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Temporal variation of management effects on soil microbial communities

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ABSTRACT

Alpha and beta diversities are widely used to assess microbial community dynamics. However, little is known about the optimum sampling times for microbial alpha and beta diversity analysis between various cropland management systems across seasons, and whether changes in alpha and beta diversities of bacteria and fungi in response to temporal variation are synchronized. To investigate shifts in microbial alpha and beta diversities between soil environments caused by cropland management during the transition from winter to summer, a long-term field experiment was conducted under three different conditions: (1) natural regeneration after the cropland was abandoned, (2) mineral fertilizer application alone, and (3) 7500 kg ha^{-1} of wheat straw combined with mineral fertilizers incorporated into the cropland. Illumina HiSeq sequencing was performed, targeting the bacterial 16S rRNA V4-5 and fungal ITS1 regions. The results showed that the alpha and beta diversities of bacteria and fungi responded differently to seasonal change, and the temporal changes in beta diversity between treatments were not synchronized with those of alpha diversity. Compared to fungi, seasonal change had a more complex influence on soil bacterial beta diversity due to the interaction between land management and sampling time. Thus, using only one or a few sampling times within a season is an oversimplified approach when assessing bacterial beta diversity between land management systems and the impacts of environmental factors on bacterial diversity. For soil fungi, it was possible to assess their beta diversity between management practices without considering temporal variation. This research provides an opportunity to assess the effects of temporal variation on microbial diversity under various land management styles.

1. Introduction

Soil microbes play an important role in maintaining soil functions by driving soil processes, including soil structure maintenance, organic matter decomposition, and nutrient cycling, all of which are essential for plant growth in agricultural and natural ecosystems (Sengupta and Dick, 2015; Chenu et al., 2019; Geyer et al., 2019). As the largest components of the earth's biodiversity, microbial communities are known to be sensitive to spatiotemporal variation (Averill et al., 2019; Hermans et al., 2020). Investigating the effect of spatiotemporal variation on soil microbes can assist in predicting of microbial community functions and improving ecosystem management policies. The spatial processes shaping microbial communities are closely related to temporal variation (Richter-Heitmann et al., 2020). Thus, research based on only a single sampling period may fail to account for any fluctuations in the microbial community resulting from temporal variation. To solve the above problems, Hermans et al. (2020) highlighted the importance of adequate spatiotemporal replication of soil sampling. However, there still exists a knowledge gap regarding the connection between temporal variations in soil bacterial and fungal communities and spatial heterogeneity.

To evaluate the temporal state of soil microbial community variation across a heterogeneous environment, it is critical to understand the relationship between monitoring data from a single sampling site and inter-site diversity dynamics, and how diversity is maintained on various spatial scales. In ecology, alpha diversity and beta diversity have been widely used to assess changes in microbial communities. Alpha diversity refers to the number of taxa or operational taxonomic units (OTUs) and their abundance within communities or habitats (Whittaker,

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1972; He et al., 2015), while beta diversity is defined as the community composition dissimilarity between sampling sites or samples (Whittaker 1972; Anderson et al., 2011). Thus, it is possible for shifts in beta diversity to occur while alpha diversity remains stable, or vice versa (Gossner et al., 2013). An integrated analysis of alpha and beta diversity is therefore necessary when evaluating changes over time across multiple communities.

In agricultural ecosystems, various cropland management systems combined with seasonal changes provide a typical model for studying soil microbial spatiotemporal variation on a plot spatial scale. This is attributed to specific habitats with unique environmental conditions created by various cropland management systems as the seasons change. Compared with forests, grasslands, and other ecosystems, the cropland environment is more homogenous at the regional scale. To lessen the impact of spatial heterogeneity on microbial diversity and evaluate seasonal variations in alpha and beta diversity of soil bacterial and fungal communities, we selected croplands with heterogeneous soil properties caused by different long-term (1982–present) agricultural management systems, which consisted of straw return (WS) combined with mineral fertilization, mineral fertilization alone (NPK), and natural regeneration (NR). To determine how the soil bacterial and fungal alpha and beta diversities under various agricultural management systems respond under seasonal change, this research was conducted based on two hypotheses: (1) soil bacterial and fungal alpha diversities would respond similarly to the shift from winter to summer, and (2) the responses of soil bacterial and fungal beta diversities to seasonal change would also resemble one another.

2. Materials and methods

2.1. Experimental design and soil sampling

The selected croplands with various long-term (1982–2015) management systems were affiliated with the Academy of Agricultural Science of Anhui Province, China (32°14′N, 116°37′E). They consisted of (1) natural regeneration after the cropland was abandoned (NR), (2) mineral fertilizer application alone (NPK), and (3) 7500 kg ha^{-1} of wheat straw combined with mineral fertilizers incorporated into cropland (WS). During the experimental period, the monthly precipitation in January, February, March, April, May, and June of 2015 was 0 mm, 26.6 mm, 55.2 mm, 48.1 mm, 33.54 mm, and 383.7 mm, respectively (Fig. S1). For each treatment, there were three randomly arranged plots (approximately 70 m^2 for each plot). The soil was vertisol (Li et al., 2011), and the levels of mineral nitrogen, phosphorus, and potassium fertilizers applied were 180 kg ha^{-1}, 90 kg ha^{-1}, and 135 kg ha^{-1}, respectively. From 1982 to 2015, the rotation crops were winter wheat and soybeans, except for 1993–1997, when winter wheat and corn rotation was implemented. Before annual winter wheat planting, all mineral fertilizers and wheat straw were incorporated into the cropland, and no fertilization practice was conducted during the soybean growth season.

For the WS treatment, the wheat straw was cut into small pieces of < 5 cm and annually added to the cropland in mid-October before wheat planting. Then, the cropland was thoroughly tilled with a 20 -cm-deep plough. Finally, the winter wheat was sown in the WS and NPK plots on October 15, 2015. In this study, soil samples were collected from the 5–15 -cm layer in the NR, WS, and NPK treatments at 90 (winter) (D90), 120 (winter) (D120), 150 (spring) (D150), 180 (spring) (D180), 210 (summer) (D210), and 240 (summer) (D240) days after the winter wheat was sown on October 15, 2015. Simultaneously, soil temperature at a depth of 5 cm was also measured. For each plot, soil samples with six replicates were taken and combined, and then divided into two subsamples for the analysis of soil physicochemical properties and microbial properties. Before analysis, one subsample was air-dried, while the other was stored at −80 °C for DNA extraction after removing stones, roots, and plant materials using a 4–mm mesh.

