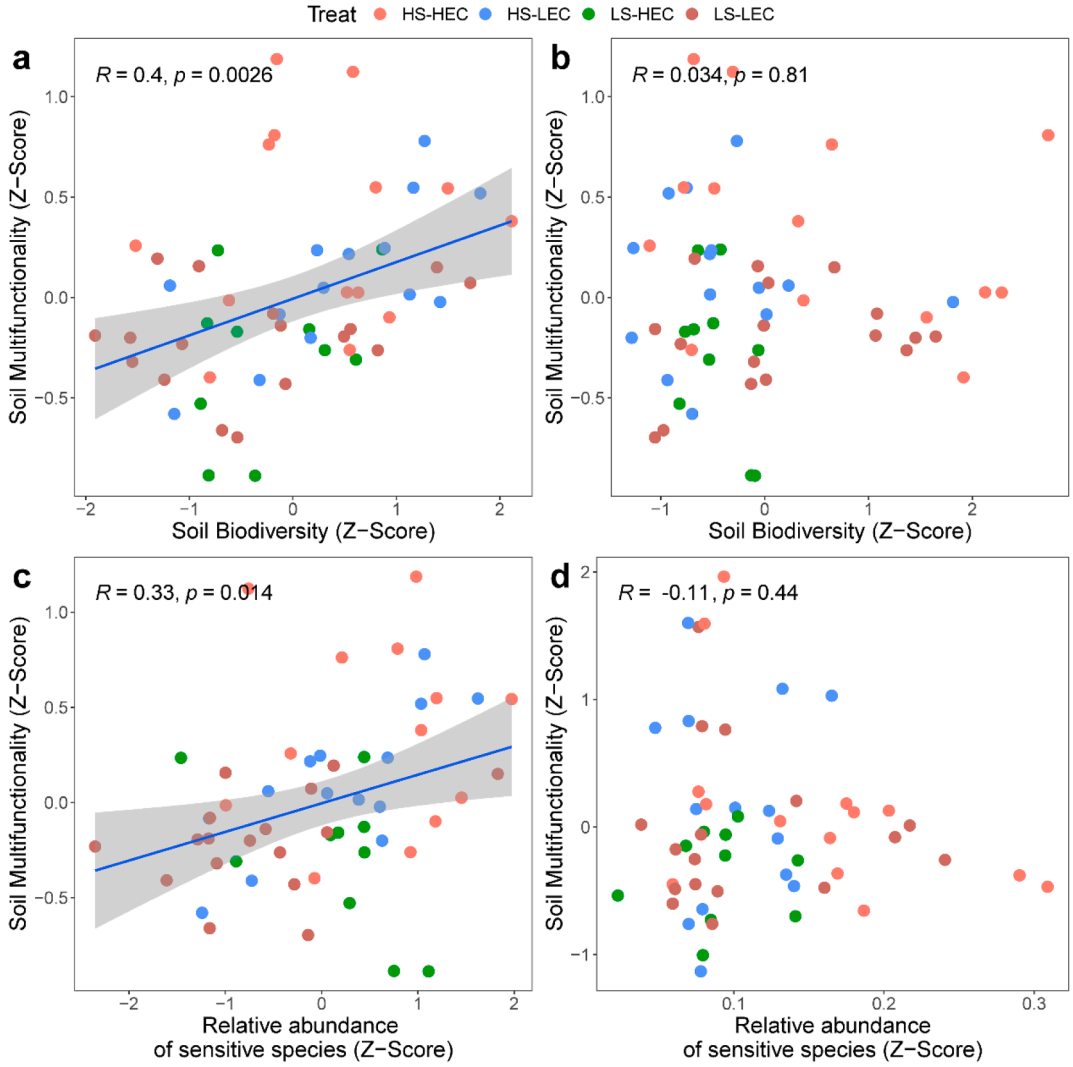


Fig. 5. Relationships between soil multifunctionality and diversity and relative abundance of bacterial (a, c) and fungal (b, d) sensitive microbes (sOTU). Four colored circles represent different groups: HS-HEC (light red), HS-LEC (light blue), LS-HEC (green), LS-LEC (dark red). Solid blue line represents the fitted ordinary least squares (OLS) linear regressions. The gray shaded area shows the 95% confidence interval of the fit.

