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Alteration of desert soil microbial community structure in response to agricultural reclamation and abandonment

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ABSTRACT

Agricultural reclamation via the conversion of desert into cropland offers a strategy to utilize arid lands and combat desertification. However, limited irrigation water resources have forced the abandonment of reclaimed agricultural lands and succession towards unmanaged natural states, which may contribute greatly to erosion potential. Soil microorganisms can affect the degradation and wind erosion potential of soils in the desert region by mediating many ecological processes. However, little is known about how soil microbial community structures respond to desert agricultural reclamation with tillage-based farming and subsequential abandonment. Using quantitative PCR (qPCR) and 16S rRNA high-throughput sequencing approaches, we investigated the changes of bacterial, archaeal and fungal community biomasses, diversities and structures in a desert farmland soil (FS). We contrasted these to soils along a 10-year farming abandonment chronosequence (2-year, 5-year and 10-year) and with adjacent soil from a native desert (control) in the Badain Jaran desert, China. Soil bacterial and archaeal community biomasses significantly increased after reclamation compared with the control and generally decreased after farming abandonment. Species richness of communities decreased for archaea and increased for fungi in response to reclamation, whereas bacterial community species richness increased during the 5-year abandonment. Microbial community structures were divergent in reclaimed and abandoned soils and were closely related to soil moisture, total carbon (C), total nitrogen (N), available phosphorus (P) and the stoichiometry of C, N and P, which explained 24.4–89.0% of their variations. Our results indicate desert soil microbial biomass, diversity and compositions differently responded to agricultural reclamation and abandonment with some irreversible changes in compositions mainly driven by soil moisture and chemical properties changes. The insights are meaningful for sustainable development of agriculture and ethical land management in arid desert regions.

1. Introduction

Deserts cover about one-quarter of the global land surface and are characterized by harsh climates and barren soil conditions. Reclaiming native desert ecosystems into cropland is the prevailing strategy to utilize these arid regions and combat desertification. However, in the past several decades, large areas of native deserts have been converted into cropland to feed the increasing global population (Köberl et al., 2011; Ding et al., 2013; Wei et al., 2018). For instance, the area of irrigated farmland in the Shiyang River watershed of northwestern China increased by 30% in the past 20 years, which is problematic owing to serious water shortages, soil salinization and competing demands for

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groundwater resources (Wei et al., 2018). In fact, high water demands are the central issue for agriculture in arid regions, which leads to significant depth declines in groundwater tables, and causes a series of eco-environmental issues (Dong et al., 2010; Wei et al., 2018). As a result, progressively more reclaimed cropland has been abandoned. Therefore, two typical contrasting types of land use (agricultural reclamation and abandonment) are ubiquitous in arid desert regions, and limited data are available to help understand the implications of their occurrences.

Soil microorganisms play key roles in maintaining plant productivity, soil fertility and health, and soil ecosystem functions by regulating many ecological processes (Biswas and Kole, 2017; Schloter et al., 2018). Microbial community diversity and structure are significantly influenced by abiotic and biotic soil environmental factors (Ramirez et al., 2010; Li et al., 2015). Thus, changes in soil physicochemical properties, such as soil moisture, pH, salinity, and nutrient availability caused by land-use changes and management, can significantly affect soil microbial community structure (Drenovsky et al., 2010; Köberl et al., 2011; Li et al., 2015; Lüneberg et al., 2018; Wang et al., 2019). However, there is no consensus on how soil microbial communities respond to farming activities (irrigation, cultivation and fertilization), with reported positive (Li et al., 2018; Wang et al., 2019), negative (Ding et al., 2013; Zhou et al., 2016) and non-significant effects (Li et al., 2015; Lazcano et al., 2013) depending on microbial taxa (Zhou et al., 2016; Wang et al., 2019) and soil type (Ramirez et al., 2010). Most previous studies have focused on typical agroecosystems (Jangid et al., 2008; Ramirez et al., 2010; Hartmann et al., 2015; Eo and Park, 2016; Hu et al., 2017), with only a few investigations on reclaimed desert agroecosystems (Köberl et al., 2011; Ding et al., 2013; Li et al., 2015). Specifically, changes to soil microbial community structures after desert farming abandonment remains poorly understood.

Soil microbial biomass, diversity and structure have been taken as indicators of soil quality that are closely related to agricultural yield (Kaschuk et al., 2010; Schloter et al., 2003; Schloter et al., 2018). Previous studies have found that farming reclamation generally enhanced soil microbial diversity in drylands due to fertilization, irrigation and cultivation (Wang et al., 2019; Köberl et al., 2011), while continuous fertilization and tillage practices tended to have opposing effects (Wang et al., 2010; Zhou et al., 2016; Wang et al., 2019). Compared to native desert soils, cultivated soils generally have higher nutrient levels owing to fertilization, crop exudates/residues and greater water contents on account of irrigation inputs, providing conditions that support more microbial growth and activity (Ding et al., 2013; Li et al., 2015). Provided that desert soil microbial communities perform important functions for erosion prevention and in ecosystem food webs (Belnap et al., 2016), it is essential to understand how reclamation alters native desert communities and if/how they rebound the following abandonment. Hence, our results will be meaningful to promote ethical land management by considering ecological impacts of both reclamation and abandonment if/when irrigation supplies cannot support the reclaimed land operations.

To access the impacts of farming reclamation and abandonment on desert soil microbial community structure, we used qPCR and Illumina MiSeq sequencing approaches to evaluate the changes in the abundances, diversities and compositions of bacterial, archaeal and fungal communities in a 10-year cultivated soil and along a 10-year farming abandonment chronosequence compared with an adjacent native desert in the southeastern edge of the Badain Jaran Desert, China. Here, we addressed the following hypotheses: 1) farming reclamation will increase soil bacterial, archaeal and fungal biomass and diversity, but this trend will reverse after farming abandonment, resulting in significantly different microbial community structures during the two contrasting processes, and 2) soil moisture and nutrient availabilities will be the key drivers in structuring desert soil microbial communities.

2. Materials and methods

2.1. Study site and soil sampling

The study was conducted at the Minqin Desert Ecosystem National Field Observation & Research Station (38°34′28″N, 102°59′05″E) with an elevation of 1370 m a.s.l., located in the southeastern fringe of the Badain Jaran Desert, China. This area is at the lower reaches of the Shiyang River and characterized as a typical transitional belt between oasis and desert. The climate conditions include a mean annual temperature of 7.6 °C with a hot summer and a cold winter. The mean annual precipitation is 113.8 mm, which mainly falls during the growing season from June to September, and mean potential annual evaporation is 2604 mm. A northwest wind with an average annual velocity of 2.5 m s^{-1} prevails. The soil is aeolian silty loam, and the mosaic distribution pattern of nebkhas and interdune lowlands dominate the landscape. The vegetation is characterized by desert plants with low coverage (<16%) and diversity, dominated by *Tamarix ramosissima* and *Nitraria tangutorum* in the nebkhas and by *Halaxylon ammodendron*, *Hedysarum scoparium, Kalidium foliatum, Reaumuria soongorice, Artemisia arenaria* and *Agriopyllum squarrosum* in the interdune lowlands (Dong et al., 2010).