2.2. Soil physicochemical analysis

The soil physicochemical properties referred to in this research were analyzed according to the method described by Bao (2005). Briefly, soil water content (SWC) was calculated using the ratio of evaporated water to dry soil after fresh soil was dried for 8 h at 105 °C. Soil pH was analyzed using a glass electrode (Mettler Toledo Instruments, Shanghai, China) with a soil to distilled water ratio of 1:2.5 (w/v). Soil organic matter (SOM) and total nitrogen (TN) were determined using the dichromate oxidation and Kjeldahl methods, respectively (Kieltec Foss 2200, Denmark) (Nelson and Sommers, 1982). The alkali distribution was used to conduct the soil available nitrogen analysis (AVN) (including NH_4^+-N, NO_3^--N, and other easily decomposable and hydrolysable forms of organic nitrogen), while the soil available phosphorus (AVP) and potassium (AVK) were measured using the molybdenum blue and flame photometry methods, respectively (Cany Precision Instrument Co., Ltd., Shanghai, China), after extracting the soil samples using sodium bicarbonate and ammonium acetate (Olsen et al., 1982). Soil dissolved organic carbon (DOC) and nitrogen (DON) were measured using a multi N/C 2100S analyzer (Analytic Jena, Überlingen, Germany) after passing a mixture of one part soil to five parts 0.5 M K_2SO_4 through 0.45-μm filters. Soil available nitrate (NO_3^--N) and ammonium (NH_4^+-N) were analyzed using a continuous flow analytical system after extracting the mixtures of 5 g fresh soil and 50 mL 2 M KCl.

2.3. PCR and amplicon library preparation

Approximately 0.5 g of fresh soil was used for total DNA extraction with an MP Fast DNA^{TM} SPIN Kit (MP Biomedicals, Solon, OH, USA). The concentration and purity of the collected DNA were measured on 1% agarose gels, and then diluted to 1 ng/μL using sterile water. The V4–V5 regions of the bacterial 16S rRNA and internal transcribed spacer region (ITS) of fungi were amplified using the primer pairs 515F/806R and ITS5/ITS2, respectively (Bellemain et al., 2010; Caporaso et al., 2011) (Supplementary Material 2). The PCR was conducted in 30-μL reaction mixtures containing 15 μL Master Mix (New England Biolabs), 0.2 μm M/l of each primer, 10 ng template DNA, and ddH_2O. The amplification conditions consisted of initial denaturation at 98 °C for 1 min, followed by 30 cycles of 98 °C for 10 s for denaturation, 50 °C for 30 s for annealing, 30 s for 72 °C for elongation, and then final extension at 72 °C for 5 min. The collected PCR products were mixed, purified using a GeneJET Gel Extraction Kit (Thermo Scientific, Waltham, MA, USA), and qualified using the Agilent Bioanalyzer 2100 system and a Qubit 2.0 Fluorometer (Thermo Scientific). Finally, the library was sequenced to generate 250-bp paired-end reads using an Illumina HiSeq Platform at Novogene Bioinformatics Technology Co., Ltd. (Beijing, China).

2.4. Processing of sequence data

After merging using FLASH, the collected paired-end reads were assigned to samples based on the unique barcodes when there were overlaps between reads 1 and 2 (Magoč and Salzberg, 2011). Raw data were processed by QIIME1 (Caporaso et al., 2010). Sequences were quality filtered, and sequences shorter than 200 bp and with a quality score lower than 25 were deleted. The chimeric and singleton sequences were also removed using UCHIME (Edgar et al., 2011). The obtained sequences of bacteria and fungi were clustered into OTUs at 97% sequence similarity. For assignment of the OTUs, the representative sequences were annotated using the RDP classifier for bacteria and the Unite database for fungi (Wang et al., 2007; Kõljalg et al., 2013). To calculate alpha diversity, including the Shannon diversity index and total observed species, all samples were rarefied to the same sequencing depth (see Fig. S2). For bacterial and fungal beta diversity, Aitchison distance was computed by the phyloseq package in R Statistical Software v 4.0.3 (R Development Core Team) (McMurdie and Holmes, 2013). To

evaluate the temporal state of bacterial and fungal taxonomic lineages as the seasons changed from winter to summer, we also calculated the beta diversity of 12 of the most abundant phyla and classes of bacteria and four of the most abundant fungal phyla. The 12 phyla of bacteria were Alphaproteobacteria, Betaproteobacteria, Gemmatimonadetes, Deltaproteobacteria, Acidobacteria, Actinobacteria, Planctomycetes, Chloroflexi, Bacteroidetes, Gemmatimonadetes, Verrucomicrobia, and Nitrospirae, and the four fungal phyla were Ascomycota, Basidiomycota, Chytridiomycota and Glomeromycota. The raw data were deposited in the Sequence Read Archive (SRA) of the National Center for Biotechnology Information (NCBI) with the BioProject accession numbers PRJNA677798 for bacteria and PRJNA637863 for fungi.

2.5. Statistical analyses

The soil microbial community composition and alpha diversity, including the Shannon indexes and the total observed species, were analyzed through a repeated-measure analysis of variance using SAS 9.4 software (SAS Institute, Cary, NC, USA). For the analysis of the effects of treatment and sampling time on the soil microbial community structure, permutational multivariate analysis of variance (PERMANOVA) was used (Anderson, 2001; Zhang et al., 2021). The pairwise dissimilarity (beta diversity) between treatments or seasons was analyzed using multi-response permutation procedure (MRPP) analysis based on Aitchison distance (McMurdie and Holmes, 2013). Prior to above analysis, the bacterial and fungal community data and subparts of these communities were transformed using a centered log-ratio transformation (Gloor et al., 2017). To further analyze the changes in community composition, the DESeq2 package in R was used to calculate and plot the enriched or depleted OTUs between treatments based on a Hellinger-transformed version of the OTU table. We used Spearman's rank correlation coefficient to examine the relationships between the environmental factors and the microbial alpha diversity indexes. The environmental factors referred to in this research included temperature, precipitation, soil pH, SWC, SOM, TN, NH_4^+-N, NO_3^--N, AVN, AVP, DOC, and DON. To test the significance of the impact of each environmental factor on microbial communities, a stepwise forward model selection based on AIC values and partial methods of constrained ordination (partial RDA) were applied using the vegan package in R software (Lai and Mi, 2005). The results of Spearman's rank correlation between environmental factors and soil bacterial and fungal alpha diversity were plotted using the pheatmap package in R software (Kolde and Kolde, 2015).

3. Results

3.1. Soil microbial alpha diversity

In all, there were 3,753,329 reads and 202,923 OTUs from 54 samples for bacteria, and 2,729,809 reads and 64,767 OTUs for fungi. The average number of high-quality sequences per sample was 69,506, ranging from 60,310 to 77,891 for bacteria, while the average was 50,552 ranging from 33,896 to 73,836 for fungi (see Table S1). Cropland management and sampling time both had significant ($p < 0.05$) effects on the alpha diversity of the bacterial community, while only sampling time significantly affected the alpha diversity of fungal communities (Table 1). From D90 to D240, the total observed species and Shannon index for bacteria decreased significantly (Figs. 1a and 2b; Table S2), whereas considerable increases were observed in both values for fungi (Fig. 1c and Table S2).