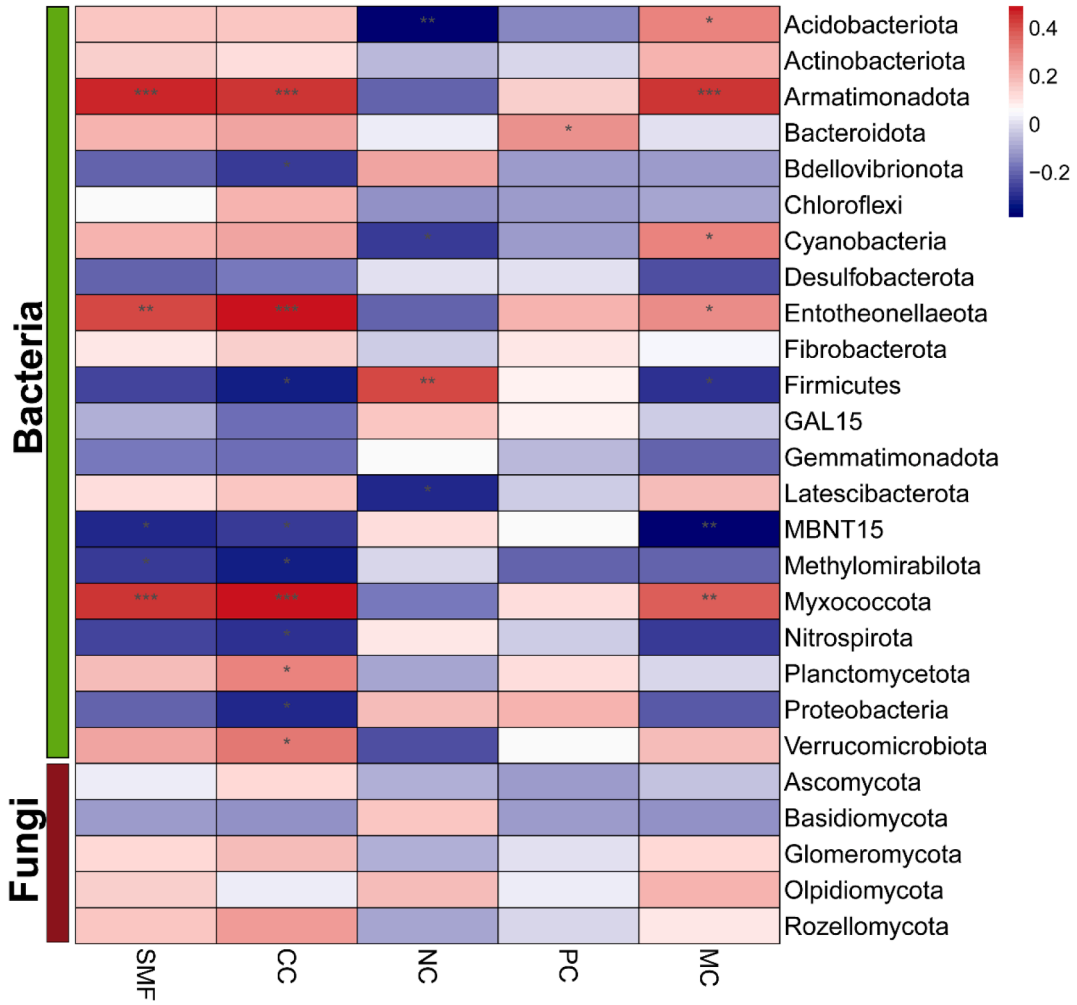


Fig. 6. Person correlations between soil functions and the abundance of sensitive microbes (sOTU) at phylum level. SMF: soil multifunctionality; CC: Carbon cycling; NC: Nitrogen cycling; PC: phosphorus cycling; MC: micronutrient cycling. "*", "**" and "***" indicate $p < 0.0$, $p < 0.01$ and $p < 0.001$ respectively.