Our study consisted of five sites that were each comprised of<1 ha^2 and distributed over a 300–600 m distance. These sites covered three abandoned farming sites (AF) and a farmland site (FS), while the adherent native desert site (DS) was considered as the control (Fig. 1). The AF and FS sites were transitioned from natural desert to farming reclamation sites in 1992. Maize was continuously grown in the FS after reclamation without rotation, with a density of approximately 70,000 plants ha^{-1} (40 cm spacing between rows and 25 cm between lines). Diammonium phosphate (375 kg ha^{-1}) and compound fertilizer (N/P_2O_5/K_2O = 15:15:15, 300 kg ha^{-1}) were applied as N, P and K fertilizers before sowing. Urea (300 kg ha^{-1}) was provided as N fertilizer topdressing two or three times during stalk formation. The farmland was irrigated seven times each year with groundwater pumped from wells and freshwater from Shiyang River. A herbicide, 24 % nicosulfuron atrazine (3.75 kg ha^{-1}) was used for weed control during the second or third irrigation after sowing. Farming activities were stopped at the AF sites for 2 (AF2), 5 (AF5) and 10 years (AF10) prior to sampling due to a shortage of irrigation water resources in the past decade. In August 2018, we collected composited soil samples from each of three replicates pre-treatment for measurements of physiochemical variables and microbial molecular analyses. In detail, three different replicate fields (10–12 m in width × 30–40 m in length) at the FS and AF sites and three replicate plots (10 × 10 m plots) at the DS site were selected. To ensure consistent spatial variations across samples, one 1 m^2 subplot was sampled at random from each replicate site, and five soil cores (4.5 cm in diameter × 10 cm in depth) were collected from the corners and center of each subplot. Soil cores from the same subplots were then composited to generate one composite soil sample. Soil samples were taken back to the laboratory on ice, immediately mixed thoroughly and sieved through 2 mm mesh to remove any visible plant roots. The sieved fresh soils were stored at −80 °C for DNA extraction or at 4 °C to determine mineral nitrogen. Soil samples for measurements of other physiochemical variables were air-dried at room temperature.

2.2. Measurements of soil properties

Soil pH and electrical conductivity (EC) was measured using a glass electrode at a soil:water ratio of 1:2.5. Soil gravimetric moisture (SM) was determined by drying soil for 24 h at 105 °C. Soil total organic C (TOC) and total N (TN) were determined with a Costech elemental analyzer (ECS 4010, Valencia, CA). Total phosphorus (TP) was determined colorimetrically after $HClO_4$–H_2SO_4 digestion, and available P (AP) was extracted with $NaHCO_3$ extraction and measured colorimetrically (Olsen and Sommers, 1982). Available K (AK) was measured by NH_4OAc extraction and the flame photometric method (Thomas, 1982).

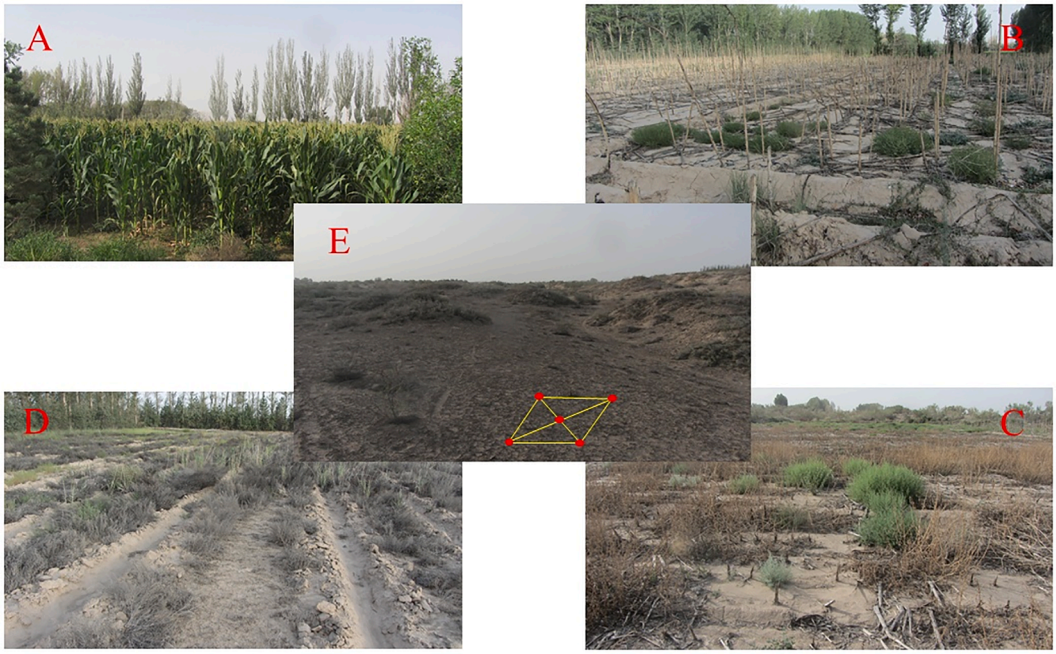

Fig. 1. The landscape of farmland site (A), 2-year (B), 5-year (C) and 10-year (D) abandoned farmland sites, and native desert (E).

Soil dissolved organic C (DOC) and N (DON), ammonia and nitrate were extracted by 2 M KCl (1:2.5, m/v) within a day or two as described previously (Jones and Willett, 2006). The concentrations of DOC and DON in the extracts were determined on a TOC analyzer (Vario TOC, Elementar, Germany), and ammonia and nitrate in the extracts were determined on an automated gas-segmented continuous flow analyzer (Skalar San++, Skalar Analytical, B.V., Netherlands).

2.3. DNA extraction and qPCR

The E.Z.N.A.® soil DNA Kit (Omega Bio-tek, Norcross, GA, USA) was used to extract total DNA from soils according to the supplied protocols. The quality of DNA extracts was checked by 1% agarose gel electrophoresis and by determining 260/280 and 260/230 nm absorbance ratios with a Nanodrop® ND-2000 spectrophotometer (NanoDrop Technologies, Wilmington, DE, USA). The DNA extracts were diluted in TE buffer (10 mM Tris-HCl, 1 mM EDTA, pH 8.0) and stored at -20 ℃ until use.

The absolute abundances of bacterial 16S rRNA, archaeal 16S rRNA and fungal ITS gene were determined by qPCR with selected primer pairs. The forward and reverse primers were Eub338 (5′-ACTCCTACGGGAGGCAGCAG-3′) and Eub806 (5′-GGACTACHVGGGTWTCTAAT-3′), Arch344 (5′-ACGGGGYGCAGCAGGCGCGA-3′) and Arch915 (5′-GTGCTCCCCCGCCAATTCCT-3′), ITS1 (5′-CTTGGTCATTTAGAGGAAGTAA-3′) and ITS2 (5′-TGCGTTCTTCATCGATGC-3′) for bacteria, archaea and fungi, respectively. The standard curves were generated from a clone with Eub, Arch, and ITS amplicon inserts using 10-fold serial dilutions of the plasmid. Each 20 μL PCR reaction mixture contained 10 μL of ChamQ SYBR Color qPCR Master Mix (Vazyme Biotech Co., Ltd, China), 0.8 μL of each forward and reverse primers (5 μM), 1 μL of template DNA and 7.4 μL ddH_2O. The reaction was conducted on a ABI7500 real-time PCR system (Applied Biosystems, Foster City, CA, USA). The amplification thermocycling consisted of initial denaturation 95 °C for 5 min followed by 40 cycles of 95 °C for 30 s, annealing temperature 55 °C for bacterial 16S rRNA and 58 °C for Archaeal 16S rRNA and fungal ITS genes for 30 s, and elongation temperature 72 °C for 1 min. All qPCRs were performed in triplicate and assayed on a StepOne Real-Time PCR System (ABI 7500, Applied Biosystems, America). The primer efficiencies ranged from 94.2 to 103.8% ($R^2 > 0.999$). The gene copy number of bacterial 16S rRNA, archaeal 16S rRNA and fungal ITS genes was calculated using a regression equation for converting the cycle threshold (Ct) value to the known number of copies in the standards.