3.2. Soil microbial beta diversity

Cropland management and sampling time both significantly altered the soil microbial community structure (Table 1, Table 2, and Table S3). For the major bacterial community groups, except for Acidobacteria and Bacteroidetes, the cropland management system, sampling time, or a combination of both factors played significant roles (Table 1). As shown in Fig. 2a and Table S4, Alphaproteobacteria, Acidobacteria, Betaproteobacteria, Gammaproteobacteria, Actinobacteria, Planctomycetes, and Deltaproteobacteria were the dominant phyla in all treatments, accounting for more than 75% of the sequences for each sample, and these were significantly affected by both cropland management and sampling time (except for Acidobacteria and Planctomycetes) (Table 1). For the Planctomycetes, which were only significantly affected by sampling time, their relative abundances under NR at D240 increased by 10.98%, while they decreased by 24.48% in the WS treatment and 31.08% in the NPK treatment in comparison with D90 (Table S4). In addition, Gemmatimonadetes were significantly affected by sampling time alone. Compared with D90, the relative abundances of

Table 1
Repeated measure ANOVA test of the effects of treatment, sampling time and their interaction on bacterial and fungal community composition at the phylum or class level.

Alpha diversity / community composition	Treatment		Time		Treatment*Time	
	F	p	F	p	F	p
Bacterial Shannon index	16.07	<0.01**	29.63	<0.001***	1.61	0.15
Bacterial Observed species	10.36	0.01*	60.55	<0.001***	1.70	0.13
Fungal Shannon index	2.01	0.21	5.25	0.02*	1.19	0.34
Fungal Observed species	0.85	0.47	8.38	<0.01**	1.06	0.42
Alphaproteobacteria	6.94	0.03*	9.98	<0.001***	1.11	0.39
Betaproteobacteria	8.35	0.02*	26.42	<0.001***	4.81	<0.001***
Gammaproteobacteria	6.90	0.03*	3.88	<0.001**	0.72	0.70
Deltaproteobacteria	23.17	<0.01**	10.70	<0.001***	2.25	0.04*
Acidobacteria	3.58	0.09	0.81	0.55	1.65	0.14
Actinobacteria	6.09	0.04*	2.80	0.03*	1.39	0.23
Planctomycetes	1.49	0.30	13.32	<0.001***	1.05	0.43
Bacteroidetes	1.21	0.36	2.17	0.08	0.31	0.97
Gemmatimonadetes	0.10	0.91	10.32	<0.001***	2.34	0.04*
Chloroflexi	35.51	<0.001***	16.61	<0.001***	1.78	0.11
Verrucomicrobia	8.75	0.02*	4.28	<0.001**	1.26	0.30
Nitrospirae	31.26	<0.001***	9.28	<0.001***	0.88	0.56
Basidiomycota	0.53	0.61	0.97	0.45	1.56	0.17
Ascomycota	0.84	0.48	0.81	0.55	2.17	0.04*
Zygomycota	0.44	0.66	4.57	<0.01**	3.89	<0.001**
Glomeromycota	0.78	0.50	3.06	0.02*	2.64	0.02**
Chytridiomycota	2.28	0.18	0.66	0.66	1.32	0.27

*$P < 0.05$, ** $P < 0.01$, *** $P < 0.001$.

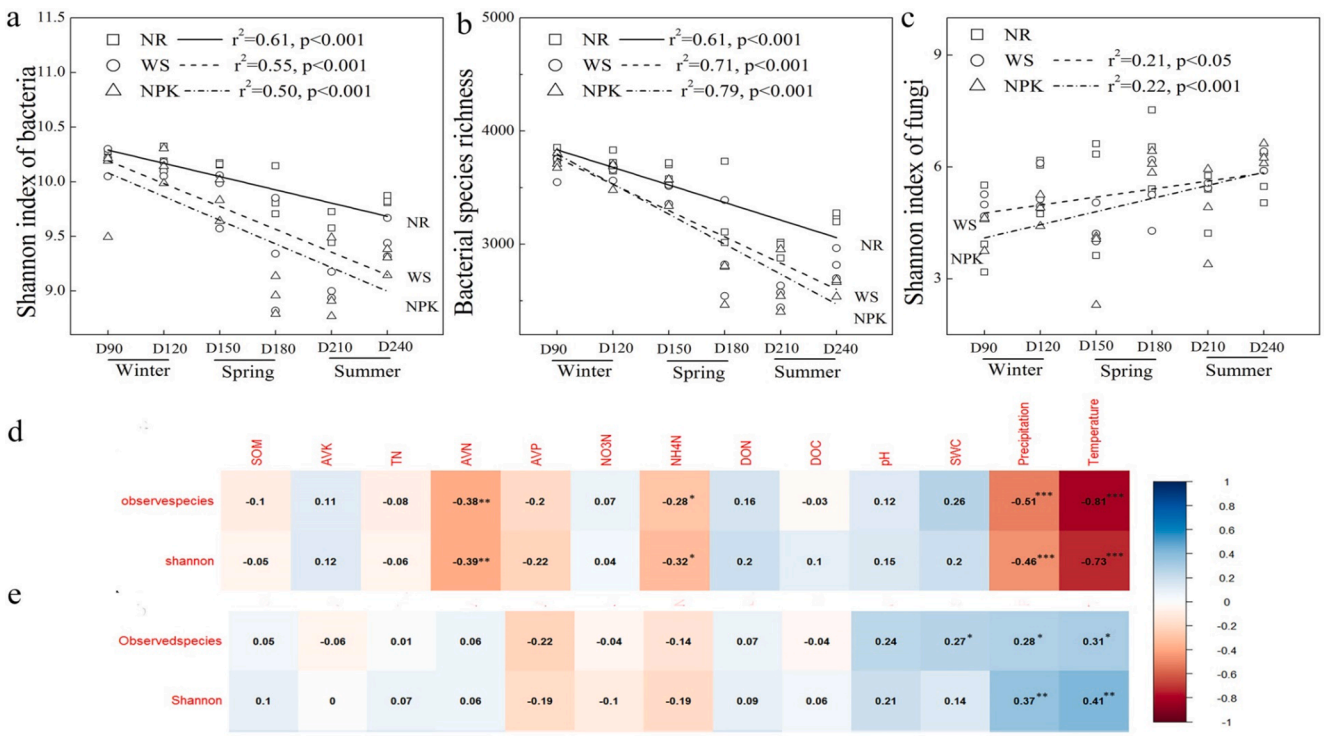

Fig. 1. Alpha diversity of soil bacterial (a and b) and fungal (c) communities at D90, D120, D150, D180, D210, and D240 under the NR, WS, and NPK treatments. Correlation analysis between alpha diversity (bacteria: d and fungi: e) and environmental factors in all treatments. *$P < 0.05$, ** $P < 0.01$, *** $P < 0.001$.

