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Bacteria drive soil multifunctionality while fungi are effective only at low pathogen abundance

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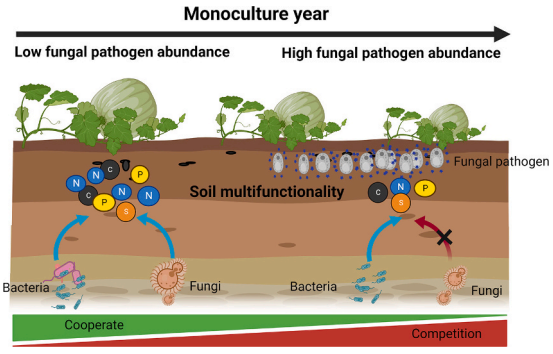
HIGHLIGHTS

- Abrupt shifts occurred at the fungal pathogen relative abundance of 0.01 based on Moving-window analysis.
- Bacterial richness contributed to multifunctionality regardless of fungal pathogen.
- Fungal richness promoted multifunctionality only in low pathogen abundance.
- Bacterial but not fungal community assembly drove soil multifunctionality.

GRAPHICAL ABSTRACT



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ABSTRACT

The positive correlation between soil biodiversity and multifunctionality has gained widespread recognition. However, the impact of plant pathogens on soil multifunctionality and its relationship with microbial diversity remains understudied. To address this knowledge gap, we collected soil samples from three Hami melon (*Cucumis melo L.*) planting sites with varying monoculture durations (1, 3, and 5 years). We sequenced the bacterial and fungal communities in these samples and quantified multifunctionality. The results revealed a significant increase in the relative abundance of fungal pathogens over the years of planting, which influenced the correlations between microbial diversity and multifunctionality at a threshold value of 0.01. Both bacterial and fungal richness positively influenced multifunctionality when fungal pathogen abundance was low (< 0.01), whereas only bacterial richness showed a positive correlation with multifunctionality under high fungal pathogen abundance (> 0.01) conditions. Both bacterial and fungal communities were primarily governed by deterministic processes. However, only bacterial community assembly drove soil multifunctionality, showing positive correlations with multifunctionality dissimilarity under low fungal pathogen abundance condition and negative correlations under high fungal pathogen abundance condition, reflecting distinct pathogen pressures. Structural

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equaling modeling further confirmed the distinct roles of bacterial and fungal richness and composition in promoting multifunctionality under different fungal pathogen condition. Our findings provide evidence that shifts in fungal pathogen abundance alter the balance and interactions between biodiversity and multifunctionality and highlight the importance of engineering biotic interactions in determining soil functioning in agroecosystems.

1. Introduction

Soil microorganisms act as engines that power and maintain multiple ecosystem functions (i.e. multifunctionality), such as nutrient cycling, litter decomposition and climate mitigation (Falkowski et al., 2008; Jensen et al., 2012; Bach et al., 2020). Soil microbial diversity, including bacteria (Jia et al., 2023), arbuscular mycorrhizal fungi (Ma et al., 2021), and fungal saprobes (Hu et al., 2021), has been found to be positively associated with SMF. However, the relationship of soil biodiversity-multifunctionality is contingent upon the specific context. Abiotic environmental factors such as fertilization (Luo et al., 2018; Chen et al., 2020), drought (Hu et al., 2021), soil pH (Dong et al., 2022), and salinity (Jia et al., 2023) can significantly impact SMF by influencing belowground microbial diversity. On the other hand, the effects of biotic factors on soil biodiversity-multifunctionality relationships have been largely unexplored. Although most crops are grown as annual plant species in monocultures, making them susceptible to pests and pathogens (Mulumba et al., 2012), the impact of pathogens on other microbial groups and community dynamics, and their subsequent consequences on soil multifunctionality, remain uncertain (Banerjee and van der Heijden, 2023). Understanding the potential effects of microbial functional groups and their interactions with ecosystem functions is essential for effective agricultural management.

The effects of fungal pathogens on SMF are likely dependent on the species and abundance of the pathogens, which are associated with the physiological conditions of the host plants (Guo et al., 2021; Wang et al., 2022). For instance, SMF was found to increase in soils infected with *Athelia rolfsii* in a peanut cropping system. The tissue rotting and necrosis caused by *A. rolfsii* enhanced the deposition of peanut residues, thereby improving nitrogen cycling (Guo et al., 2021). In contrast, SMF was significantly lower when potatoes were infected with *Alternaria solani*, which causes potato early blight and reduces the input of plant tissue into the soil (Wang et al., 2022). The discrepancies observed in different studies could be attributed to variations in pathogen characteristics and crop planting durations. Soil-borne pathogens that cause more root lesions tend to contribute to increased plant tissue decomposition, and continuous planting can lead to the accumulation of more pathogens. Moreover, an excessive presence of pathogens can impact the composition of other soil microbes, resulting in imbalances in soil nutrients and changes in soil biological enzyme activities, microbial functions, and activities (Creamer et al., 2022), with unpredictable effects on SMF. Therefore, examining the temporal dynamics of fungal pathogens on SMF is essential for predicting the responses of ecosystems to perturbations future ecosystem dynamics.

A healthy soil maintains a dynamic balance with higher microbial diversity, complex microbial networks, increased cooperation, and reduced competition among microbes. For instance, interspecific interactions and competition for resource help to control fungal pathogen populations to maintain soil health (Essarioui et al., 2020). However, in consecutive monoculture systems, pathogen populations are dynamic. In the initial years of planting with low pathogen abundance, both bacteria and fungi could function normally and promote SMF. Whilst under conditions of high fungal pathogen abundance, the proliferation and activities of non-pathogen fungal species may be restricted by competition from fungal pathogens, resulting in fungal community heterostasis and dysfunction (Grudzinska-Sterno et al., 2016). Bacterial species may further exploit the resources of certain fungal species due to niche overlap between bacteria and fungi (Boer et al., 2005; Guo et al., 2021). This asymmetric competition suggests that bacteria may play a more significant role than fungi under high pathogen conditions.

Furthermore, SMF can be influenced by microbial community assembly during ecosystem development and ecological succession (Metcalf et al., 2016; Graham and Stegen, 2017). However, the relationship between microbial assembly and ecosystem functions is not yet definitively established. Stochastic assembly processes dominate in communities with more positive species covariation, as they can mitigate the adverse effects of environmental changes and maintain ecosystem functions (Zhou et al., 2014). However, unbalanced stochastic processes with excessive dispersal may reduce ecosystem functioning by altering species composition (Leibold et al., 2017). Similarly, deterministic processes can enhance ecosystem functions by favoring certain species that perform well under specific environmental conditions (Graham et al., 2017) or reduce ecosystem functions if the selected species are not highly functional (Knelman and Nemergut, 2014). Under the influence of fungal pathogens, stronger selective forces may occur due to the occurrence of diseases, leading to increased environmental heterogeneity (Berendsen et al., 2018). Deterministic processes may increase with the abundance of pathogens due to intensified competition among species and environmental filtering. However, the regulation and impact of microbial community assembly processes under different fungal pathogen conditions on soil SMF performance have yet to be explored.

Continuous cropping could cause the accumulation of plant pathogens of Hami melon, in particular fungal pathogens (Li et al., 2023). Previous studies documented *Fusarium* and *Alternaria* were the two most deleterious pathogens for Hami melons inducing root rot and leaf spot diseases (Hanson et al., 2018; Naeem et al., 2019), and their absolute abundance increased significantly with the continuous cropping duration (Korir et al., 2020; Ku et al., 2022). In order to elucidate the soil fungal pathogen effect on the relationships between microbial biodiversity, community assembly processes and SMF, we sampled soils from Hami melon fields with different monoculture durations (1, 3, and 5 years).We quantified SMF based on carbon, nitrogen, phosphorus, and sulfur cycling functions, and sequenced microbial communities to assess the impacts of fungal pathogens on multifunctionality and the relationship between microbial communities and SMF. In this study, we hypothesize that (1) fungal pathogens will significantly impact soil microbial communities and multifunctionality, (2) both bacteria and fungi will promote SMF under low fungal pathogen condition, while bacteria will contribute more to multifunctionality than fungi under high fungal pathogen condition, and (3) deterministic processes of microbial community assembly will increase with the abundance of fungal pathogens and mediate SMF responses.