2.4. PCR amplification and Illumina MiSeq sequencing

Amplicon libraries were created by using the same bacterial, archaeal and fungal specific primers utilized for qPCR. In brief, a 10 ng of aliquot of previously extracted DNA from each soil sample was used as a template to amplify bacterial 16S rRNA, archaeal 16S rRNA and fungal ITS genes. The PCR amplification was performed in triplicate on a GeneAmp® 9700 PCR system (Applied Biosystems, Foster City, CA.). The reaction mixture contained 4 μL of 5 × FastPfu Buffer, 2 μL of 2.5 mM dNTPs, 0.8 μL of each primer (5 μM), 0.4 μL of FastPfu Polymerase, 10 ng of template DNA and ddH_2O to reach a total volume of 20 μL. Thermocycling consisted of 95 ℃ for 3 min, followed by 29 cycles for bacterial 16S rRNA and 35 cycles for archaeal 16S rRNA and fungal ITS genes at 95 ℃ for 30 s for denaturation, 55 ℃ for 30 s for annealing, and 72 ℃ for 45 s and a final extension at 72 ℃ for 10 min. The PCR products were extracted from 2% agarose gels and purified using the AxyPrep DNA Gel Extraction Kit (Axygen Biosciences, Union City, CA, USA) and quantified using QuantiFluor™-ST (Promega Corporation, Madison, WI, USA) according to the manufacturer's protocols. Purified amplicons were then pooled in equimolar ratios and paired-end sequenced (2 × 300) on an Illumina MiSeq platform (Illumina, San Diego, USA) according to the standard protocols at Majorbio Bio-Pharm Technology Co. Ltd., Shanghai, China (http://www.majorbio.com). The raw MiSeq sequencing results were deposited in the NCBI Sequence Read Archive (SRA) database under accession number SRP252549.

2.5. Processing of sequencing data

Raw sequence FASTQ files were quality-filtered by Trimmomatic and merged by FLASH v. 1.2.11 with the following criteria: (i) The reads were truncated at any site receiving an average quality score < 20 over a 50 bp sliding window. (ii) Sequences with overlap ≥ 10 bp were merged according to their overlap disallowing > 2 bp overlaps. (iii) Sequences of each sample were separated according to barcodes (exactly matching)

and primers (allowing 2 nucleotide mismatching), and reads containing ambiguous bases were removed. The trimmed and unique sequences were clustered using UPARSE (version 7.0.1090 http://drive5.com/uparse/) at 97% identity to generate operational taxonomic units (OTUs). The taxonomy identity of each phylotype was assigned using a BLAST comparison against the NCBI GenBank database.

2.6. Statistical analysis

We used the online platform, Majorbio Cloud Platform (www.majorbio.com), to analysis the MiSeq sequencing data. Briefly, rarified OTU tables of bacterial, archaeal and fungal sequence reads were randomly selected to calculate number of OTUs, Chao1, Shannon and Simpson diversity indices (α-diversity) using Mothur v.1.30.2 (https://mothur.org/wiki/calculators/), and Bray-Curtis dissimilarities between different sites (β-diversity). The normality of soil properties, bacterial, archaeal and fungal gene abundances, α-diversity indices and microbial community abundance data was confirmed by Shapiro-Wilk test. One-Way analysis of variance (ANOVA) with Least Significance Difference (LSD) and nonparametric Kruskal-Wallis H test (SPSS 22.0 Inc., Chicago, IL, USA) were performed to test differences across sites at a 95 % confidence interval when data were normality distributed or not, respectively. Bray-Curtis distances between samples were visualized using principal coordinates analysis (PCoA) to determine the effects of farming reclamation and abandonment on bacterial, archaeal and fungal β-diversity at the OTU level. Bray-Curtis distances were defined as follows:

$$D_{Bray-Curtis} = 1 - 2\frac{\sum min(S_{A,i}S_{B,i})}{\sum S_{A,i} + \sum S_{B,i}}$$

where $S_{A,i}$ and $S_{B,i}$ represent the sequence number of the i-th OTU of sample A and B, respectively.

Linear discriminant analysis (LDA) with effect size (LEfSe) measurement analysis (http://huttenhower.sph.harvard.edu/galaxy/root?tool_id = lefse_upload) was used to identify the classified microbial groups with significant abundance differences at the phylum and class level in different sites with the LDA threshold of 2.0. The Mantel test and Spearman correlation analysis were adopted to evaluate the correlations of microbial community structures and soil properties. Stepwise linear regression was used to reveal the relationships between microbial biomass and diversity (Shannon index) and soil properties. Associations between bacterial, archaeal and fungal communities and soil properties were analyzed using redundancy analysis (RDA) and canonical correspondence analyze (CCA) with vegan package in R 3.3.1.

3. Results

3.1. Characteristics of soil properties

Farming reclamation and abandonment significantly affected soil SM, TOC, TN, AP, C/P and N/P. Significant effects of farming reclamation on soil EC and C/N, and farming abandonment on pH, TP and DOC were also observed (Table S1). Increased SM, TOC, TN, AP, C/P and N/P were found in FS soil compared with the DS soil. In general, soil SM, TOC, TN, DOC and N/P decreased with the progression of farming abandonment though there were no significant differences among abandoned farming sites (AF2, AF5 and AF10) in most cases. Only 5 of the 45 comparisons of soil properties significantly differed across AF2, AF5 and AF10, which were typically observed between AF2 and AF10 (Table 1).

3.2. Gene abundance and diversity of the microbial community

The qPCR results revealed that farming reclamation and abandonment soils had significantly higher bacterial and archaeal gene abundances than did DS, with a few exceptions, while only AF5 had significantly higher fungal biomass than DS (Fig. 2). The bacterial and archaeal taxonomic gene copies and the ratio of bacteria to fungal gene copies significantly linearly decreased in abundance with the duration of farming abandonment. In contrast, fungal biomass exhibited a weak linear increase with the time in response to farming abandonment (Fig. S2).

Although there were mostly no significant effects of farming

Table 1
Soil properties of different sampling sites. Values are means of three replicates with standard errors shown in parentheses. Different lowercase letters indicate significant differences across sites ($p < 0.05$).

Index	FS	AF2	AF5	AF10	DS
pH	8.6(0.2)^{b}	8.8(0.3)^{b}	9.1(0.1)^{ab}	9.3(0.3)^{a}	8.8(0.1)^{b}
EC (us/cm)	177.8 (49.5)	152.7 (46.3)	96.5 (14.8)	222.6 (112.3)	86.6 (17.9)
SM (%)	16.2(0.8)^{a}	6.4(0.4)^{b}	5.9(0.3)^{b}	5.9(0.6)^{b}	3.9(0.2)^{c}
TOC (%)	2.0(0.4)^{a}	1.1 (0.03)^{b}	1.0(0.2)^{b}	1.3(0.2)^{b}	0.6(0.1)^{c}
TN (‰)	0.6(0.1)^{a}	0.4 (0.02)^{b}	0.3(0.1)^{b}	0.3(0.03)^{b}	0.1 (0.04)^{c}
TP (g/kg)	0.7 (0.04)^{b}	0.8 (0.02)^{b}	0.9 (0.10)^{ab}	1.0(0.05)^{a}	0.7(0.1)^{b}
DOC (mg/kg)	14.6(3.5)^{a}	9.7(1.1)^{b}	8.4(3.3)^{b}	6.8(2.8)^{b}	15.2 (1.2)^{a}
DON (mg/kg)	24.5 (20.9)^{ab}	42.9 (21.6)^{a}	21.5 (8.8)^{ab}	14.5 (0.2)^{ab}	7.5(2.1)^{b}
AP (mg/kg)	16.1 (5.1)^{d}	51.7 (10.4)^{b}	66.5 (8.5)^{a}	36.5(3.4)^{c}	2.4(0.9)^{e}
AK (mg/kg)	202.3 (28.0)	252.3 (60.5)	195.7 (20.6)	246.0 (26.0)	194.0 (6.1)
Ammonia (mg/kg)	0.3(0.2)	0.1(0.06)	0.1(0.01)	0.1(0.01)	0.1(0.03)
Nitrate (mg/kg)	5.5(3.1)	8.1(3.2)	2.4(0.3)	3.5(0.7)	1.2(0.3)
C/N	32.6(8.4)	28.4(1.4)	31.1(3.2)	38.9(1.5)	76.5 (25.4)
C/P	2.7(0.6)^{a}	1.4 (0.02)^{ab}	1.1(0.3)^{ab}	1.3(0.3)^{ab}	0.8 (0.02)^{b}
N/P	0.08 (0.01)^{a}	0.05 (0.00)^{b}	0.04 (0.01)^{b}	0.03 (0.00)^{c}	0.01 (0.01)^{d}