Gemmatimonadetes in D240 with NR and NPK both decreased considerably, by 17.48% and 6.54%, respectively. Evaluation of the fungal community composition revealed that the dominant phyla across all samples were Asomycota, Basidiomycota, Zygomycota, and Chytridiomycota, which accounted for more than 90% of the sequences from each sample (Fig. 3a and Table S4). Among them, Zygomycota and Glomeromycota were significantly affected by sampling time and the interaction of cropland management and sampling time (Table 1).

For the beta diversity of the soil bacterial and fungal communities between each pair of treatments, we found different responses to seasonal shifts (Figs. 2b and 3b). For soil bacteria, the beta diversity of NR vs WS, NR vs NPK, and WS vs NPK increased as the season changed from winter to summer, whereas the fungal beta diversity of NR vs WS and NR vs NPK decreased. Fungal beta diversity initially decreased from winter to spring and subsequently increased from spring to summer for WS vs NPK. The seasonal changes in bacterial and fungal beta diversity may be attributed to various impacts of seasonal change on bacterial and fungal OTUs. Our results showed that the number of enriched (NR) or depleted (WS and NPK) bacterial OTUs, as demonstrated by a pairwise comparison of treatments, increased greatly as the season changed from winter to summer (Fig. 2c), whereas few OTUs changed for fungi (Fig. 3c). Consequently, the expected delta value of the MRPP test, which is a parameter measuring the bacterial community variation between treatments, increased from 358.46 in winter to 399.47 in summer for WS vs NR, from 357.88 to 397.06 for NPK vs NR, and from 348.10 to 393.77 for WS vs NPK. For the fungal community, the expected delta values of WS vs NR and NPK vs NR decreased during the shift from winter to summer (Table 3).

For the 12 phyla or classes of the bacterial community, a pairwise comparison of treatments revealed that the beta diversities of most bacterial taxa, including Betaproteobacteria, Gemmatimonadetes, Verrucomicrobia, Acidobacteria, Planctomycetes, Nitrospirae, and Chloroflexi, as well as Alphaproteobacteria, Bacteroidetes, Deltaproteobacteria, Gammaproteobacteria, and Actinobacteria in NR vs WS and NR vs NPK, all increased linearly ($p < 0.05$) as the season transitioned from winter to summer. Only the beta diversities of Alphaproteobacteria, Actinobacteria, Bacteroidetes, and Gammaproteobacteria in WS vs NPK decreased from winter to summer (Fig. 4). For fungi, a pairwise comparison of treatments showed that the beta diversities of Glomeromycota between treatments, and those of Basidiomycota and Chytridiomycota between NR and NPK all decreased linearly ($p < 0.05$) as the season changed from winter to summer (Fig. 4).

These results further showed that the responses of bacterial unique OTUs in each treatment to seasonal shifts were closely related to cropland management. In NR, the average unique OTUs increased from 895 in winter to 1114 in summer, whereas they decreased from 800 in winter to 639 in summer and from 885 in winter to 597 in summer for WS and NPK, respectively (Fig. 2d). For fungi, where the number of unique OTUs were almost the same across summer and winter, the number of unique OTUs in spring increased greatly under NR, whereas it decreased considerably for both the WS and NPK treatments (Fig. 3d).

3.3. Soil microbial community and environmental factors

The correlation analysis showed that bacterial community alpha diversity, including the Shannon index and observed species, were both negatively correlated with soil AVN, NH_4^+-N, precipitation, and soil temperature (Fig. 2d and S3), whereas a positive correlation was found between fungal alpha diversity and climatic parameters, such as precipitation and soil temperature (Fig. 2e).

The significance of the relationships between soil microbial communities and environmental factors was tested (Table 4). Our results revealed that the environmental factors that significantly affected soil microbial communities were completely different in each treatment or each season. For NR, the soil bacterial community across seasons was significantly affected by AVP, NH_4^+-N, SWC, precipitation, and soil temperature, while it was significantly affected by NH_4^+-N, DOC, SWC, precipitation, and soil temperature for WS and AVN, and by NO_3^--N for NPK. For the fungal community, the significant environmental factors in