abundance of sOTUs (R = 0.60, $p = 0.03$) (Table 2). For single functions, we observed positive relationships in the HS-LEC group between carbon cycling and bacterial sOTUs biodiversity (R = 0.57, $p = 0.04$) and the relative abundance (R = 0.73, $p < 0.01$) (Table S6). When we explored the single threshold approach, significant correlations were observed between the bacterial as well as sOTU abundance and SMF at thresholds of 20 % (R = 0.69, $p < 0.01$; R = 0.57, $p = 0.04$) and 40 % (R = 0.66, $p = 0.01$; R = 0.6, $p = 0.03$) in HS-LEC group (Table 3). And bacterial sOTU diversity was positively correlated with SMF at thresholds of 20 % (R = 0.55, $p = 0.05$), 40 % (R = 0.60, $p = 0.03$) and 60 % (R = 0.60, $p = 0.03$). We also observed significantly negative relationships between the fungal diversity and SMF (R = -0.62, $p = 0.02$) at 80 % (Table 3). In addition, specific taxa of bacterial sOTUs showed positive relationships with SMF and carbon cycling. The abundance of *Bdellovibrionoda* and *Myxococcota* were positively correlated with SMF, and the abundance of *Entotheonellaeota* and *Fibrobacterota* were positively correlated with carbon cycling (Fig. S9).

3.4. Direct and indirect effects of multiple drivers on soil multifunctionality

The SEM model was constructed to test the positive relationship between soil multifunctionality and bacterial diversity. The model explained 51 % and 73.0 % of the variance in SMF across all soil samples and in HS-LEC group (Fig. 7a; Fig. S10). SOM, diversity, and relative abundance of bacterial sOTU showed significantly positive effects on SMF (Fig. 7; Fig. S10). EC showed an indirect effect on SMF by affecting bacterial sOTU diversity. Bacterial sOTU diversity was the most important biotic factor contributing to SMF. These results indicated that diversity and relative abundance of bacterial sOTU rather than fungal sOTU explained SMF (Fig. 7; Fig. S10).

4. Discussion

4.1. Combined effects of EC and SOM on the soil biodiversity-multifunctionality relationship

The positive relationships between soil microbial diversity and SMF were affected by EC and SOM, and only occurred under HS-LEC condition (Table 2), which supports predictions from our first hypothesis. Consistent with our results, SOM increases enzyme activities in soils with low EC (<2.05 ds/m) (Dong et al. 2022). The importance of SOM in contributing to SMF is well established (Luo et al. 2018; Chen et al. 2020). As an indispensable energy and nutrient source for microorganisms, SOM availability is a key factor shaping microbial communities (Burns et al., 2016; Drenovsky et al., 2004). Soil organic matter tends to improve microbial diversity, and organic matter application in previously cultivated lands can increases diversity of soil organisms and soil substrates, which may stimulate growth of indigenous organisms (Bastida et al., 2021).

However, we observed low or no effects of high SOM on SMF under higher EC conditions, suggesting that the negative effect of soil salinity

Table 2
Relationships between soil multifunctionality and the bacterial and fungal diversity and diversity as well as relative abundance of sensitive microbes (sOTU). Value in bold indicates a positive relationship. * indicate $p < 0.05$.