Notes: FS, farmland site; AF2, 2-year abandoned farmland site; AF5, 5-year abandoned farmland site; AF10, 10-year abandoned farmland site; DS, native desert site; EC, electrical conductivity; SM, soil moisture; TOC, total organic carbon; TN, total nitrogen; TP, total phosphorus; DOC, dissolved organic carbon; DON, dissolved organic nitrogen; AP, available phosphorus; AK, available potassium

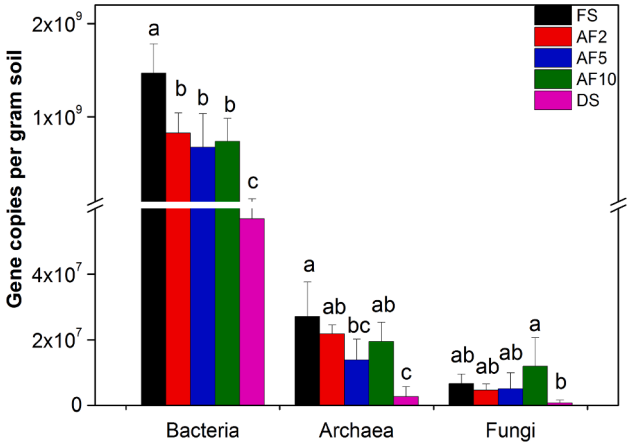

Fig. 2. The gene abundances (copies/g soil) of bacterial, archaeal and fungal taxonomic markers for different sites determined by qPCR. Bars represent standard deviations. Different lowercase letters indicate significant differences between different sites ($p < 0.05$).

reclamation and abandonment on microbial α-diversity, farming abandonment significantly affected bacterial OTUs, Chao1, and Ace species richness and archaeal Simpson index (Table S2). Significantly lower archaeal Ace species richness and higher fungal Chao1 species richness were detected in the FS soil than were found in the DS soil, while no significant differences in other α-diversity indices were found between FS and DS samples. In most cases, microbial α-diversity remained unchanged among FS and farming abandoned sites (AF2, AF5 and AF10). However, bacterial OTUs, Chao1, and Ace species richness increased during 5-year abandonment and then decreased after 10-year abandonment (Table 2).

The Bray-Curtis based PCoA indicated distinct dissimilarity of bacterial, archaeal and fungal communities based on the sampling site. This revealed that the within site variance in microbial community compositions was less than the variances between sites, signifying greater community variation associated with reclamation and abandonment. The first principal coordinates analysis axis (PCoA 1) explained 36.3, 51.0 and 22.8% of the variations, and the second axis (PCoA 2) represented 18.0, 24.5 and 15.3% of the variations in bacterial, archaeal and fungal communities, respectively (Fig. 3).

3.3. Taxonomic characteristics of microbial communities

In total, 770,566 bacterial, 628,687 archaeal and 1,044,937 fungal sequences were obtained across 15 soil samples after quality trimming and removing chimeric sequences and singletons, with an average number of 51,371, 41,912 and 69,662 sequences per site. These sequences were clustered into 3,330 bacterial, 877 archaeal and 1,531 fungal OTUs at 97% identity thresholds. The lowest number of sequences in one sample (19,390 for bacteria, 10,072 for archaea and 56,839 for fungi) were used in the downstream analysis to compare all soil samples without bias. In total, 35 bacterial, 5 archaeal, and 8 fungal phyla were detected across all soil samples, which consisted of 549 bacterial, 27 archaeal and 307 fungal genera. Out of the OTUs with > 1% abundance in one sample for each site, 32.8% bacterial, 11.7% archaeal and 7.1% fungal OTUs were shared by all samples. The unclassified bacterial, archaeal and fungal communities on average accounted for 14.5, 2.0 and 10.3% of the total relative abundance across all sampling sites at the phylum level, respectively.

Bacterial communities were dominated by *Proteobacteria* (28.8%), followed by *Actinobacteria* (22.2%), *Chloroflexi* (15.1%) and *Acidobacteria* (11.5%). Archaeal communities were dominated by *Thaumarchaeota* (80.5%) and *Euryarchaeota* (12.0%), and fungal communities were dominated by *Ascomycota* (82.6%) across all sites (Fig. 4). Heatmaps revealed that bacterial, archaeal and fungal community structures in the FS soil were most similar to the AF2 soil and

Table 2
The α-diversity of microbial communities in different sampling sites. Values are means of three replicates with standard errors shown in parentheses. Different lowercase letters indicate significant differences across sites ($p < 0.05$).

	OTUs	Chao1	Shannon	Simpson	Ace
Bacteria					
FS	1680 (70)^{bc}	2019 (86)^{bc}	6.38(0.08)	0.004 (0.001)	1999(88)^{bc}
AF2	1814(4)^{ab}	2248 (53)^{ab}	6.42(0.01)	0.005 (0.000)	2199(19)^{ab}
AF5	1850(40)^{a}	2293(38)^{a}	6.33(0.10)	0.007 (0.002)	2264(41)^{a}
AF10	1627(65)^{c}	2022 (84)^{bc}	6.14(0.03)	0.007 (0.000)	2002(89)^{bc}
DS	1631(55)^{c}	1954(97)^{c}	6.20(0.05)	0.006 (0.001)	1936 (105)^{c}
Archaea					
FS	179(21)	240(33)	2.99(0.24)	0.172 (0.063)	247(28)^{b}
AF2	218(27)	302(51)	3.15(0.05)	0.100 (0.004)	331(67)^{ab}
AF5	253(48)	350(60)	3.01(0.10)	0.116 (0.007)	370(66)^{ab}
AF10	143(39)	222(71)	2.51(0.16)	0.176 (0.016)	262(86)^{ab}
DS	322(110)	433(117)	2.96(0.39)	0.194 (0.031)	488(104)^{a}
Fungi					
FS	441(28)	495(27)^{a}	3.65 (0.21)^{ab}	0.069 (0.014)	494(28)
AF2	358(20)	397(17)^{ab}	3.41 (0.23)^{ab}	0.082 (0.019)	405(19)
AF5	396(8)	442(23)^{a}	3.89(0.08)^{a}	0.045 (0.006)	441(23)
AF10	357(31)	409(27)^{ab}	3.27(0.16)^{b}	0.089 (0.013)	407(31)
DS	260(90)	273(99)^{b}	3.88(0.04)^{a}	0.042 (0.005)	273(98)