2. Materials and methods

2.1. Field experiment and samples collection

Soils were sampled in September 2022 from three sites located in Gaochang district, Turpan, Xinjiang province. The region experiences a continental arid climate characterized by an average annual temperature of 13.4 °C and an annual precipitation of 16.6 mm. The sampling sites were in three different towns: Erbao (ER), Qiatekale (KT), and Tuyugou (TY). The Hami melon fields at these sites had been subjected to monoculture planting for one (M1), three (M3), and five years (M5). Detailed information about the sampling sites can be found in the supplementary materials (Table S1). Each treatment had four blocks as

replicates. Five soil cores to a depth of 20 cm were collected and pooled to one composite sample in each plot using a 5 cm auger. Soil samples were sieved through 6 mm mesh in the field to remove plant roots, soil macrofauna and rocks, stored in a sealed container filled with dry ice and transported to the lab immediately after collection. The soil sample of each plot was divided into three subsamples, one part (~ 50 g) was used subsample was kept at 4 °C for soil multifunctionality measurement, the second one part (~ 150 g) was air-dried for soil property analysis, and the rest was stored at a temperature of −80 °C for DNA extraction.

2.2. Soil properties measurement and multifunctionality assessment

Soil pH, organic carbon (SOC), total nitrogen (TN), ammonium (NH_4^+) and nitrate (NO_3^-), available phosphorus (AP) and potassium (AK) were measured (Bei et al., 2018). Soil multifunctionality was quantified using the single function and averaging approach based on C, N, P, S cycling, soil basic respiration and denitrification (Byrnes et al., 2014; Delgado-Baquerizo et al., 2017). The four element cyclings were assessed based on soil extracellular enzyme activities (Bell et al., 2013). Carbon cycling process was estimated using *α-1,4 Glucosidase* (sugar degradation), *β-1,4 Xylosidase* (hemicellulose degradation), *β-1,4 Glucosidase* (sugar degradation), *β-Cellubiosidase* (cellulose degradation) and soil basic respiration. Nitrogen cycling process included *β-1,4-Nacetylglucosaminidase* (chitin degradation), *leucine-aminopeptidas* (nitrogen mineralization) and denitrification capacity. P cycling process used *acid phosphatase activities* (phosphorus mineralization) and S cycling used *sulfatase* (sulfate hydrolysis). Soil basal respiration was assessed by incubating 10 g of soil in a sealed serum bottle with a volume of 100 ml for 24 h at 25 °C. Denitrification capacity was measured using a short-term anaerobic assay protocol, briefly, 10 g soil was amended with 10 ml of 1.0 mM KNO_3 and 1.0 mM glucose, and 10 ml acetylene was incubated in a 100 ml evacuated serum bottle for 5 h. Carbon dioxide (CO_2) and nitrous oxide (N_2O) was measured by a gas chromatograph (7890 A; Agilent Technologies, Santa Clara, CA, USA) (Chen et al., 2020). The value of N_2O was done to reverse because an increase in N_2O levels reflects a negative effect of climate change, while a decrease represents the opposite. All these soil indicators were normalized to a range of 0–1 by maximum method ($f(x) = x_i/x_{max}$). Soil multifunctionality index and single-function index were calculated by taking the average of all the previously normalized values (Maestre et al., 2012).

2.3. Soil DNA extraction, sequencing and processing

Soil microbial DNA was extracted from 0.5 g of soil using the MoBio PowerSoil DNA Isolation Kit (MoBio Laboratories, Carlsbad, CA, USA) and kept at −80 °C for subsequent analysis. PCR amplifications were conducted using the primer pair 515F (5′-GTGCCAGCMGCCGCGGTAA-3′) and 806R (5′-GGACTACHVGGGTATCTAAT-3′) targeted the V4 region for bacteria and ITS3F (GCATCGATGAAGAACGCAGC) and ITS4 (TCCTCCGCTTATTGATATGC) primers targeted the ITS region for fungi. The PCR reactions of both bacteria and fungi were performed in a 20-μL volume with 2 μl dNTPs (2.5 mM), 4 μl 5 × FastPfu Buffer, 0.8 ul each per primer (5 μM), and 10 ng of template DNA. And then sample was amplified under the following conditions of 95 °C for 5 min, 37 cycles of 95 °C for 45 s, 50 °C for 30 s, and 72 °C for 45 s for bacteria and 94 °C for 3 min, 30 cycles of 94 °C for 45 s, 50 °C for 30 s and 72 °C for 45 s for fungi. All PCR products were sequenced on the Illumina Miseq platform (Illumina, San Diego, CA, USA). After the initial sequencing, the pair-end reads were subjected to quality control using Trimmomatic v0.39 (Bolger et al., 2014) to eliminate sequences with a quality score lower than 20. Subsequently, the pair-end reads were combined using Fast Length Adjustment of Short Read (FLASH v1.2.7). The merged sequences were then processed for denoising and chimaera filtering utilizing the 'USEARCH' algorithm (Edgar, 2010). Any reads that were shorter than 200 bp were excluded from further analysis. The high-quality reads were subsequently grouped into amplicon sequence variants (ASVs) using a 100 % identity threshold. Bacterial and fungal ASVs were assigned to SILVA database and the UNITE database, respectively.

Melons are prone to be attacked by soil fungal pathogens (Bezirganoglu et al., 2013). The FUNGuild database was utilized to classify the functional guilds of the fungal community based on trophic modes (Nguyen et al., 2016). Specifically, ASVs with a trophic mode classified as 'Pathotroph' and a guild assigned as 'Plant Pathogen' were identified as potential crop pathogens. The remaining ASVs were categorized into 'Symbiotroph' and 'Saprotroph'.

2.4. Statistical analysis

Two-way ANOVA was employed to examine the differences in soil microbial richness, SMF, and signal function and soil fungal pathogen abundance, with sampling site and monoculture duration year as the fixed variables. Non-metric multidimensional scaling (NMDS) based on Bray-Curtis dissimilarity was performed to assess the impacts of sampling site and monoculture year on soil microbial community structure in the "vegan" package in R. A moving-window analysis was performed to examine the variability of the biodiversity-multifunctionality relationship across different fungal pathogen abundance levels as described by Berdugo et al. (2019). For a subset window of 18 study sites with the lowest fungal pathogen values (chosen for adequate statistical power), we applied a linear mixed-effects model, as described in Eq. (1), and performed the calculations repeatedly for each remaining site (Berdugo et al., 2020; Hu et al., 2021).

$$\begin{aligned}\text{Soil multifunctionality} \sim\ & \text{pH} + \text{SOC} + \text{bacterial richness} + \text{fungal richness} \\ & + \text{fungal pathogen abundance} + \text{fungal pathogen abundance} \times \text{bacterial richness} \\ & + \text{fungal pathogen abundance} \times \text{fungal richness} + \text{fungal pathogen abundance} \\ & \times \text{bacterial richness} \times \text{fungal richness} + (1|\text{site}) + (1|\text{monoculture year})\end{aligned} \quad (1)$$

We also explored whether the presence of fungal pathogen modified the relationship between microbial diversity and SMF by linear regression. The model yielded a tipping point (i.e., threshold) of relative abundance of fungal pathogen that corroborated the shift in a given nonlinear relationship evaluated. To enhance the validation of the established thresholds for fungal pathogens as delineated in this study, we undertook an additional analysis involving the assessment of bootstrapped standardized coefficients concerning biodiversity. Moreover, we examined the interaction between biodiversity and fungal pathogens within each subset window, with a confidence level set at 95 %. Subsequently, we conducted *t*-tests to compare the slope and projected value before and after the implementation of each respective threshold. This approach aimed to further substantiate the findings and implications of our research. In order to further estimate the accuracy of the threshold, the "chngpt" was used to estimate threshold regression model and fit segmented regressions, and simultaneously, linear regressions at both sides of each threshold for each variable were bootstrapped to further check the validity of the thresholds identified. When fitting segmented regressions to models that are better fitted to smooth nonlinear continuous trends, segmented regressions provide the point of maximum curvature of the fit. This point can be considered a threshold in the sense that it shows a peak of change in the response of the variable to fungal pathogens abundance. Ordinary least squares (OLS) linear regressions were utilized to assess the associations between SMF and different microbial groups. Structural equation models (SEMs) were employed to evaluate relationships between soil properties, soil microbial diversity and SMF using AMOS 17.0 (SPSS, Chicago, IL, USA). Random forest regressions were performed to identify the primary microbial predictors of SMF at the family level. We constructed microbial co-occurrence networks using ASVs that were present at a relative abundance >0.01 % based on random matrix theory (RMT) to test the