Group	Microbial diversity	Soil multifunctionality	
		R	*p*
HS-HEC	Bacterial diversity	−0.17	0.60
	Fungal diversity	0.00	0.99
	Bacterial sOTU diversity	0.02	0.95
	Bacterial sOTU relative abundance	−0.22	0.49
	Fungal sOTU diversity	−0.24	0.46
	Fungal sOTU relative abundance	−0.54	0.07
HS-LEC	Bacteria diversity	**0.60**	**0.03***
	Fungal diversity	−0.073	0.812
	Bacterial sOTU diversity	**0.66**	**0.01***
	Bacterial sOTU relative abundance	**0.60**	**0.03***
	Fungal sOTU diversity	−0.074	0.811
	Fungal sOTU relative abundance	−0.353	0.237
LS-LEC	Bacterial diversity	0.22	0.49
	Fungal diversity	−0.21	0.50
	Bacterial sOTU diversity	0.15	0.65
	Bacterial sOTU relative abundance	−0.12	0.71
	Fungal sOTU diversity	−0.27	0.39
	Fungal sOTU relative abundance	−0.13	0.69
LS-HEC	Bacterial diversity	0.16	0.53
	Fungal diversity	−0.39	0.11
	Bacterial sOTU diversity	0.12	0.65
	Bacterial sOTU relative abundance	0.23	0.36
	Fungal sOTU diversity	0.29	0.25
	Fungal sOTU relative abundance	0.43	0.08

could diminish the positive effects of SOM (Table 2). It is likely that high salinity reduced microbial metabolism decreasing rates of organic matter degradation and nutrient release (Wichern et al., 2006; Dong et al., 2022). Consequently, the low fertility and buffering capacity of soils could exasperate the negative effects of salinity on SMF. The functional trade-offs could be another reason, as soil microorganisms allocate more energy to tolerate high salinity, resulting in the depletion of other soil functions (Kempf and Bremer, 1998; Oren, 2008). Lastly, low average SOM content (14 g/kg) observed in the study may constrain our ability to detect changes in SMF with the reduction of salt stress. In this study we added no external organic matter input, except for root residues. The addition of organic amendments (manures, vermicompost, compost) could alleviate the negative effect of soil salinity on soil microbial activities and functions by improving soil fertility and SOM (Azadi and Raiesi, 2021; Srivastava et al., 2016; Tejada et al., 2006).

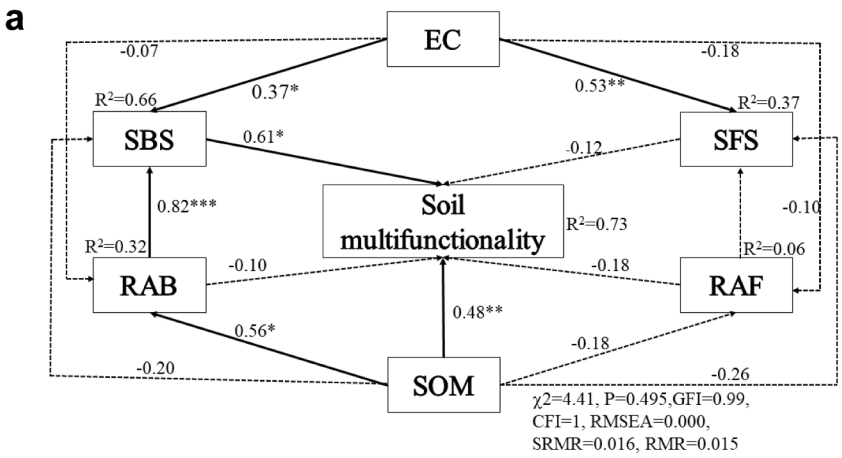
4.2. Sensitive bacteria drive soil multifunctionality

We found that bacterial, not fungal diversity was positively related to SMF in agroecosystems, which supported our second hypothesis. Consistent with our results, Han et al. (2022) found bacterial rather than fungal diversity drove SMF in a tea plantation. Agricultural soils suffer from frequent anthropogenic disturbances and disrupted microbial habitats, which impose more pressures that drive the turnover of soil community structure. Compared with fungi, bacterial community showed higher phylogenetic and taxonomic turnover under with frequent disturbance, resulting in higher niche complementarity in bacterial communities (Han et al., 2022). As a result, bacterial communities may have higher functional redundancy than fungal communities, making them better suited to withstand changes in the soil environment while maintaining SMF (Li et al., 2021b).