Notes: FS, farmland site; AF2, 2-year abandoned farmland site; AF5, 5-year abandoned farmland site; AF10, 10-year abandoned farmland site; DS, native desert site

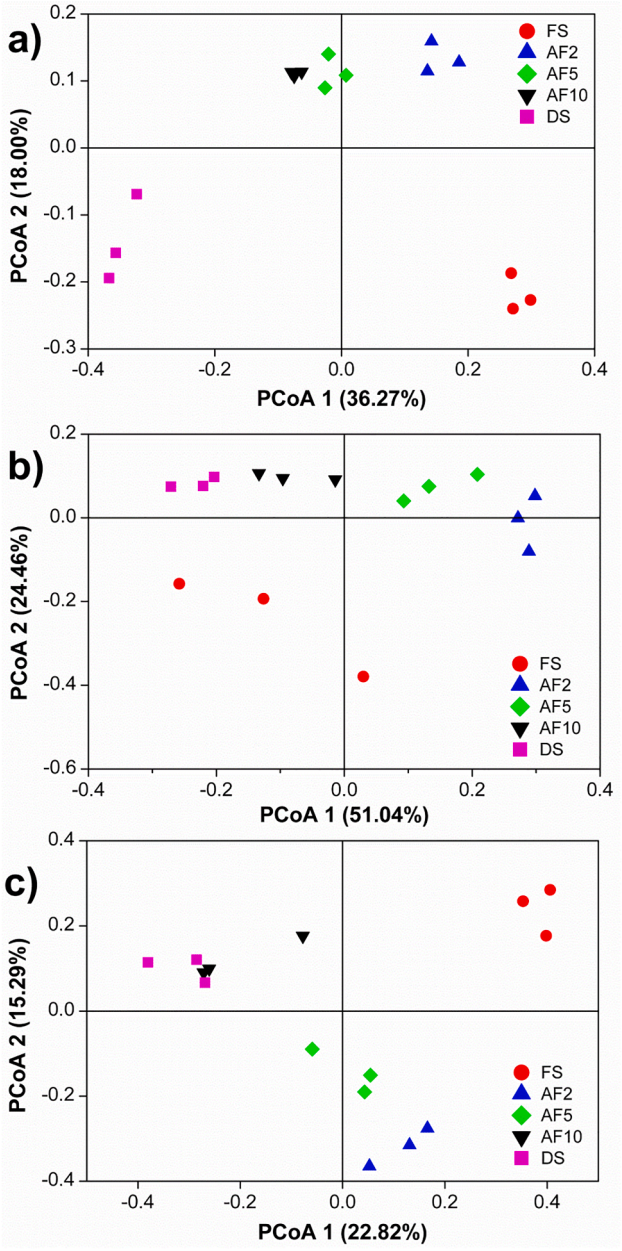

Fig. 3. Principal coordinate analysis (PCoA) of bacterial (a), archaeal (b) and fungal (c) communities based on Bray–Curtis distances at the OTU level.

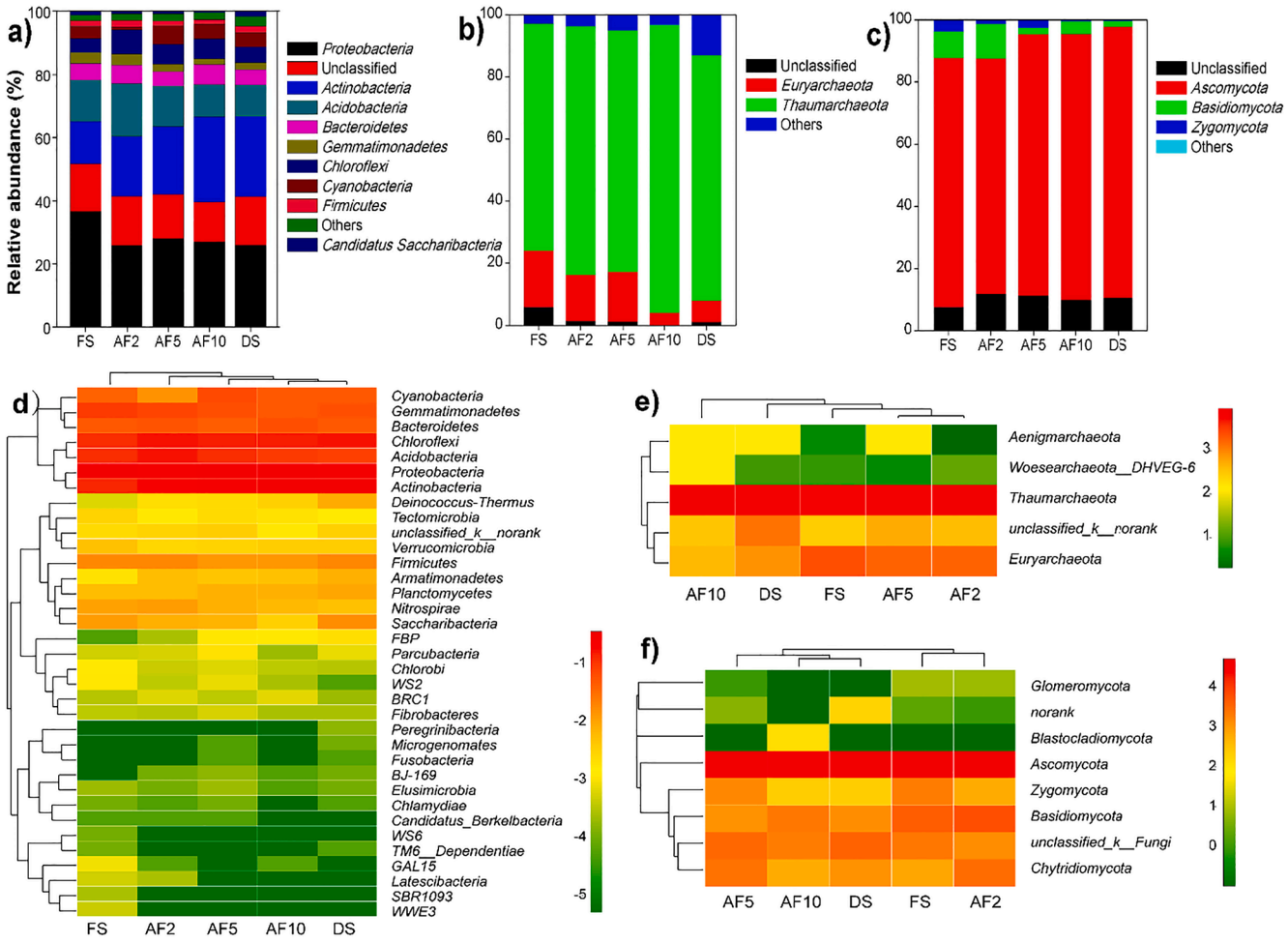

Fig. 4. Relative abundances of bacterial (a), archaeal (b) and fungal (c) communities at the phylum level and heatmaps of bacterial (d), archaeal (e) and fungal (f) phyla. Only taxa with 1% relative abundance at least in one soil sample are shown.

least similar to the DS soil, while that in the AF10 soil were more similar to the DS soil (Fig. 4d-f), suggesting microbial community structures succeed towards the native desert soil after farming abandonment.

3.4. Statistically significant differences in microbial communities

LEfSe analysis revealed 26 bacterial, 4 archaeal and 3 fungal groups had significantly different relative abundance based on their sampling sites (Fig. 5). The FS soil had the most distinct community compositions, comprising most archaeal and fungal taxa that had significant effect sizes in delineating sampling site. Many bacterial taxa were significantly more abundant in the DS and AF2 soils, and several archaeal and fungal taxa were also significantly enriched in the AF2 soil. At the class level, 7 bacterial, 3 archaeal and 3 fungal classes of the top 20 bacterial, 5 archaeal and 15 fungal dominant classes showed significant differences in their proportions among different sites (Fig. S3).