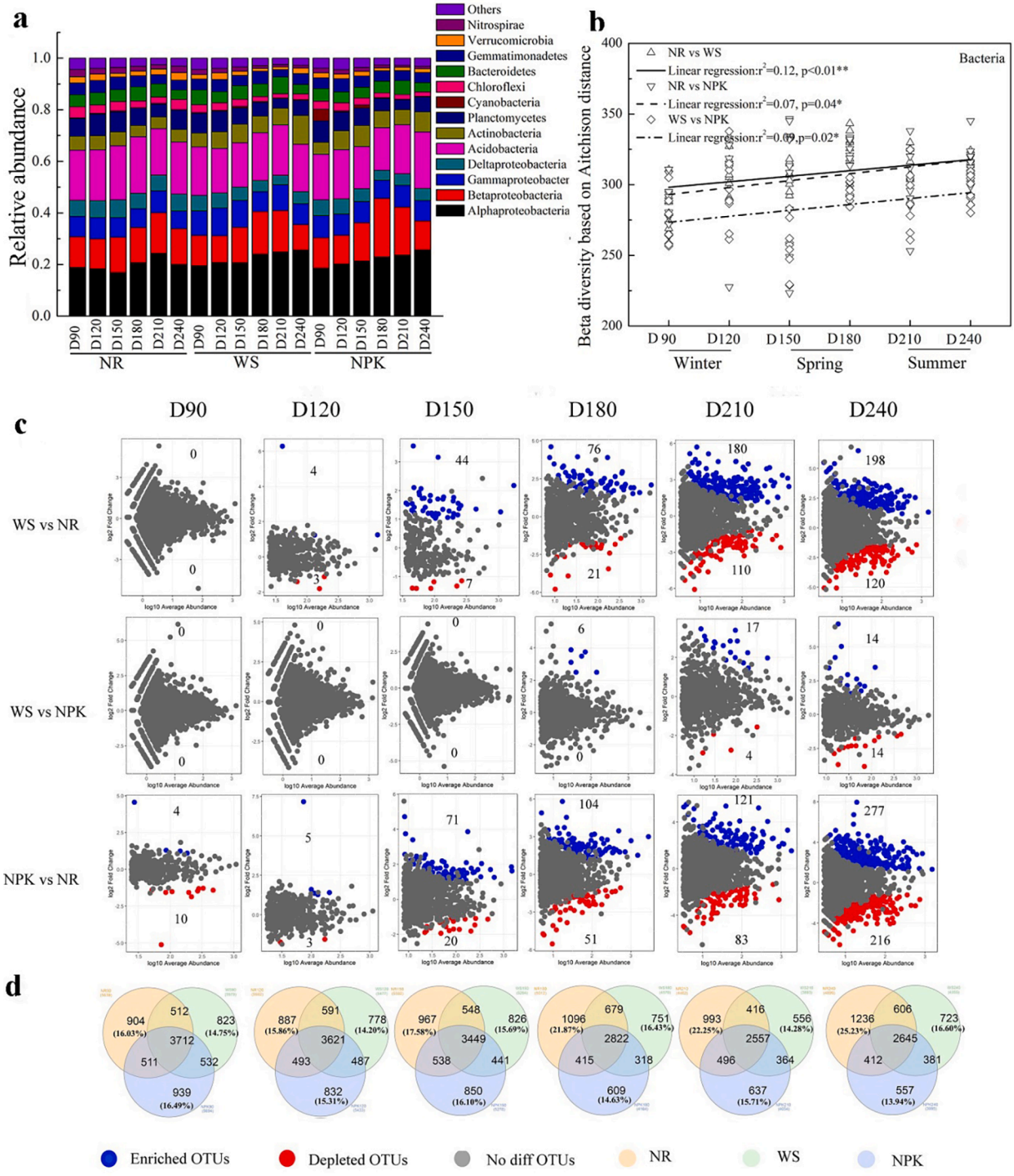

Fig. 2. Soil bacterial community composition at the phylum/class level (a), beta diversities (b), enriched and depleted OTU analysis (c) and Venn diagram showing unique and shared bacterial OTUs (c) at sampling times of D90, D120, D150, D180, D210, and D240 under the NR, WS, and NPK treatments.

Table 2
PERMANOVA test of the effects of treatment and sampling time on bacterial and fungal communities based on the Aitchison distance.

Community	Treatment		Time		Treatment*Time	
	R^2	p	R^2	p	R^2	p
Bacterial community	0.05	<0.001***	0.15	<0.00***	0.16	0.03*
Fungal community	0.07	<0.001***	0.14	<0.001***	0.17	0.91

*$P < 0.05$, ** $P < 0.01$, *** $P < 0.001$.

NPK were precipitation and temperature. When considering the temporal variation, the environmental factors that significantly affected the bacterial community were SOM, NO_3^-N, and pH in winter and pH in summer. Meanwhile, the significant environmental factors for the fungal community were SOM, AVN, and pH in winter, pH in spring, and AVP, DOC, pH, and precipitation in summer.

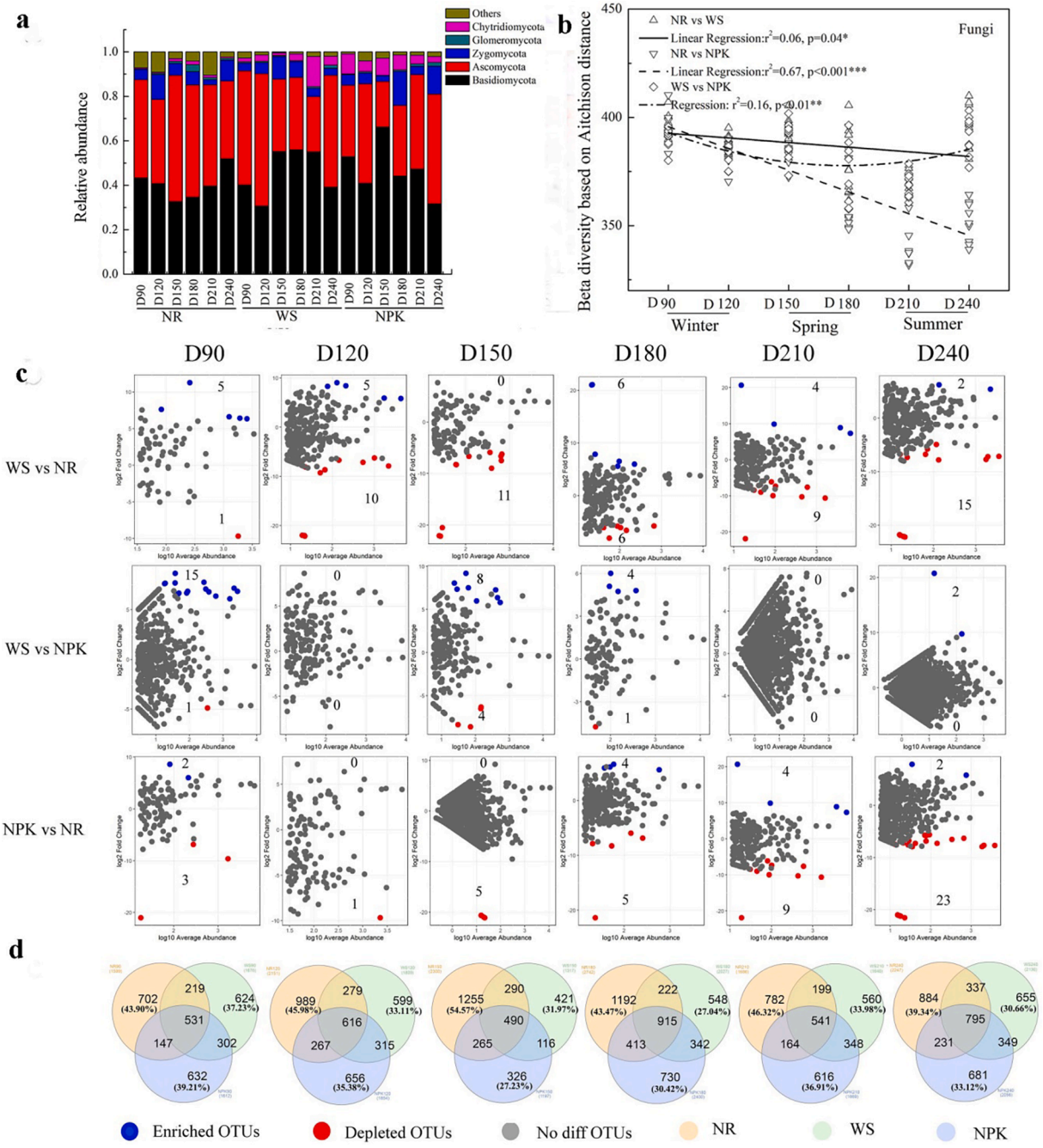

Fig. 3. Soil fungal community composition at phylum level (a), beta diversities (b), enriched and depleted OTU analysis (c), and Venn analysis of unique and shared OTUs (c) at sampling times of D90, D120, D150, D180, D210, and D240 under the NR, WS, and NPK treatments.