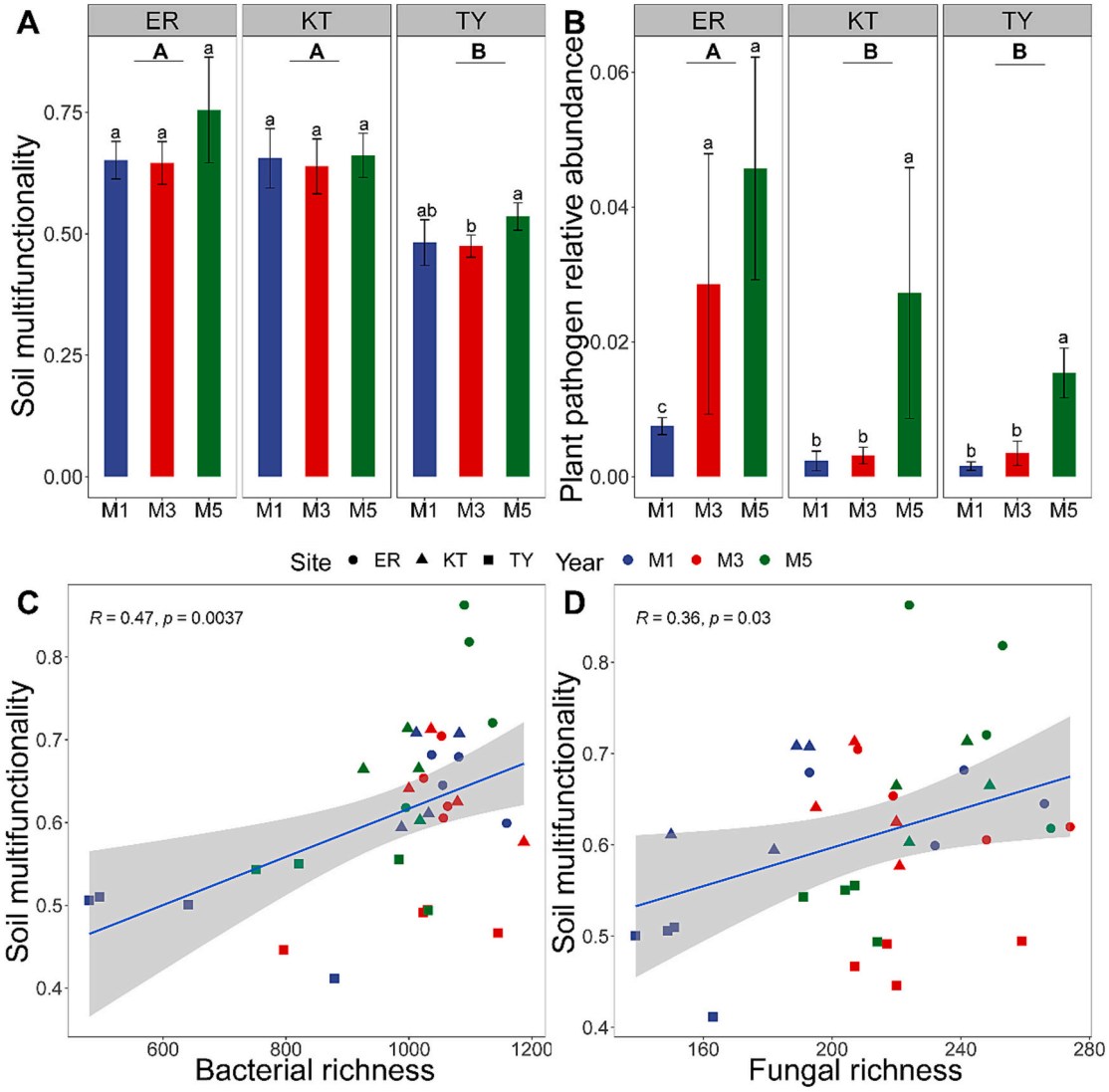

Fig. 1. Levels of soil multifunctionality (A) and the relative abundance of plant pathogens (B) were assessed across different monoculture years at three sampling sites. The relationships between soil bacterial diversity (C), fungal diversity (D), and soil multifunctionality were examined. The solid line represents the fitted ordinary least squares (OLS) linear regression, while the gray shaded area represents the 95 % confidence interval. Three shapes represent different sampling sites: ER (cycle), KT (triangle), TY (square) and three colors represent different monoculture year: M1 (dark blue), M3 (dark red), M5 (dark green).

Table 1
Linear mixed-effects model for the relationships between multiple biotic (bacterial richness, fungal richness, and fungal pathogen) and abiotic (pH, SOC) factors and soil multifunctionality with considering soil and vegetation types as random terms. * indicates $p < 0.05$; ** indicates $p < 0.01$, *** indicates $p < 0.001$, respectively.

	Estimate	Std. Error	df	t_{value}	Pr (>F)
(Intercept)	0.07	0.25	2.81	0.29	
pH	−0.11	0.34	25.88	−0.33	0.70
SOC	0.28	0.17	24.98	−0.76	0.01**
Bacterial richness	0.57	0.31	24.27	1.83	0.00**
Fungal richness	−0.19	0.25	25.95	−0.74	0.93
Fungal pathogens abundance	0.38	0.32	26.00	1.18	0.01*
Fungal pathogens abundance× Bacterial richness	0.28	0.44	25.83	0.63	0.52
Fungal pathogens abundance × Fungal richness	−0.24	0.27	24.83	−0.92	0.02*
Fungal pathogens abundance × Bacterial richness × Fungal richness	0.00	0.46	25.96	0.00	1.00

microbial interaction using the "microeco" package (Liu et al., 2021a). Network properties were assessed using the "igraph" package. Gephi software (version 0.9.1) was utilized for visualization of the correlation networks.

The "iCAMP" approach was employed to statistically quantify different ecological processes in shaping the soil microbial metacommunity based on Null model analysis (Ning et al., 2020). We generated the null model expectation by performing 999 randomizations, calculated β-Nearest-Taxa-Index (βNTI) as the difference between the observed β-Mean-Nearest-Taxon-Distance (βMNTD) and the average value of the null distribution of βMNTD, measured in units of standard deviation. A βNTI >2 indicates a significantly higher phylogenetic turnover than expected, suggesting the influence of heterogeneous selection in the community assembly process. Conversely, a βNTI < −2 indicates a significantly lower phylogenetic turnover than expected, indicating the presence of homogeneous selection. When |βNTI| < 2, stochastic processes shape the change of microbial community. We further calculated Bray–Curtis-based Raup–Crick (RC_{bray}) by measuring