Farming reclamation significantly increased bacterial proportions of *Proteobacteria* (36.7% FS vs 25.9% DS) and *Nitrospirae* (1.0% FS vs 0.5% DS), and decreased that of *Actinobacteria* (13.8% FS vs 26.8% DS), *Armatimonadetes* (0.2% FS vs 0.7% DS) and *Deinococcus-Thermus* (0.1% FS vs 0.8% DS). Although the proportions of fungal phylum *Glomeromycota* showed a significant increase in the FS soil (0.01% FS vs 0% DS), no significant differences in other archaeal and fungal phyla proportions between the FS soil and the DS soil were found. After farming abandonment, the proportion of bacterial class *Actinobacteria* gradually increased with the duration of abandonment, while some other bacterial classes (*Acidobacteria, Gemmatimonadetes*, *Betaproteobacteria*, *Gammaproteobacteria*, *Anaerolineae* and *Nitrospirae*) declined in relative abundance. However, no stark variations in the proportions of dominant archaeal and fungal classes were detected (Fig. S3).

3.5. Relationships between microbial communities and soil properties

The abundances of bacterial, archaeal and fungal populations linearly decreased with increased soil C/N ($p < 0.001$), and bacterial abundance linearly increased with increased soil TOC ($p < 0.001$). Linear equations based on microbial gene abundance and soil C/N and TOC across all sites explained >60% of the variations in bacterial, archaeal and fungal gene abundances. Although no significant associations were revealed between bacterial or archaeal community diversities (Shannon index) and soil properties, fungal diversity linearly decreased with increased SM and AK ($p = 0.01$, Table 3).

The results of Mantel tests indicated that soil properties strongly correlated with microbial community structure. Bacterial, archaeal and fungal communities positively correlated with SM, TOC, TN, AP and the ratios of C, N and P ($p < 0.05$). Bacterial communities also positively correlated with TP and nitrate, and archaeal communities were positively correlated with DON ($p < 0.05$, Table 4). However, the relationships between microbial communities and soil properties varied for different taxa. For instance, bacterial classes of *Actinobacteria*, *Thermomicrobia* and *Chloroflexia* were significantly negatively correlated with TN, while the classes of *Gemmatimonadetes*, *Betaproteobacteria*, *Gammaproteobacteria*, *Anaerolineae* and *Nitrospira* positively correlated to TN (Table S3). While archaeal class of *Thermoplasmta* positively

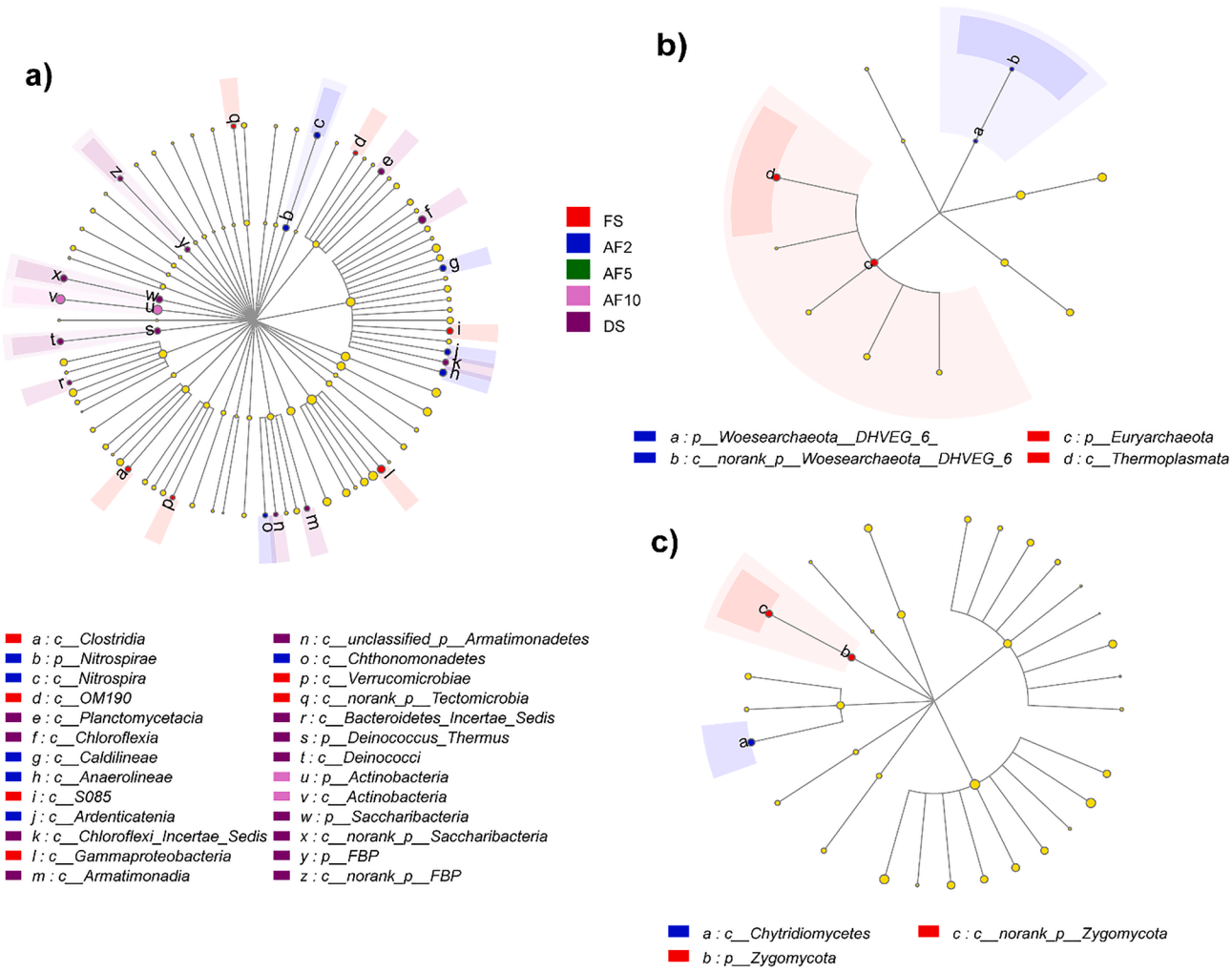

Fig. 5. LEfSe analysis of microbial taxa significantly enriched in each individual site. a), b) and (c) are the cladograms of bacterial, archaeal and fungal communities, respectively.

Table 3
Stepwise linear regressions between microbial gene abundance and diversity of microbial communities and soil properties, only significant equations are shown.

Microbialgroup	Ln (qPCR abundance)			Shannon index		
	Equation	R^2	*p*	Equation	R^2	*p*
Bacteria	Y = -0.06*C/N + 1.16*TOC + 20.89	0.90	<0.001	-	-	-
Archaea	Y = -0.06*C/N + 18.76	0.90	<0.001	-	-	-
Fungi	Y = -0.05*C/N + 17.15	0.61	0.001	Y = -0.002*SM-0.004*AK + 4.89	0.53	0.011

Notes: TOC, total organic carbon; SM, soil moisture; AK, available potassium

associated with AP, the class of *Methanomicrobia* was negatively correlated with AP (Table S4). Fungal classes of *Sordariomycetes, Agaricomycetes* and *Blastocladiomycetes* positively associated with SM, while the class of *Dothideomycetes* negatively correlated with SM (Table S5). The first two axes of RDA or CCA explained 48.8, 89.0 and 24.4% of the variations in bacterial, archaeal and fungal community structures, respectively (Fig. 6).