4. Discussion

4.1. Soil microbial alpha diversity, agricultural management, and temporal variation

Soil microbial diversity is an important factor in driving ecosystem function and is positively correlated with plant production (Delgado-Baquerizo et al., 2016; Duchene et al., 2017). Greater soil diversity can result in a more stable ecosystem. In the present study, it was found that fungal alpha diversity increased during the seasonal transition from winter to summer, while the bacterial alpha diversity decreased. These findings conflicted with our hypotheses. The significant decrease in bacterial diversity from D90 to D240 across all treatments may be attributed to rising soil aridity as a result of variations in temperature and soil water content that are associated with seasonal change (Fig. S3). As previously reported, there was a negative relationship between increasing aridity and bacterial diversity (Maestre et al., 2015). It was also possible that considerable exhaustion of available soil nutrients occurred, such as the NO_3^--N content, as plants absorbed more nutrients from the soil during the transition from winter to summer, which resulted in fierce competition between plants and bacteria (Van Der Heijden et al., 2008; Ai et al., 2018). It was also found that the bacterial alpha diversity under NR was higher than that in the WS and NPK treatments from D90 to D240. This result is consistent with previous reports of peak diversity occurring in soils with near-neutral pHs (Lauber et al., 2009; Ni et al., 2021) and could be ascribed to the narrow optimal pH ranges for bacterial growth (Wheeler et al., 1991) (Figure S3, pH is 6.1–6.7 ranging from D90 to D240 with NR, 4.6–5.1 with WS, and

Table 3
Multi-response permutation procedure (MRPP) analysis of the differences in soil bacterial and fungal community structure between treatments and seasons based on the Aitchison distance.

	Season/Treatment	Treatments/Season	A	Observed delta	Expected Delta	p
Bacteria	Winter (D90 + D120)	WS vs NR	−0.00	361.38	358.46	0.75
		WS vs NPK	−0.00	348.74	348.10	0.94
		NPK vs NR	−0.00	358.51	357.88	0.75
	Spring (D150 + D180)	WS vs NR	0.00	386.08	394.13	<0.01**
		WS vs NPK	−0.00	383.66	382.79	0.63
		NPK vs NR	0.01	386.20	390.10	0.04*
	Summer (D210 + D240)	WS vs NR	0.03	389.90	399.47	<0.01**
		WS vs NPK	0.00	392.62	393.77	0.15
		NPK vs NR	0.04	390.55	397.06	<0.01**
	NR	Winter vs Spring	0.01	389.69	390.48	0.01*
		Winter vs Summer	0.03	379.50	392.12	<0.01**
		Spring vs Summer	0.01	378.43	382.90	<0.01**
	WS	Winter vs Spring	0.01	386.86	389.18	<0.01**
		Winter vs Summer	0.05	369.43	390.44	<0.01**
		Spring vs Summer	0.02	366.11	373.96	<0.01**
	NPK	Winter vs Spring	0.01	390.57	392.65	0.02*
		Winter vs Summer	0.18	372.45	394.98	<0.01**
		Spring vs Summer	0.07	365.65	370.14	0.02*
Fungi	Winter (D90 + D120)	WS vs NR	0.02	307.15	313.67	<0.01**
		WS vs NPK	0.01	280.01	282.63	<0.01**
		NPK vs NR	0.02	320.02	323.40	0.04*
	Spring (D150 + D180)	WS vs NR	0.02	302.40	306.75	0.01*
		WS vs NPK	0.01	280.77	281.64	0.20
		NPK vs NR	0.00	299.38	305.00	0.03*
	Summer (D210 + D240)	WS vs NR	0.01	290.25	294.93	0.03*
		WS vs NPK	−0.00	296.82	295.92	0.50
		NPK vs NR	0.02	299.79	306.95	<0.01**
	NR	Winter vs Spring	0.00	329.01	329.04	0.32
		Winter vs Summer	−0.00	307.99	307.29	0.46
		Spring vs Summer	0.00	327.38	328.38	0.32
	WS	Winter vs Spring	0.01	269.39	270.18	0.06
		Winter vs Summer	0.01	285.66	286.68	0.06
		Spring vs Summer	0.01	282.16	285.95	0.02*
	NPK	Winter vs Spring	0.00	292.40	293.74	0.26
		Winter vs Summer	0.01	291.18	293.24	0.19
		Spring vs Summer	0.01	294.43	298.60	0.13

*$P < 0.05$, ** $P < 0.01$, *** $P < 0.001$.

5.1–5.4 with NPK).

Although there were no significant differences in alpha diversity for soil fungi among the WS, NR, and NPK treatments, significant increases in alpha diversity were observed as the seasons changed from winter to summer, especially at D240. These findings may be explained by the higher input of organic materials due to greater plant growth in summer compared to winter, as well as the interactive mechanism between bacteria and fungi during the decomposition of organic material (Žifčáková et al., 2017). In summer, fungi were the primary drivers of recalcitrant biopolymer decomposition, while bacteria replaced fungi in this role during winter. This was supported by the finding that high temperature had a positive effect on fungal alpha diversity (Fig. 2e).

4.2. Soil microbial beta diversity and seasonal changes in the environment

Conflicting with the second hypothesis, the results of this study are consistent with those of Shigyo et al. (2019), who found that seasonal patterns of beta diversity were not synchronized between fungi and bacteria. In this research, the bacterial beta diversity between treatments increased as the season shifted from winter to summer, which may have been due to the higher number of enriched OTUs compared to depleted OTUs in spring and summer. The higher number of enriched OTUs in spring and summer than in winter for NR vs NPK and NR vs WS may be attributed to lower temperatures in winter, which restrict the survival of species or genera sensitive to cold conditions (Li et al., 2015). The reduced number of enriched OTUs in WS vs NPK than NR vs WS and NR vs NPK in spring and summer may have been caused by the significantly lower soil pH under the WS and NPK treatments. Wheeler et al. (1991) pointed out that bacteria exhibit a narrow optimal pH range for growth, and changes in soil pH can explain and predict the abundance distribution of most OTUs (Mod et al., 2021; Ni et al., 2021). In contrast to bacteria, the decreasing fungal beta diversity of NR vs WS and NR vs NPK may have been related to the higher number of depleted OTUs compared to enriched OTUs in spring and summer. The beta diversity of WS vs NPK decreased in the spring, and subsequently increased during summer. This may have been due to the lower number of unique OTUs during spring compared to winter and summer. Furthermore, by comparing the number of enriched and depleted OTUs between bacteria and fungi as the seasons changed, the results showed that fungi were more tolerant of environmental changes than bacteria, which suggested that seasonal changes strengthened bacterial community variation but not fungal community variation (Landesman et al., 2019). Fungi may owe their increased tolerance of environmental changes to their hyphae formation and durable viable spores (Sun et al., 2017).