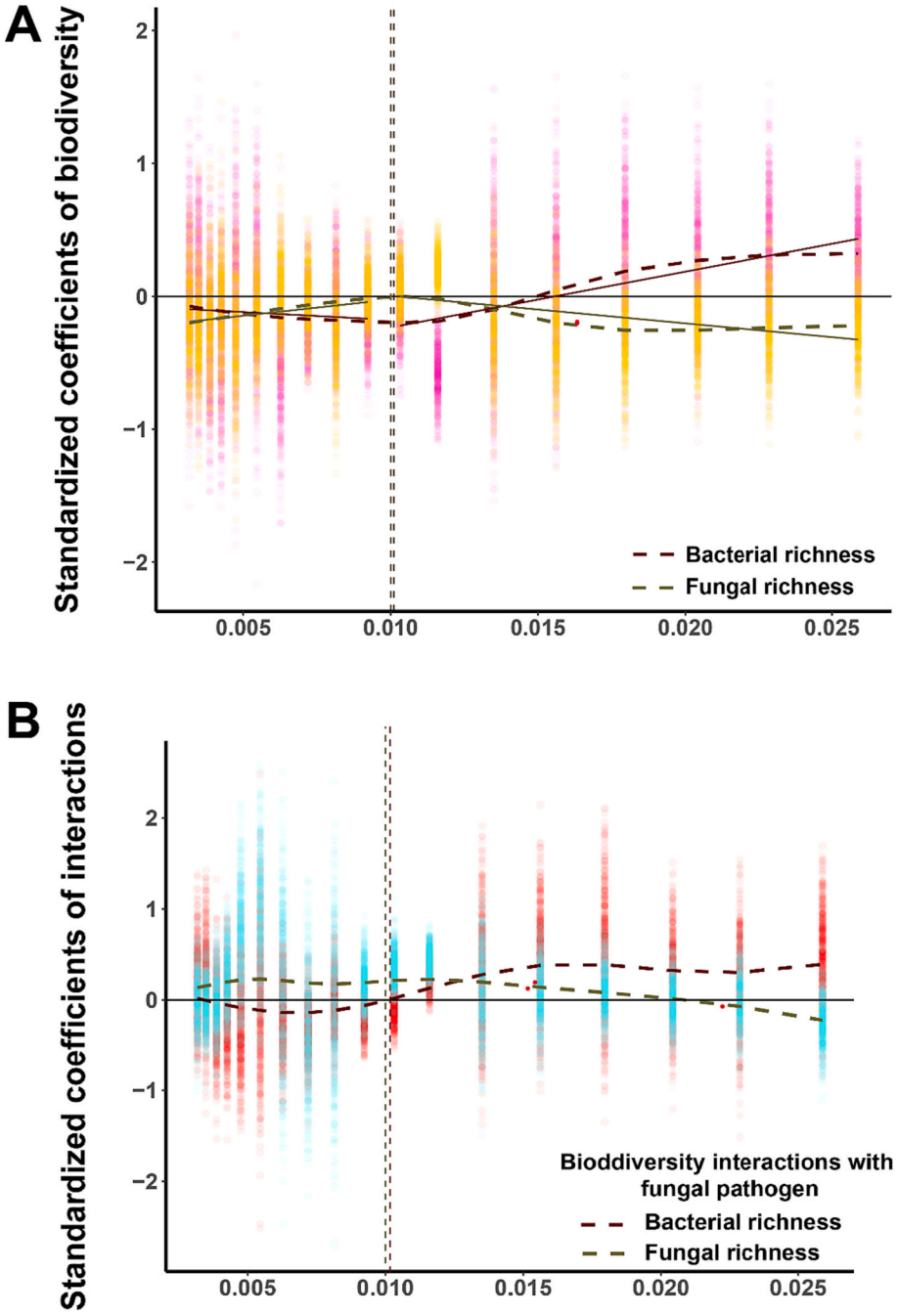

Fig. 2. Nonlinear changes in the standardized coefficients of biodiversity (A) and the interaction between biodiversity and fungal pathogens (B) were obtained using a linear mixed-effects model across a moving subset window of the surveyed field sites along the gradients of fungal pathogens.

the deviation between the observed Bray-Curtis dissimilarity and the null distribution to analyze the assembly processes within communities. When $|\beta NTI| < 2$ and $RC_{bray} < -0.95$, microbial community is shaped by a homogenizing dispersal process. Furthermore, when $|\beta NTI| < 2$ and $RC_{bray} > 0.95$, the community assembly is primarily driven by dispersal limitation processes, and $|\beta NTI| < 2$ and $RC_{bray} > -0.95$ refer to the drift processes (Stegen et al., 2013). A two-way ANOVA was employed to examine the differences in bacterial and fungal βNTI with sampling site and monoculture duration year as the fixed variables. Pearson correlations between microbial assembly processes and SMF were conducted using the Mantel test by "vegan" package, and the correlation coefficients and the significance were obtained with lm function.

3. Result

3.1. Assessment of soil properties, multifunctionality and characteristics of microbial community

Soil NO_3^-, NH_4^+, pH, AP, TN and SOC were significantly affected by both sampling sites and monoculture year while available phosphorus was only affected by sampling sites (Tables S2; S3). Across three sites, NO_3^- content was the highest in M3 treatment and NH_4^+ was the lowest in M3 treatment. There is not significantly different of soil pH, AP and TN in ER and KT site. In TY site, pH was the highest in M1 while the lowest in M3. The content of AP and TN was the lowest in M1 and the highest in M5. AK was only affected by monoculture year in ER site, which showed the highest in M1 and the lowest in M5. In ER site, SOC decreased with

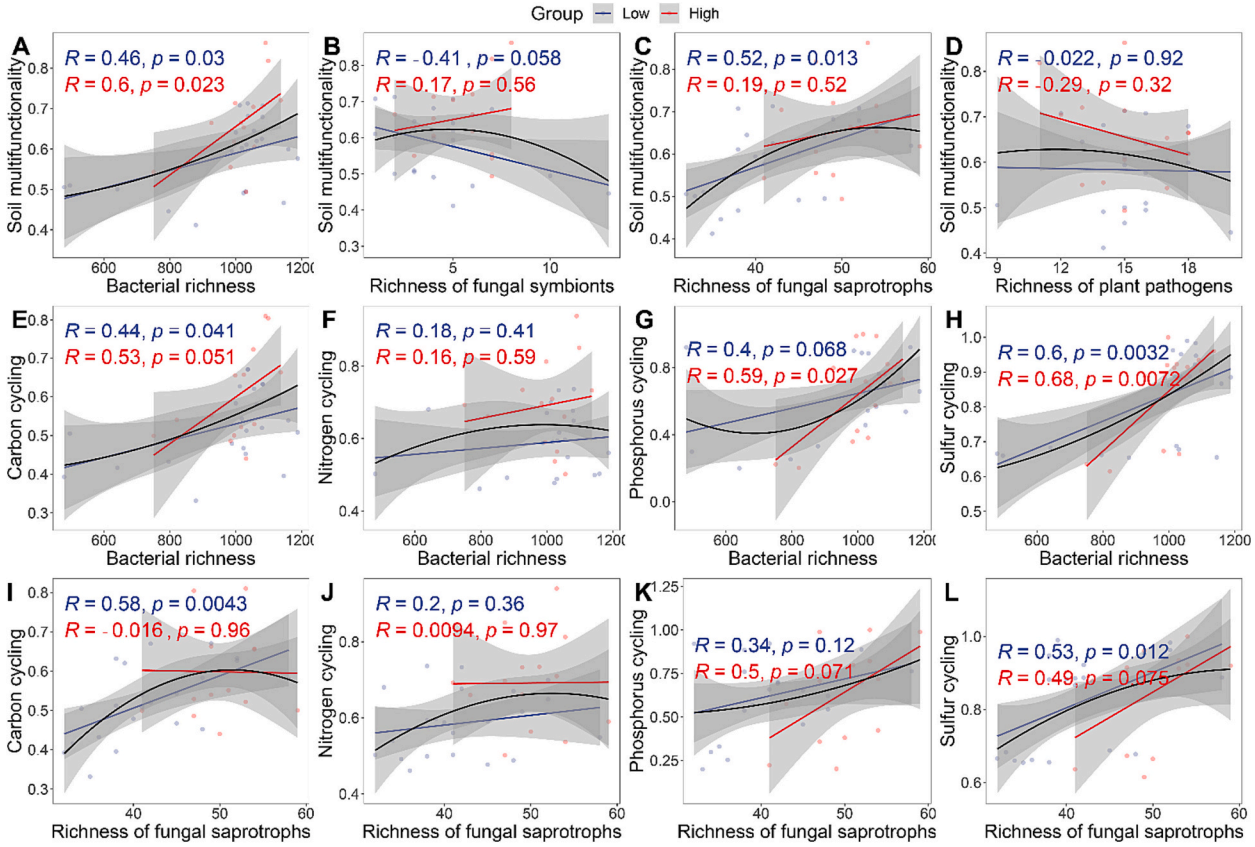

Fig. 3. Relationships between bacterial richness (A), richness of fungal symbionts (B), fungal saprotrophs (C) and fungal plant pathogens (D) and soil multifunctionality at sites with fungal pathogen abundance <0.01 (dark blue line) and > 0.01 (dark red line), as well as across all field sites (black line). Correlations between bacterial richness (E, F, G, H) and richness of fungal saprotrophs (I, J, K, L) and carbon, nitrogen, phosphorus and sulfur cycling at sites with fungal pathogen abundance <0.01 (dark blue line) and > 0.01(dark red line), as well as across all field sites (black line). Lines represent the fitted linear OLS mode Shaded areas denote the 95 % confidence interval of the regression lines.