The positive correlation between bacterial diversity and SMF was mainly driven by sensitive microbes that were responsive to changes in EC and SOM (Fig. 5; Table 2). Among them, rare taxa accounted for a large proportion (80.3 %) of sensitive microbes (Table S3), which is further shown by the Chen et al. (2020) and Shu et al. (2021) as drivers of SMF. Rare taxa contain a broader range of metabolic functions compared to the abundant species (Chen et al. 2020; Shu et al. 2021). However, rare species have a limited ability to disperse and occupy relatively narrower ranging niches, which makes rare taxa more susceptible to changes in edaphic conditions (Wu et al., 2017; Wan et al., 2021a). The co-occurrence network supported this argument as we found sensitive OTUs formed different modules that were clustered together and were similarly responsive to SOM and/or EC conditions; which might reflect different functions. We observed the relative abundance of some sensitive bacteria in M3 and M4 of the network increased in the high SOM treatment and most microorganisms within have been found to play crucial roles in carbon cycling. Species from the genus of *Microlunatus* can produce glucosidase (Cui et al., 2007), while *Myxococcota* and *Latescibacterota* could be involved in the degradation of

Table 3
Relationships between soil multifunctionality and the bacterial and fungal diversity and diversity as well as relative abundance of sensitive microbes (sOTU) based on single threshold approaches. Value in bold indicates a positive relationship. * indicate $p < 0.05$; ** indicate $p < 0.01$.

		20 %		40 %		60 %		80 %	
Group	Microbial diversity	R	*p*	R	*p*	R	*p*	R	*p*
HS-HEC	Bacterial diversity	−0.35	0.26	−0.22	0.48	−0.21	0.52	−0.14	0.66
	Fungal diversity	0.03	0.93	−0.023	0.94	−0.08	0.8	−0.01	0.97
	Bacterial sOTU diversity	−0.15	0.65	−0.08	0.81	0.01	0.99	0.04	0.91
	Bacterial sOTU relative abundance	−0.27	0.39	−0.22	0.49	−0.32	0.32	−0.29	0.35
	Fungal sOTU diversity	−0.12	0.72	−0.28	0.37	−0.31	0.33	−0.33	0.29
	Fungal sOTU relative abundance	−0.48	0.11	−0.47	0.12	−0.51	0.09	−0.54	0.07
HS-LEC	Bacterial diversity	**0.69**	**<0.01****	**0.66**	**0.01***	0.53	0.06	0.47	0.11
	Fungal diversity	−0.02	0.96	0.05	0.88	0.16	0.6	0.29	0.34
	Bacterial sOTU diversity	**0.55**	**0.05***	**0.60**	**0.03***	**0.63**	**0.02***	0.52	0.07
	Bacterial sOTU relative abundance	**0.57**	**0.04***	**0.60**	**0.03***	0.53	0.06	0.47	0.11
	Fungal sOTU diversity	−0.16	0.6	−0.07	0.82	0.07	0.82	−0.1	0.73
	Fungal sOTU relative abundance	−0.27	0.37	−0.35	0.24	−0.54	0.06	**−0.62**	**0.02***
LS-HEC	Bacterial diversity	0.15	0.65	0.17	0.59	0.23	0.47	0.28	0.38
	Fungal diversity	−0.3	0.23	−0.28	0.27	−0.28	0.26	−0.26	0.3
	Bacterial sOTU diversity	−0.03	0.92	−0.04	0.89	−0.09	0.79	−0.14	0.65
	Bacterial sOTU relative abundance	−0.19	0.55	−0.22	0.5	−0.18	0.58	0.02	0.96
	Fungal sOTU diversity	−0.11	0.74	−0.03	0.94	0.09	0.77	0.14	0.66
	Fungal sOTU relative abundance	−0.11	0.73	−0.04	0.89	0.01	0.98	0.01	0.97
LS-LEC	Bacterial diversity	0.2	0.42	0.21	0.4	0.13	0.62	0.15	0.55
	Fungal diversity	−0.02	0.96	0.05	0.88	0.16	0.6	0.29	0.34
	Bacterial sOTU diversity	0.18	0.47	0.2	0.44	0.08	0.76	0.08	0.76
	Bacterial sOTU relative abundance	0.25	0.33	0.27	0.28	0.25	0.32	0.2	0.43
	Fungal sOTU diversity	−0.01	0.97	−0.1	0.7	−0.12	0.65	−0.11	0.66
	Fungal sOTU relative abundance	0.29	0.25	0.16	0.54	0.1	0.69	0.07	0.78