For the beta diversities of major bacterial phyla, an interesting phenomenon was found. Unlike the linearly increasing beta diversities observed for the bacterial community in NR vs WS, NR vs NPK, and WS vs NPK during the transition from winter to summer, the beta diversities of some bacterial phyla of WS vs NPK, such as Alphaproteobacteria, Gammaproteobacteria, Actinobacteria, and Bacteroidetes, exhibited decreases, while the beta diversities increased for WS vs NR and NR vs NPK. This may be attributed to the cropland management systems. Compared with NR, fertilization management systems such as WS and NPK can result in high nutrient availability, which benefits proliferation of copiotrophs such as Alphaproteobacteria, Gammaproteobacteria, Actinobacteria, and Bacteroidetes as opposed to oligotrophs (Fierer et al., 2007; Kurm et al., 2017). Tillage activity combined with a lower soil pH in WS and NPK may be another reason for this finding. Some

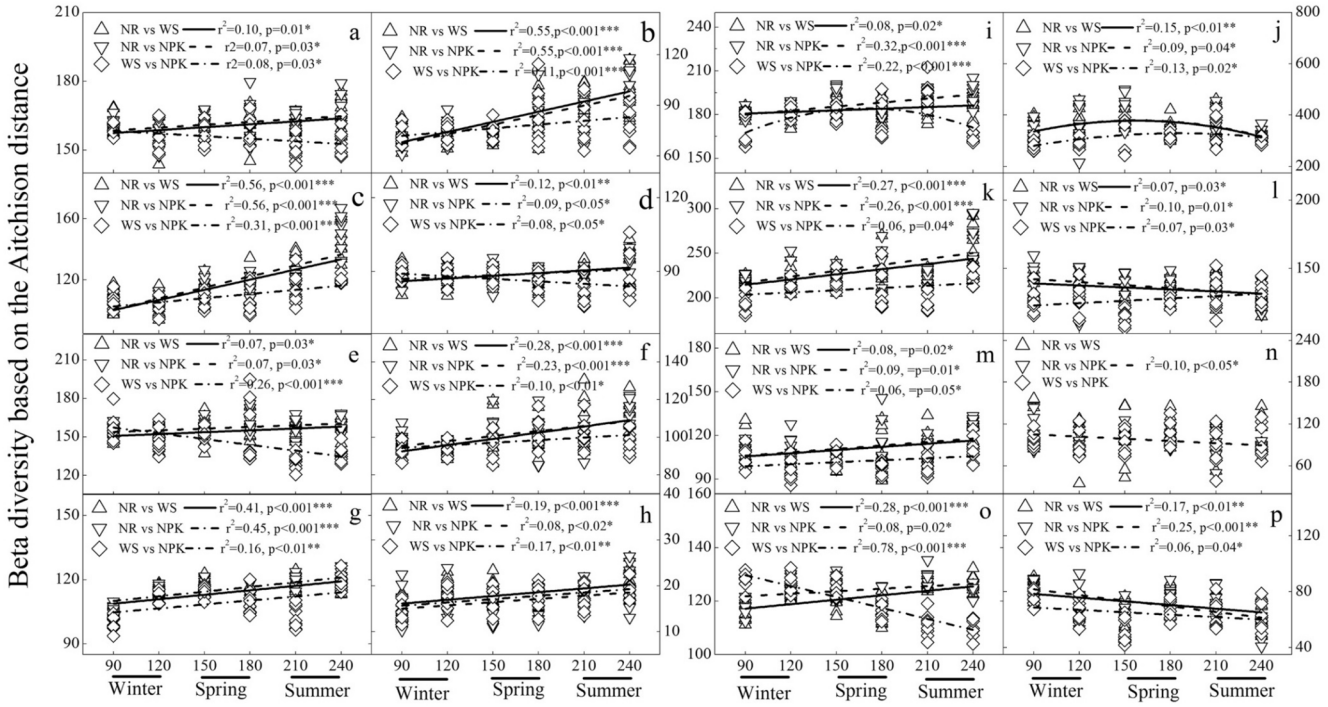

Fig. 4. Beta diversities of Alphaproteobacteria (a), Betaproteobacteria (b), Acidobacteria (c), Actinobacteria (d), Bacteroidetes (e), Gemmatimonadetes (f), Chloroflexi (g), Nitrospirae (h), Detaproteobacteria (i), Ascomycota (j), Planctomycetes (k), Basidiomycota (l), Verrucomicrobia (m), Chytridiomycota (n), Gammaproteobacteria (o), and Glomeromycota (p) at sampling times of D90, D120, D150, D180, D210, and D240.

Table 4
Significance test of the relationship between environmental factors and soil bacterial and fungal communities based on the Aitchison distance.