the increase of monoculture year. In KT and TY sites, SOC was the highest in M5 and M1 while the lowest in M3. Both sampling site and monoculture year exhibited a significant impact on SMF, with a larger effect from the sampling site (Fig. 1A; Table S4). The SMF was significantly lower in TY compared to the other two sites, while no significant difference was found between ER and KT. However, in the TY site, the SMF in the M5 treatment was significantly greater compared to the M3 treatments (Fig. 1A). Regarding single functions, carbon, phosphorus, and sulfur cycling were only affected by the sampling site, while nitrogen cycling was influenced by both the sampling site and monoculture year (Fig. S1; Table S4). Carbon and nitrogen cycling were higher in the M5 treatment compared to the M1 and M3 treatments in the ER site (Fig. S1). Additionally, nitrogen cycling in the M3 treatment was the lowest in the TY site. Phosphorus cycling exhibited a declining pattern, with the lowest value observed in the M5 treatment. However, there was no significant difference in sulfur cycling across all treatments.

Microbial richness was influenced by both the sampling site and monoculture year (Fig. S2A, B; Table S5). Bacterial richness showed no significant difference among all monoculture years in the ER sites, while it was lower in the M1 treatment compared to the M3 and M5 treatments in the TY site. Furthermore, bacterial richness in M3 was significantly lower than M1 and M5. Fungal richness did not significantly differ among the treatments in the ER site. However, fungal richness was lowest in the M1 treatment in the KT and TY sites, while it was highest in M5 in the KT site and M3 in the TY site. Both soil bacterial and fungal communities were clearly separated based on monoculture year and sampling site, as supported by permutational multivariate analysis of variance (Fig. S2C, D). Fungal pathogens relative abundance was also significantly affected by the sampling site and monoculture year, showing an increasing trend with an increase in monoculture year across all three sites (Fig. 1B; Table S5). The abundance of five fungal pathogens including *Fusarium*, *Alternari*, *Podosphaera*, *Verticillium* and *Scopulariopsis* increased with the monoculture years (Table S6). *Fusarium* and *Alternari* were two most enriched genera in the M5 treatment.

3.2. *The effect of fungal pathogen on relationship of biodiversity-multifunctionality*

The results of OLS regression models revealed significant positive correlations between bacterial and fungal richness and SMF (Fig. 1C, D). The effects of bacteria on SMF were independent, while the effects of fungi interacted with fungal pathogen abundance (Table 1; Fig. 2; Fig. S3; Table S7). A moving-window analysis indicated an abrupt shift in the slope of the correlation between bacterial, fungal richness and SMF at a threshold value of 0.01 (Fig. 2A). The effect of bacterial and fungal richness on multifunctionality changed at 0.01. Before 0.01, the coefficients of bacterial richness gradually decreased, while the coefficients of fungal richness increased. After 0.01, the coefficients of bacterial and fungal richness showed opposite trends, which showed the coefficients of bacterial richness increased gradually, while fungal richness decreased. The patterns of standard coefficients of interactions between fungal pathogens and bacterial and fungal richness also shifted across the pathogen gradient, with an increasing trend for bacteria and a decreasing trend for fungi (Fig. 2B). The interaction term between plant pathogens and bacterial richness was statistically significant in both high and low fungal pathogen condition (Fig. S3). Additionally, the interaction term between plant pathogens and fungal richness was only statistically significant under conditions with low plant pathogens.

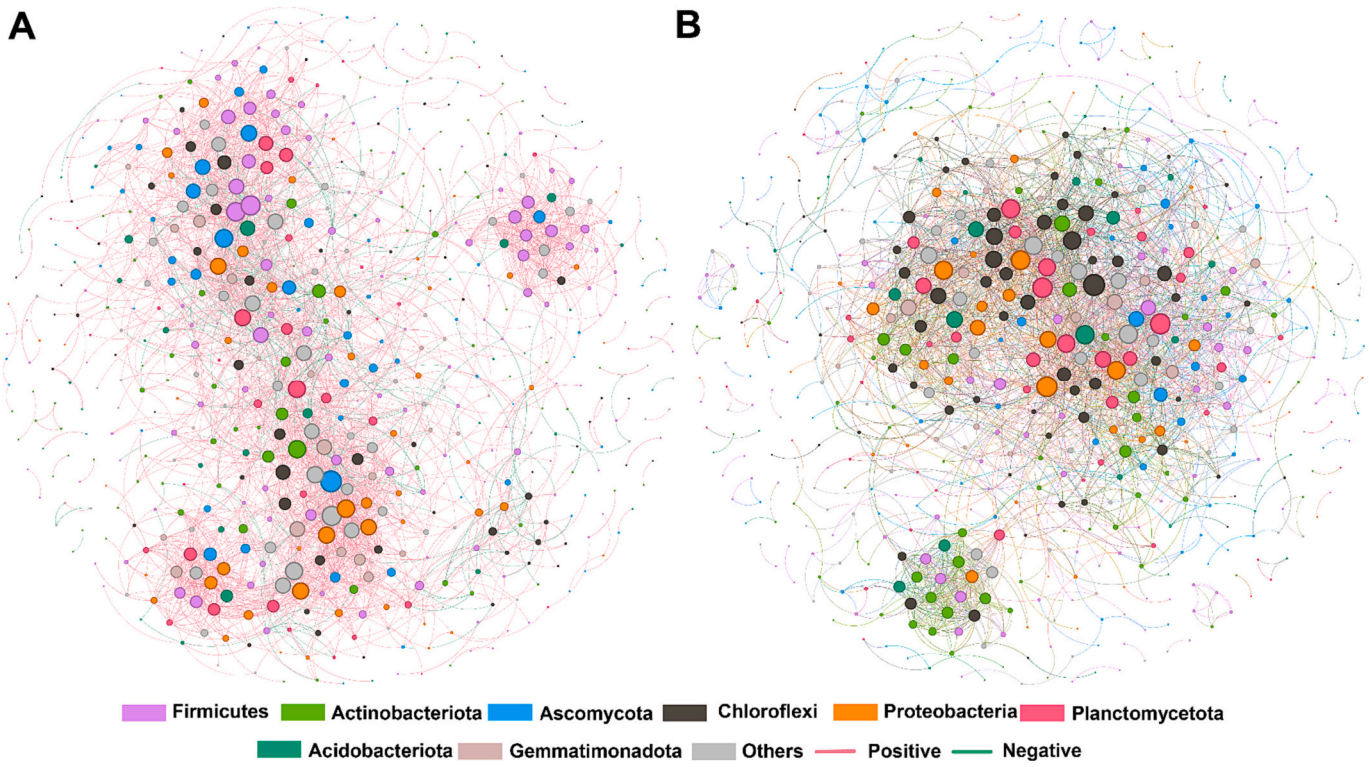

Fig. 4. Network visualization of microbial co-occurrence patterns under low (A) and high (B) abundance pathogens condition. The size of a node is proportional to the relative abundance of OTUs, and the width of each edge is proportional to the Spearman's correlation coefficient.

Table 2
Properties of soil microbial co-occurrence networks.

	Node	Positive edge	Negative edge	Average degree	Clustering coefficient	Betweenness centralization	Degree centralization	Modularity
Low	591	2517	318	9.59	0.41	0.08	0.07	0.58
High	582	2203	496	9.27	0.41	0.12	0.06	0.53

The study sites were further divided into two groups based on the relative abundance of 0.01: high vs. low plant pathogen conditions (Fig. 3; Fig. S4). SMF was observed to be positively related to bacterial richness and fungal saprotroph richness under low fungal pathogen condition (Fig. 3A, C), while it was only significantly correlated with bacterial richness under high pathogen conditions (Fig. 3A). Bacterial richness mainly contributed to carbon and sulfur cycling under low pathogen conditions (Fig. 3E, H) and to phosphorus and sulfur cycling under high pathogen conditions (Fig. 3G, H). Additionally, the richness of fungal saprotrophs contributed to carbon and sulfur cycling (Fig. 3I, L).