4. Discussion

4.1. Impacts of farming reclamation on soil chemical and microbial properties

Prior studies have found that N fertilization decreased soil pH in comparison with unmanaged desert (Li et al., 2015; Wang et al., 2019) and other non-fertilized biomes (Ramirez et al., 2010). However, we did not find significant change in soil pH after farmland reclamation, which suggests that short-term fertilization had no effects on desert soil pH in the arid region. As we expected, a significant improvement of soil fertility characterized by C and N enrichments was observed after farming reclamation probably due to fertilization and accumulation of organic matter from crop residues and roots (Wang et al., 2019). Also, the higher TOC observed in the FS soils may be derived from crop root exudations and rhizodeposition (e.g. sloughed root material and exudates) and their corresponding influence on microbial activity and biomass that contribute to soil C and its stabilization. The observed N enrichments might be ascribed to the applied N from fertilization, returns to soil N from crop residues, and enhanced microbial N due to microbial community stimulus. Likely, most of the observable increase in soil N can be attributed to N fertilization with a minor component

Table 4
Mantel tests of UniFrac distances of microbial communities and their relationships with soil properties, with the *r* values reported. Values in bold represent significant differences at $p < 0.05$ (*) and $p < 0.01$(**).

Variables	Bacteria	Archaea	Fungi
pH	0.02	0.04	0.16
EC	0.25	0.04	0.01
SM	**0.76****	**0.56****	**0.62****
TOC	**0.77****	**0.46****	**0.57****
TN	**0.76****	**0.38****	**0.54****
TP	**0.22***	0.09	0.17
DOC	-0.02	0.08	0.08
DON	-0.02	**0.39****	0.14
Ammonia	0.03	-0.07	0.10
Nitrate	**0.33***	0.16	0.17
AP	**0.66****	**0.57****	**0.46****
AK	-0.18	-0.08	-0.13
C/N	**0.59****	**0.29***	**0.40****
C/P	**0.70****	**0.46****	**0.54****
N/P	**0.84****	**0.46****	**0.68****

Notes: EC, electrical conductivity; SM, soil moisture; TOC, total organic carbon; TN, total nitrogen; TP, total phosphorus; DOC, dissolved organic carbon; DON, dissolved organic nitrogen; AP, available phosphorus; AK, available potassium

associated with C accumulation, which lead to significant decreases in soil C/N and increases in N/P.

In supporting our first hypothesis, the qPCR-based estimations revealed that microbial biomass significantly increased when native desert was converted into cropland. The enhanced microbial biomass in cropland soil was likely attributed to continuous irrigation and fertilization and increased plant biomass (Hu et al., 2017; Lazcano et al., 2013). In general, soil water availability and nutrients are limiting factors for microbial growth in drylands (Angel et al., 2013; Maestre et al., 2015). Additional water supply and fertilization can improve water and nutrient availabilities that sustain greater microbes by populations densities. Moreover, the increased root growth and return of crop residues also enhance inputs of exudates and substrates to soil that can be utilized by soil microorganisms (Ding et al., 2013; Li et al., 2015). Farming reclamation did not impose significant changes in bacterial and archaeal α-diversity, which is inconsistent with other studies (Köberl et al., 2011; Wang et al., 2019). However, fungal richness increased in the farmland compared to that in native desert, which is similar to previous reports (Li et al., 2018; Wang et al., 2019). These findings indicate that soil fungal diversity was more sensitive to land-use transformation for agriculture than bacterial and archaeal communities in the arid desert. These findings revealed that land-use transformation from desert into cropland did not necessarily result in increased microbial community diversity, though shifts in abundant taxa and in microbial biomass occurred (Li et al., 2015; Li et al., 2018).

High-throughput sequencing analysis revealed a strong and significant effect of farming reclamation on microbial community structure. One of the possible explanations is the difference in plant composition. In desert ecosystem, farming introduced a novel rhizosphere environment, which is considered as a main factor in shaping microbial community structures (Costa et al., 2006; Mendes et al., 2011). The diverse and indigenous desert vegetation in the native desert was replaced by maize after farming reclamation. The shift to a virtual monoculuture may be responsible for significant losses of some indigenous microbial communities in the rhizosphere of desert plants and enrichments of other crop rhizosphere microbial communities, evidenced by our results of the LEfSe analysis. There were fewer changes in fungal taxa abundances than revealed for bacterial taxa, which might reflect the capacity of fungal taxa to thrive on diverse substrates and under variable environmental conditions (Wu, 2011; Chen et al., 2014). Alternatively, the copiotrophic-oligotrophic hypothesis may explain differential responses of bacterial communities to farming reclamation. Bacterial taxa have been grouped based on life-strategies, where copiotrophs have high

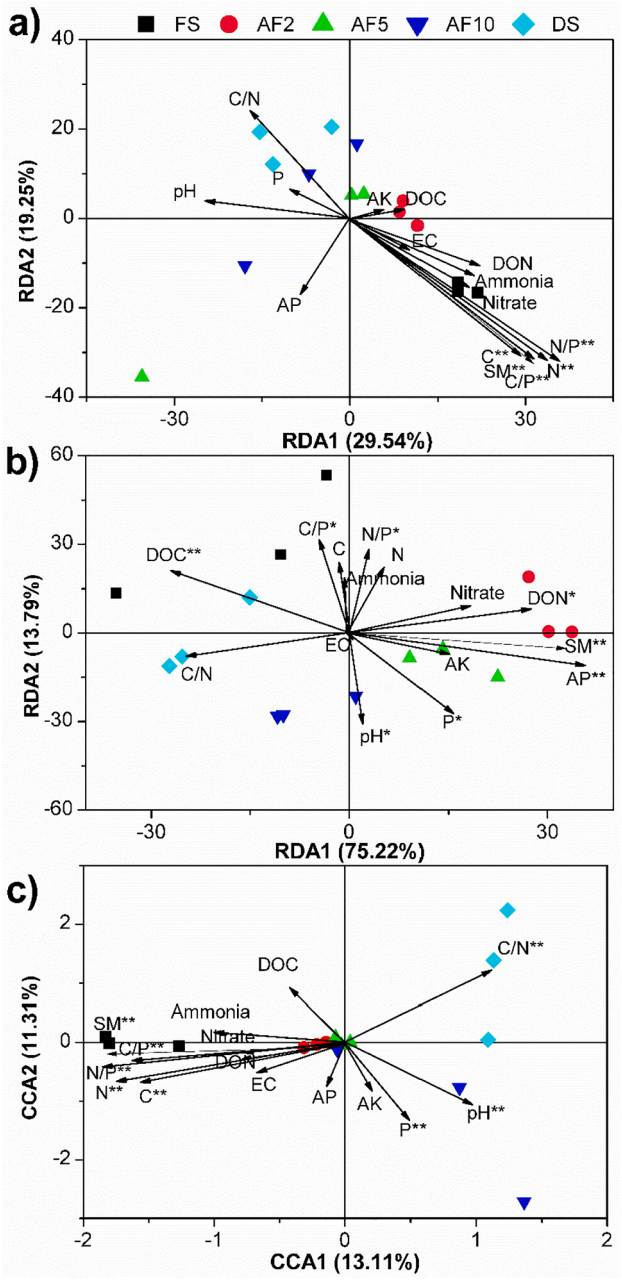

Fig. 6. Redundancy analysis (RDA) and canonical correspondence analysis (CCA) for bacterial (a), archaeal (b) and fungal (c) communities and soil properties. Significant differences are shown at $p < 0.05$ (*) and $p < 0.01$ (**).