Soil Microbe	Soil properties	NR		WS		NPK		Winter		Spring		Summer	
		F	*p*	F	*p*	F	*p*	F	*p*	F	*p*	F	*p*
Bacteria	SOM	0.59	0.87	1.20	0.31	0.73	0.52	3.13	0.01*	1.18	0.32	2.15	0.09
	AVK	1.11	0.34	1.70	0.13	1.48	0.23	0.46	0.75	1.11	0.41	1.59	0.16
	TN	1.20	0.32	0.98	0.48	0.32	0.90	0.71	0.53	1.00	0.42	0.66	0.83
	AVN	0.80	0.65	1.68	0.07	4.14	0.01**	0.67	0.62	1.07	0.37	0.82	0.65
	AVP	3.19	0.01*	0.43	0.81	1.37	0.23	0.63	0.61	1.61	0.24	1.36	0.18
	NO_3^--N	0.63	0.83	1.64	0.13	3.92	<0.01**	12.15	<0.01**	1.07	0.42	0.92	0.52
	NH_4^+-N	2.52	0.02*	2.14	0.03*	0.69	0.64	0.66	0.61	1.31	0.25	0.74	0.79
	DON	0.82	0.66	1.27	0.28	1.83	0.09	0.41	0.85	2.27	0.13	0.83	0.71
	DOC	0.78	0.73	3.99	<0.01**	0.89	0.49	0.61	0.61	1.25	0.38	1.26	0.22
	pH	1.03	0.49	1.55	0.20	3.35	0.09	5.90	<0.01**	1.40	0.27	10.03	<0.01***
	SWC	2.31	0.04*	2.49	0.03*	0.74	0.53	2.20	0.12	1.26	0.35	1.29	0.17
	Precipitation	2.59	0.01**	3.24	0.01**	0.42	0.84	0.56	0.62	0.91	0.51	0.60	0.83
	Temperature	3.47	<0.01**	2.62	0.03*	1.08	0.36	0.79	0.53	0.53	0.76	2.11	0.06
Fungi	SOM	0.83	0.82	1.12	0.36	1.05	0.36	1.35	0.04*	0.76	0.80	1.05	0.44
	AVK	0.90	0.73	0.86	0.82	1.15	0.21	1.10	0.33	0.94	0.59	1.11	0.21
	TN	0.69	0.99	1.46	0.11	0.78	0.66	1.14	0.21	1.04	0.32	0.83	0.76
	AVN	0.77	0.94	0.81	0.80	0.92	0.70	1.46	0.02*	0.84	0.76	0.96	0.63
	AVP	1.58	0.08	1.40	0.07	0.96	0.42	1.21	0.25	0.89	0.62	1.48	<0.01**
	NO_3^--N	0.78	0.94	0.82	0.82	1.00	0.46	0.49	0.98	0.64	0.95	1.11	0.36
	NH_4^+-N	1.32	0.06	0.87	0.79	0.90	0.68	1.18	0.22	0.54	0.99	1.17	0.10
	DON	1.03	0.43	1.03	0.39	0.71	0.78	1.27	0.21	0.71	0.87	0.75	0.69
	DOC	0.86	0.76	1.21	0.17	1.54	0.09	1.35	0.12	1.35	0.15	1.57	0.03*
	pH	1.17	0.16	1.32	0.11	0.93	0.62	2.06	<0.01**	2.18	<0.01**	1.70	<0.01**
	SWC	1.17	0.23	1.30	0.12	0.86	0.62	1.35	0.08	1.10	0.29	0.88	0.76
	Precipitation	0.99	0.47	0.99	0.52	1.83	0.03*	1.02	0.50	1.05	0.46	1.19	0.04*
	Temperature	0.95	0.62	0.95	0.60	1.80	<0.01**	1.14	0.21	0.88	0.55	1.18	0.06

*$P < 0.05$, ** $P < 0.01$, *** $P < 0.001$.

studies have reported that Alphaproteobacteria were more abundant in tilled soil (Souza et al., 2013), while the abundances of Actinobacteria and Bacteriodetes were positively correlated with soil pH (Lauber et al., 2009; Shen et al., 2013).

For the fungal phyla of Basidiomycota and Glomeromycota, the beta diversities of WS vs NR and NR vs NPK decreased from winter to summer, which may have been caused by the lack of tillage under NR and the straw return management under WS. As reported previously, Basidiomycota are the primary agents of lignin decomposition and play an important role in degrading lignin under anaerobic conditions (Boer

et al., 2005; Blackwood et al., 2007), while Glomeromycota contain arbuscular mycorrhizal fungi and play a key role in soil aggregate formation and stabilization (Douds and Millner, 1999; Rillig and Mummey, 2006; Rillig et al., 2015). Because crop residue retention and no-tillage management improve soil aggregate formation and stability (Singh et al., 2018; Xiao et al., 2019), no tillage and plant residue retention with NR and straw return with WS may create a microenvironment that promotes Basidomycota and Glomeromycota growth by providing anaerobic and high lignin content conditions (Zhang et al., 2013; Degrune et al., 2015; Wang et al., 2017). For Ascomycota, as the key decomposers of organic matter in agricultural soils, the initial increase and subsequent decrease in beta diversity for WS vs NR and WS vs NPK may be due to their lifestyles and ability to decompose cellulose (Jones et al., 2009; Ma et al., 2013; Qin, 2016). Previous research has shown that the Ascomycota are copiotrophs and thrive in soils with added straw, and their growth rate is correlated with nitrogen availability (Yao et al., 2017). As most of the returned crop straw decomposition occurs from winter to summer (Wang et al., 2012), the positive effect of wheat straw combined with mineral fertilizers on Ascomycota may decrease over time.

4.3. Soil microbial community variation and environmental factors

The soil microbial community is a key biomarker of soil quality and ecosystem functioning, and its structure can be modified by seasonal change and various agricultural management practices (Sun et al., 2015; Wang et al., 2017; Žifčáková et al., 2017; Ai et al., 2018). However, unlike previous studies that found that pH was the determining factor in structuring bacterial communities (Lauber et al., 2009; Shen et al., 2013; Sun et al., 2015), this study demonstrated that pH was the most significant factor structuring the bacterial community only during winter and summer, even though a significantly lower pH was found in the WS and NPK treatments compared to the NR treatment across seasons. This was likely because the time span of this research stretched across winter, spring, and summer, and soil organic matter as a nutrient resource became more important for plant productivity in the spring than in other seasons (Pan et al., 2015). For fungi, the significant factor in structuring the fungal community across winter, spring, and summer was also pH, which may have been attributable to preferable neutral soil conditions rather than the acidic environment and higher soil pH with NR (Hu et al., 2017; Cai et al., 2018).

Temperature and precipitation represent the typical environmental factors under seasonal change that significantly influence the microbial community composition and the activity of different taxa that make up the community (Yergeau et al., 2012; Xiong et al., 2014; Stark et al., 2015). However, we found that the effects of precipitation and temperature on soil bacterial and fungal communities were closely related to cropland management. Under NR and WS treatment, the reason for the significant effect of temperature and precipitation on the bacterial community may be related to untreated natural cover and crop straw return management, as temperature plays an important role in organic material decomposition (Guan et al., 2020). For the fungal community under NPK treatment, the significant effects of precipitation and temperature may be due to the predominant role of fungi in the decomposition of organic material during summer and the increasing input of fresh organic material as wheat grows during spring and is harvested in summer (Žifčáková et al., 2017).

5. Conclusion

The results of this study revealed that the alpha and beta diversities of bacteria and fungi have contrasting responses to seasonal changes. The temporal state of beta diversity could not be determined based on changes in alpha diversity. Compared to fungi, temporal variation during seasonal change had a more complex influence on soil bacterial beta diversity due to the interaction between land management systems and sampling time. This suggests that using one or a few sampling times within a season to assess bacterial beta diversity and the impacts of environmental factors on bacterial diversity could be an oversimplified approach. For soil fungi, it was sufficient to assess the fungal beta diversity between land management systems without considering temporal variation. This study provides an opportunity for researchers to assess the effects of temporal variation on microbial diversities under various land management systems. As this experiment lasted less than one year, this research was limited in time scale. Thus, an experiment with several years of repeated sampling should be conducted to provide stronger evidence.

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.

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Appendix A. Supplementary data

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