Microbial co-occurrence patterns were examined to further characterize microbial interactions under different fungal pathogen condition (Fig. 4). The results showed that fungal pathogens had a strong effect on network complexity. Microbial network complexity was higher at low pathogen abundance compared to high pathogen abundance (Fig. 4; Table 2). Moreover, it was observed that there were higher positive and lower negative interactions at low pathogen abundance, while high negative and lower positive interactions at high pathogen abundance (Fig. 4; Table 2).

The SEM model explained 45 %, 59 %, and 67 % of the variation in SMF, respectively (Fig. 5). Across all samples, soil organic carbon (SOC), bacterial richness, saprotroph richness, and fungal pathogen abundance had positive effects, while pH and fungal pathogen richness had negative effects on SMF (Fig. 5A). Consistent with the results of OLS regressions, bacterial richness and saprotroph richness were found to contribute to SMF under low fungal pathogen condition, while bacterial richness was positively related to SMF under high fungal pathogen condition (Fig. 5B, C).

3.3. Microbial community assembly processes and its correlations with SMF

We found deterministic processes of homogeneous selection were dominant in shaping both bacterial (100 %) and fungal (72 %) community assembly (Table S8). Compared to M1, the contribution of deterministic processes to the assembly of fungal communities increased by 45.90 % and 9.83 % in M3 and M5, respectively. Additionally, bacterial βNTI decreased with an increase in monoculture year, indicating that deterministic processes became stronger over time (Fig. S5). Consistent with the results of monoculture year analysis, it was also observed that the assembly of bacterial communities was primarily influenced by deterministic processes driven by homogeneous selection, which varied under different fungal pathogen conditions (Table S9). Furthermore, we performed mantel tests to assess the correlations between bacterial, fungal βNTI and SMF. It was found that bacterial βNTI, rather than fungal βNTI, was strongly associated with the variation in multifunctionality (Fig. 6A). Bacterial βNTI showed a positive relationship with multifunctionality dissimilarity under low fungal pathogen condition and a negative relationship under high fungal pathogen condition (Fig. 6B).

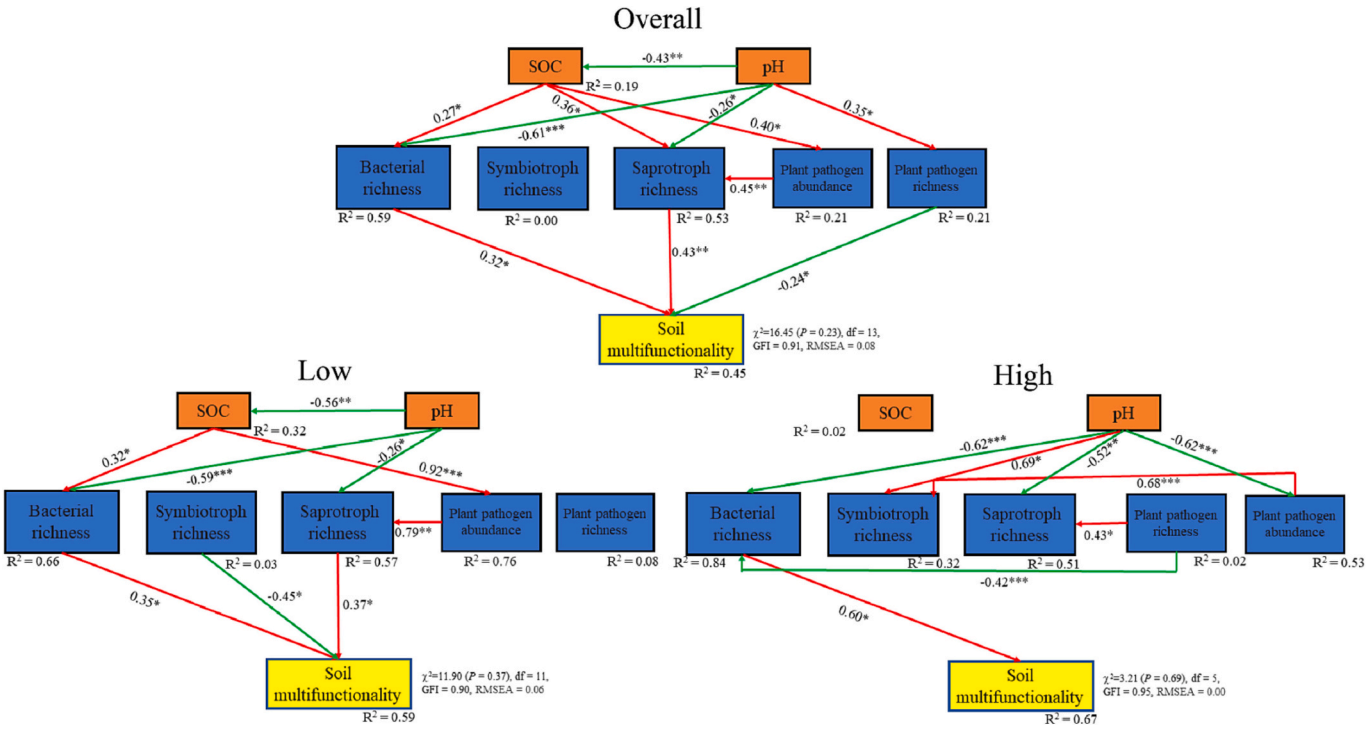

Fig. 5. Effects of abiotic and biotic factors on soil multifunctionality across overall sites and under low fungal abundance condition (sites with relative abundance of fungal abundance <0.01) as well as under high pathogen abundance condition (sites with relative abundance of fungal abundance >0.01). * indicates $p < 0.05$; ** indicates $p < 0.01$, *** indicates $p < 0.001$, respectively. Red and blue lines indicate positive and negative relationships, respectively. R^2 denotes the proportion of variance explained.

4. Predictors for soil multifunctionality

Random forest regressions were employed to identify microbial families which played crucial roles in driving SMF. The model explained 59.69 % of the variation in SMF across all samples. We identified twenty bacterial families and five fungal families as significant predictors of SMF (Fig. S6). Notably, bacterial species from *Planococcaceae* as well as fungal species from *Nectriaceae* emerged as the most important predictors at the family level. We further investigated the key microbial families as predictors of SMF under low and high abundances of fungal pathogens (Fig. 7). While both bacteria and fungi contributed to SMF in both conditions, more bacterial families were identified as predictors compared to fungal families. Specifically, 22 bacterial and 8 fungal families, along with 25 bacterial and 5 fungal families, were identified as essential predictors of SMF under low and high pathogen abundance condition, respectively. Moreover, more fungal predictors were observed under low pathogen abundance condition relative to high pathogen condition.

5. Discussion

5.1. Fungal pathogen abundance shifts the relationship between biodiversity and multifunctionality

The relationships between bacterial and fungal diversity and SMF varied depending on the abundance of fungal pathogens. Bacteria positively influenced SMF regardless of fungal pathogen levels, whereas fungi contributed to SMF only under conditions of low fungal pathogen abundance. Notably, the contribution of fungi to SMF at low pathogen abundance was mainly driven by fungal saprotrophs and their involvement in carbon and sulfur cycling (Figs. 3; 5). In conditions of low fungal pathogen abundance, microbial associations exhibited greater resilience to environmental changes and resource competition, resulting in more stable and beneficial relationships among microorganisms (Reynolds et al., 2003). This was reflected in the occurrence network, which displayed a more complex structure with increased positive connections (Fig. 4 and Table 2). Positive interactions among coexisting species, such as facilitation and mutualism, enhance the efficiency and performance of ecosystem functions (Zhang et al., 2022a, 2022b). The higher modularity of coexisting species indicates the occupation of distinct niches and the ecological functions of soil taxa with strong interactions, potentially enhancing community functional performance (Bruno et al., 2003; Ghoul and Mitri, 2016). Furthermore, the coexistence of multiple species enhances ecosystem stability and resilience (de Vos et al., 2017). A diverse community is better equipped to withstand disturbances, as the loss or decline of one species can be compensated by others, thereby contributing to the overall functioning and performance of the community (Elmqvist et al., 2003). In these contexts, both bacteria and fungi play roles in contributing to soil functions (SMF).