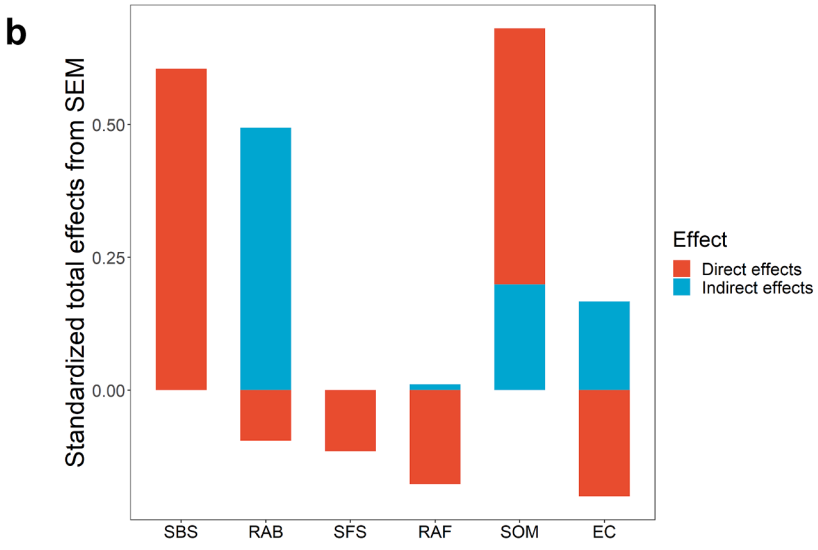


Fig. 7. Effects of abiotic and biotic factors on soil multifunctionality in HS-LEC group (a). * indicates $p < 0.05$; ** indicates $p < 0.01$, *** indicates $p < 0.001$, respectively. Continuous and dashed lines indicate significant and nonsignificant relationships, respectively. R^2 denotes the proportion of variance explained. (b) Standardized total effects (direct and indirect effects combined) derived from the structural equation model depicted above. SBS: bacterial sOTU diversity; SFS: fungal sOTU diversity; RAB: relative abundance of bacterial sOTU; RAF: relative abundance of fungal sOTU.

methyl and aniline, respectively (Langwig et al., 2022; Liu et al., 2021). However, we did not find evidence that fungal communities are driving SMF. It is well known that fungi play important roles in regulating energy and nutrient transport through their hypha structures (Cairney, 2005; Dighton, 2007; Holden et al., 2013). However, intensive agricultural practices, such as tillage and fungicide application, have destroyed soil structure and fungal hyphal extension, which would consequently affect fungal community functioning (Sofo et al., 2021). Additionality, fungi normally grow slower than bacteria (Smithee et al., 2014), and when measuring soil functioning in a short incubation period (*e.g.*, soil respiration), bacteria may be as stronger drivers because they recover faster after soil perturbation (sampling, sieving, *etc.*), while the fungal communities take longer (Sun et al., 2017).