However, under conditions of high soil pathogen abundance, only bacteria, and not fungi, drove the positive relationship between microbial richness and SMF. The accumulation of pathogens can inhibit crop growth and limit carbon investment belowground, leading to increased resource competition among microorganisms (Mille-Lindblom et al., 2006). Bacteria, with higher phylogenetic and taxonomic turnover rates, exhibit greater versatility in resource utilization, enabling them to adapt quickly to changed conditions, establish themselves, and compete effectively (Han et al., 2022). Bacteria can exhibit antifungal activity through the production of antimicrobial substances or engage in direct interactions such as biofilm formation or the secretion of extracellular enzymes that degrade fungal cell walls (Schmidt et al., 2015; Köhl et al., 2019). The competitive advantage of bacteria and the inhibition of fungal growth and activities indirectly strengthen bacterial cooperation and activities (Hibbing et al., 2010), resulting in a positive effect on SMF.

Under conditions of high pathogen abundance, the intense competition for resources between fungal pathogens and non-pathogenic fungi often reduces microbial growth and functions (Becker et al., 2012; Yu

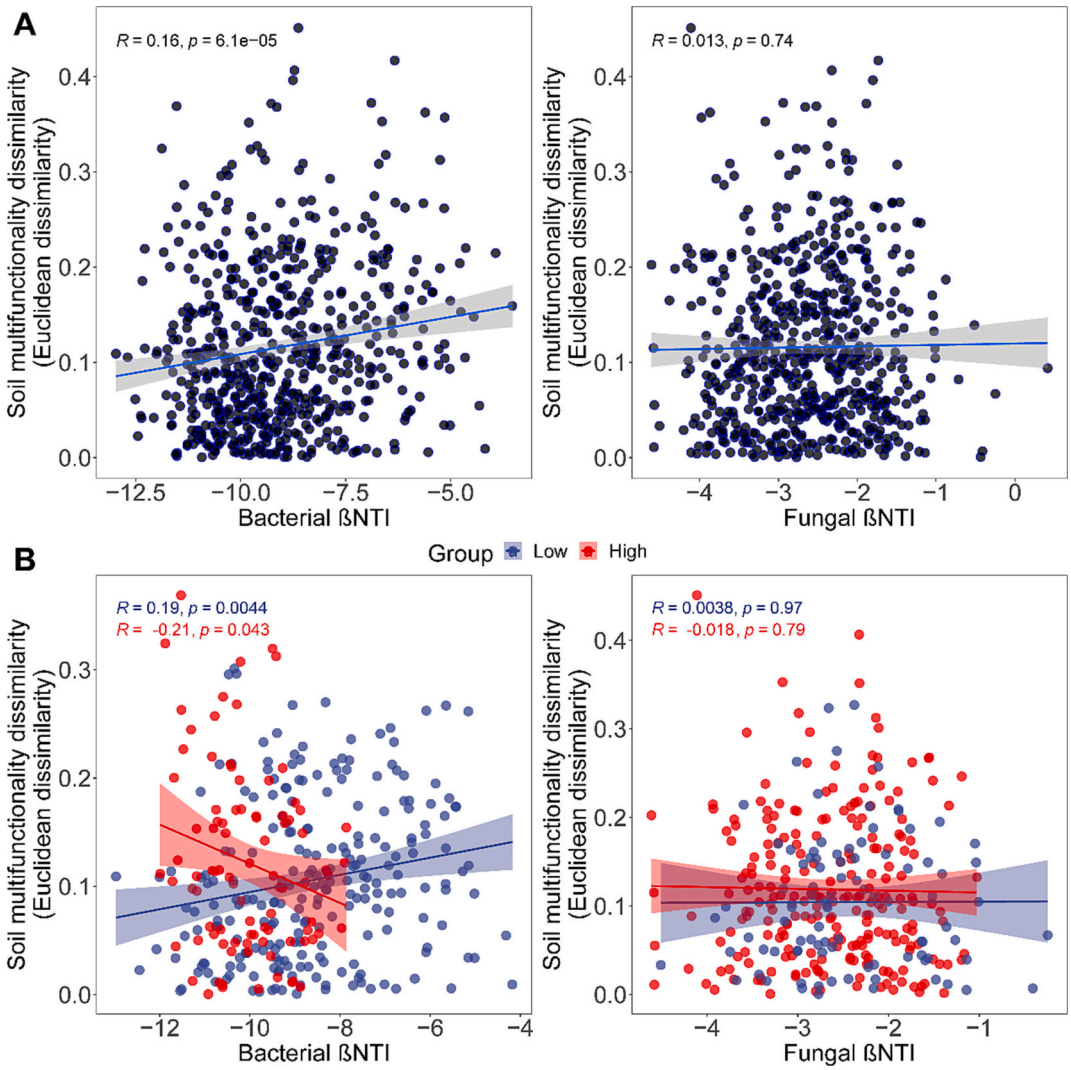

Fig. 6. Relationship between bacterial (A, C) and fungal (B, D) community phylogenetic turnover (βNTI) and multifunctionality dissimilarity at sites with fungal pathogen abundance <0.01 (dark blue line) and > 0.01 (dark red line), as well as across all field sites.

et al., 2019). Specifically, the abundant fungal pathogens can hinder the colonization and proliferation of arbuscular mycorrhizal fungi (AMF) due to their antagonistic effect on symbiotic associations (Porras-Alfaro and Bayman, 2011), thereby creating unfavorable conditions for mycorrhizal functions. Saprophytic fungi primarily rely on crop tissues or necrotic tissues as their main source of nutrients. Under low pathogen conditions, the decomposition of plant debris and growth of saprophytic fungi are stimulated, leading to an increase in SMF (Fig. 3C). However, under high pathogen conditions, soil pathogens can suppress the sporulation and growth of saprophytic fungi (Zeilinger et al., 2016), thereby limiting their contribution to carbon and nutrient cycling (Fig. 3I-L).

Furthermore, we observed that the impact of soil properties (pH and SOC) on SMF was consistent regardless of changes in pathogen abundance. Soil pH had negative effects on SMF while SOM showed positive effects. The soils were sampled from Xinjiang province which are mostly belong to alkaline soils. The reduction of soil pH in alkaline soils has shown to improve nutrient availability and cycling and enhance soil multifunctionality (Li et al., 2021). Soil pH can also influence soil multifunctionality by indirectly affecting soil biological richness. The positive effects of SOC on SMF have been widely documented. SOC act as an indispensable energy and nutrient source for microorganisms (Burns et al., 2016). SOC improvement tends to improve microbial diversity and soil substrates which may stimulate growth of indigenous organisms (Bastida et al., 2021). In this study, we mainly focused on the fungal pathogen because the host-specific pathogens of Hami melons are potentially to be fungi. However, pathogens are not just fungal pathogens. Although we did not study other pathogens (e.g. bacterial pathogens, oomycete), we speculated that the effect of soil microbial diversity on multifunctionality was similar under different pathogen abundance conditions. Under low bacterial pathogen condition, both bacterial and fungal diversity may promote soil multifunctionality while under high bacterial pathogen condition, the bacterial functions may be highly inhibited by pathogens and only fungal diversity could contribute to multifunctionality.

6. The bacterial ecological process contributes to soil multifunctionality

Deterministic and stochastic processes both affect the functions of microbial communities in biogeochemical cycles (Tilman, 2004; Zhang et al., 2016; Zhang et al., 2018). In our study, we observed significant positive relationship between bacterial βNTI and multifunctionality dissimilarity (Fig. 6A). Deterministic processes involve the influence of abiotic and biotic factors on the presence, absence, and relative abundance of microbial species (Dini-Andreote et al., 2015). In our study, the enhanced contribution of deterministic processes to bacterial assembly may result from the intensified environmental selection exerted by fungal pathogens. These selection pressures from fungal pathogens play

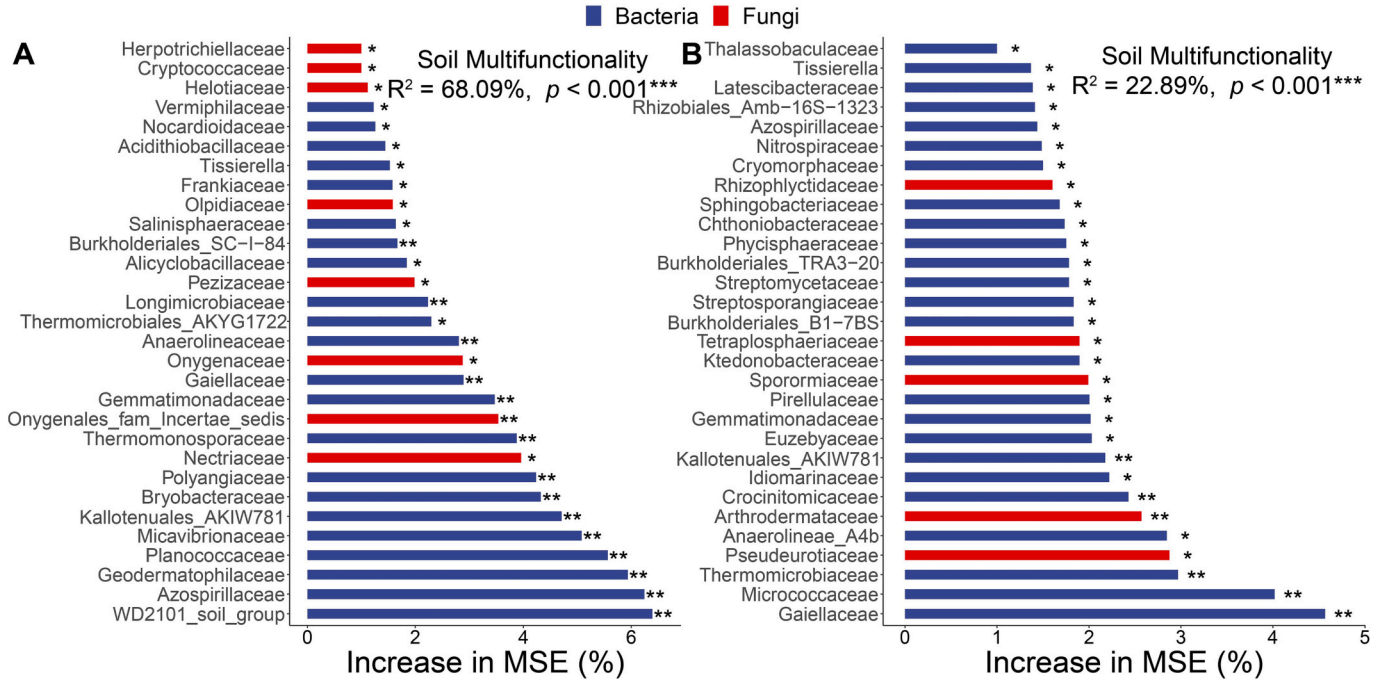

Fig. 7. Important microbial taxa as predictors of soil multifunctionality characterized by random forest regression under low (A) and high (B) fungal pathogen abundance. The figure shows the random forest mean predictor importance (% of Increase o MSE) of microbial families to soil multifunctionality. The colors are used to indicate different domains. Significance is indicated by $p < 0.05$*, $p < 0.01$**, and $p < 0.001$***.

a significant role in shaping the composition and structure of the bacterial community. Assembly dominated by determinism may lead to functional convergence, with high rates of functions but limited diversity (Liu et al., 2021b; Liu et al., 2022), which could negatively impact SMF under stronger determinism (Fig. 6A). However, this effect is context-dependent. The relationship between bacterial βNTI and dissimilarity in soil multifunctionality under low soil pathogen conditions aligns with the entire community, but the relationship turns positive under high soil pathogen conditions (Fig. 6B). The pressure exerted by fungal pathogens may lead to the recruitment of beneficial bacteria capable of suppressing pathogens (Liu et al., 2021c). The selected bacterial taxa through determinism-dominated assembly processes, driven by fungal pathogens, could enhance bacterial metabolism through species sorting mechanisms that optimize the microbiome for a given environment, thereby increasing ecosystem functions by favoring these particular bacterial species (Fig. 7B) (Lindström and Langenheder, 2012; Van der Gucht et al., 2007). In summary, the microbial assembly process appears to be related to soil multifunctionality by the alternations of bacterial community diversity and structure regulated by fungal pathogens.

6.1. The potential predictors of soil multifunctionality

Across all samples, the bacterial families *Planococcaceae* and *Azospirillum*, as well as the fungal families *Nectriaceae* and *Onygenales fam Incertae sedis*, were the main predictors of soil multifunctionality (Fig. S6). *Planococcaceae*, primarily consisting of the genus *Planococcus*, is enriched in healthy soil and includes denitrifying bacteria, which contribute to functions such as carbon degradation and phosphorus cycling (Ismail et al., 2021; Silva et al., 2022). *Azospirillum*, on the other hand, can enhance plant growth indirectly by altering the availability of nutrients like nitrogen and phosphorus, as well as by reducing plant diseases (Saharan and Nehra, 2011; Fukami et al., 2018). *Nectriaceae* is identified as a group of pathogens with the potential to degrade resistant plant material (Habtewold et al., 2020). Similarly, *Onygenales fam Incertae sedis*, which includes cellulolytic soil saprophytic fungi, tends to be enriched in diseased plant sites (Greif and Currah, 2007).

Furthermore, different bacteria and fungi were identified as predictors of soil multifunctionality under different conditions of fungal pathogen abundance (Fig. 7). The random forest regression model revealed that soil microorganisms had a higher explanatory power for soil multifunctionality under conditions of low fungal pathogen abundance compared to high fungal pathogen abundance. Under low fungal pathogen abundance, the bacterial *taxon WD21–01* was recognized as the most important predictor (Fig. 7A), likely due to its involvement in the degradation of plant cell wall components (Lewin et al., 2021). On the other hand, *Gaiellaceae* emerged as the most important bacterial taxon under high fungal pathogen abundance (Fig. 7B), and it has been found to be indicative of the carbon-to-nitrogen ratio and capable of decomposing plant residues (Hermans et al., 2017; Obermeier et al., 2020). Additionally, more fungal taxa were found to contribute to soil multifunctionality under conditions of low fungal pathogen abundance compared to high fungal pathogen abundance, providing partial support for our second hypothesis.

7. Conclusion

Overall, we found fungal pathogens are crucial factors in influencing the soil microbial diversity and multifunctionality relationships by mediating community structure and assembly processes. We observed a distinct shift for the soil biodiversity-multifunctionality relationships at a threshold of fungal pathogens relative abundance approximately 0.01 under field conditions. Both bacterial and fungal richness can promote soil multifunctionality under conditions of low fungal pathogen abundance (< 0.01), whereas only bacterial richness contributes to soil multifunctionality under conditions of high fungal pathogen abundance (> 0.01). Moreover, bacterial βNTI exhibits a positive relationship with multifunctionality under conditions of low fungal pathogen abundance, but a negative relationship under conditions of high fungal pathogen abundance. This study emphasizes the importance of fungal pathogens in mediating the biodiversity-multifunctionality relationship and highlights the need for implementing biodiversity conservation strategies to

mitigate the negative impacts of fungal pathogens on soil functioning and ecosystem services in agricultural ecosystems.

CRediT authorship contribution statement

Jiyu Jia: Methodology, Data curation, Investigation, Writing – original draft. **Guozhi Hu:** Methodology, Data curation, Investigation. **Gang Ni:** Investigation, Resources. **Muxi Xie:** Investigation, Resources. **Ruipeng Li:** Investigation, Resources. **Guangzhou Wang:** Resources, Supervision, Writing – review & editing. **Junling Zhang:** Supervision, Writing – review & editing.

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.scitotenv.2023.167596.

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