4.3. The effects of responsive species on individual soil function

In our study, sensitive species were significantly correlated with different soil functions, which suggests that the performance of multiple soil functions may be widely distributed across different functional groups within the community (Bender et al., 2016; Delgado-Baquerizo et al., 2016). We found that carbon cycling showed similar patterns to those observed for the overall SMF (Fig. 6; Table S6), indicating the crucial role carbon cycling plays in agroecosystems (Luo et al., 2018). Furthermore, sensitive taxa from the phylum of *Armatimonadota*, *Entotheonellaeota*, *Planctomycetota*, *Verrucomicrobiota* and *Myxococcota* were the major contributors to carbon cycling (Fig. 6). In general, bacteria obtain energy from the decomposition of labile organic matter, while recalcitrant organic compounds usually act as primary energy source of fungi (Rousk et al., 2016). There is less recalcitrant organic materials and more labile substrates derived from straw decomposition in agricultural ecosystems (Li et al., 2022), which may stimulate bacterial rather than fungal growth, thus promoting carbon cycling. Species from *Armatimonadota*, *Entotheonellaeota*, *Myxococcota*, *Acidobacteriota* and *Cyanobacteria* promoted micronutrients cycling (Fig. 6). Micronutrient such as Fe, Cu, Mn, Zn are essential metabolites for both plants and microbes. Microbes have evolved various biosynthetic pathways to improve the bioavailability of metals, such as releasing chelating molecules, exudation of organic anions, and the promotion of reductive processes that facilitate mobilization (Rakshit et al., 2009; Hider and Kong, 2010; Sánchez-Rodríguez et al., 2013; Boiteau et al., 2018;). In calcareous soil with low micronutrient availability, microorganisms likely play a critical role driving micronutrient transport within the plant-soil system. And indeed, microbially driven micronutrient cycling has been linked to improving the micro-element content of crops (de Santiago et al., 2019).

Although some species like *Firmicutes* and *Bacteroidota* were involved in N and P cycling (Fig. 6), N and P functions were not predicted by overall microbial diversity. This was consistent with previous studies (Li et al., 2020; Chen et al., 2020) and likely largely due to a high input of chemical fertilizers in the fields managed by small farmers. Fertilization is one of the most common agricultural practices and has accelerated the degradation of soils resulting in both soil salinization and acidification (Guo et al. 2010). Salinization and acidification influence soil microbial community diversity and composition (Fig. S12), as well as a broad

range of critical ecosystem functions (Zhou et al., 2020). Furthermore, excessive nitrogen and phosphorus applications would alter ecosystem functions by causing nutrient imbalances (Huang et al. 2018). Microbial populations involved in soil nitrogen and phosphorus cycling change with altered soil C: N: P stoichiometry (Luo et al., 2020). Alternatively, the uncorrelated relationships between N and P cycling and microbial diversity suggest that a majority of microbes are involved in N and P turnover processes (Li et al., 2019), resulting in functional redundancy. Even loss of some species has negligible effect on overall functionality as other groups can replace the roles (Louca et al., 2018). These results indirectly emphasize the importance of organic matter in improving SMF and soil health in agriculture, by providing many functions like improvement of soil biodiversity and nutrient cycling, plant disease suppression, carbon sequestration enhancement, and the alleviation of soil salinization (Sall et al., 2015; Luo et al., 2018; Chen et al., 2020; Tao et al., 2020; Yang et al., 2021). Our results highlight the importance of improving SOM for improving SMF especially in previously cultivated lands.

5. Conclusions

In conclusion, our results demonstrate that soil salinity and organic matter have interactive effects on the positive relationship between soil biodiversity and multifunctionality in soils with low EC and high SOM. Additionally, we found soil multifunctionality responded positively to increased soil bacterial diversity but not fungal diversity, and sensitive bacteria were the main drivers. Soil multifunctionality was mainly derived from soil carbon and micronutrient cycling, but not by N and P cycling, suggesting negative effects of extensive chemical fertilizer application impair soil functions. These results highlight the importance of increasing both organic matter inputs and decreasing soil salinization to improve multifunctionality.

Declaration of Competing Interest

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

Data availability

Data will be made available on request.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.geoderma.2022.116273.

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