growth rates and prefer nutrient-rich conditions and oligotrophs have slow growth rates but thrive in nutrient-poor environments (Fierer et al., 2007; Ding et al., 2013; Lienhard et al., 2014). Thus, an enhanced proportion of copiotrophic bacteria and reduced proportion of oligotrophs were expected in the FS soils due to increased nutrient availability from agriculture fertilization, crops residues and root exudates compared to the DS nature ecosystem (Fierer et al., 2012; Koyama et al., 2014). *Proteobacteria* and *Actinobacteria* have been reported as the dominant bacteria phyla in dryland soils (Maestre et al., 2015; Lüneberg et al., 2018) and are often classified as copiotrophs (Fierer et al., 2007; Ramirez et al., 2012; Lienhard et al., 2014), while *Acidobacteria* and *Nitrospirae* are considered as oligotrophs (Fierer et al., 2007; Ding et al., 2013; Lienhard et al., 2014). However, our study revealed that farming reclamation significantly enhanced the proportions of *Proteobacteria* expectedly, but also increased *Nitrospirae* relative abundances, and

reduced relative abundances of several other bacterial phyla (*Actinobacteria*, *Armatimonadetes* and *Deinococcus-Thermus*). Moreover, farmland reclamation increased the proportions of *Acidobacteria* though no significant difference was found between the farmland soil and the native desert soil, which is inconsistent with other studies (Bissett et al., 2011; Ding et al., 2013). Higher proportions of *Nitrospirae* in the farmland soil than the native desert soil might be attributed to high N supply from fertilization (Maestre et al., 2015). In addition, the changes to the soil water content imposed by irrigation could also be responsible for the shifts of microbial community structure. The contrasting responses of *Actinobacteria* and *Acidobacteria* might be attributed to their contrasting differences in ribosomal synthesis in response to irrigation inputs/soil wetting, a decrease for *Actinobacteria* and increase of *Acidobacteria* relative abundances in response to rewetting were previously reported (Barnard et al., 2013). Our study revealed enriched *Euryarchaeota* in farmland soil compared to the native desert soil. Many organisms within this phylum are closely involved in methane production under anaerobic condition (Angel et al., 2011). Higher soil moisture in farmland might create anaerobic environments in water filled pore spaces that promote some methanogenic archaeal communities (e.g. the classes of *Methanobacteria* and *Thermoplasmata*). Our results also confirmed that farming reclamation increased propotions of *Zygomycota*, which was associated with higher nutrient availability delivered by fertilization (Richardson, 2009). In this study, greater returns of crop debris after farming reclamation may have enriched *Zygomycota*, which are able to decompose this crop debris.

4.2. Impacts of farming abandonment on soil chemical and microbial properties

A weak increase in pH after farming abandonment might have resulted from salt enrichment in the soil surface once a lack of irrigation reduced salt leaching through the soil profile. The decreased soil nutrients and moisture revealed promptly after farming abandonment indicated a fast rate at which desert farmland soil would return to a state with low fertility and dry conditions. Declines in soil DOC with the duration of farming abandonment signified reduced substrates for microbial respiration.

In support of our first hypothesis, the increase in bacterial and archaeal biomass associated with reclamation was followed by a decline as a consequence of abandonment. This was supported in other studies, wherein increased biomass was attributed to enhanced soil fertility across a revegetation chronosequence (Hu et al., 2019). Exhausted soil nutrients and drier soil conditions might contribute to the declines in microbial biomass after farming abandonment (Maestre et al., 2015). However, fungal biomass showed a weak increase after abandonment, which might be ascribed to elimination of tillage disturbance (Chen et al., 2020). A previous recent study revealed that decreased microbial diversity was associated with declined soil moisture across biogeographic space (Maestre et al., 2015). However, bacterial species richness increased and then decreased across the abandonment chronosequence though declines in soil moisture occurred immediately following farming abandonment. Still, there were no significant differences in most archaeal and fungal α-diversity metrics among the different sites. These findings might reflect microbial adaption, wherein microorganisms from the harsh desert environment had strong desiccation resistances and as such the soils maintained a seed bank with high diversity even when water and nutrient resources became scarce. The increased bacterial diversity might have resulted from the cease of tillage, similar to previous reports (Lu et al., 2019; Li et al., 2020).

The proportion of *Actinobacteria* gradually increased, while those of *Acidobacteria, Gemmatimonadetes*, *Saccharibacteria* and *Nitrospirae* decreased with the duration of farming abandonment. Similar changes in the proportions of *Actinobacteria* and *Acidobacteria* were demonstrated in response to dry-down (Barnard et al., 2013) and N fertilization (Ramirez et al., 2012) in other biomes. Although reclamation resulted in increased *Acidobacteria* and decreased *Actinobacteria* relative abundances, this trend was reversed with abandonment, where *Acidobacteria* declined and *Actinobacteria* increased with abandonment duration, further supporting the copiotrophic-oligotrophic theory and/or their differential responses to desiccation and wetting (Barnard et al., 2013). However, the responses of archaeal and fungal communities did not parallel those of bacteria as they showed no significant trends in response to farming abandonment, implying reduced sensitivity of fungal and archaeal communities to the environmental shifts compared to the bacterial communities (Barnard et al., 2013). This might also indirectly reflect a competitive advantage of fungal microorganisms in nutrient acquisition over many bacteria (Wu, 2011; Chen et al., 2014). Overall, water desiccation responses and life-strategies emerged as important taxa characteristics to explain shifts in bacterial community structures in response to land-use transformation.

4.3. Association of microbial community abundance, diversity, and compositions with soil properties

Soil microbial biomass significantly linearly decreased with an increase in soil C/N, which indirectly implies N limitation for microbial growth in the desert soil. Strong relationships between microbial biomass and soil C/N ratios ($R^2 > 0.61$) reflect that desert soil microbial biomass can be evaluated by taking soil C/N as a good predictor. Moreover, bacterial biomass was positively related to soil TOC, confirming that bacterial growth may have been limited by a lack of available C substrates (Lazcano et al., 2013). However, bacterial and archaeal α-diversities (Shannon index) were not associated with soil properties, indicating that there were some other unknown factors in determining their diversities in the arid desert. Based on the negative relationships between fungal diversity and soil moisture and available K, we predicted that long-term irrigation and K fertilizers used for agriculture might lead to a reduction of desert soil fungal diversity owing to the inputs creating a relatively homogenous soil environment compared to the native desert soil, which may exacerbate the impacts of tillage.

Many soil factors including pH, salinity, soil moisture, C content and C/N have been widely reported to be key determinants of soil microbial community structure in drylands (Richardson, 2009; Drenovsky et al., 2010; Köberl et al., 2011; Maestre et al., 2015; Lüneberg et al., 2018; Li et al., 2018; Zhang et al., 2019). In support of our second hypothesis, we found soil moisture, TOC, TN and AP to be the key factors in structuring soil microbial communities, emphasizing the key roles of irrigation and fertilization in shaping desert soil microbial community structure (Köberl et al., 2011). Possibly, fertilization drove the shifts of microbial community structure through changing soil stoichiometry of C, N and P, as suggested by results of the Mantel tests. Ramirez et al. (2010) found that soil bacterial communities are more structured by N and/or soil C availability than by pH in grassland and other agroecosystems. Soil salinity has been reported as another key determinant for desert soil microbial community structure across biogeographic space (Zhang et al., 2019) as it alters soil solutes and differentially impacts microorganisms with varying osmotic tolerances (Yan et al., 2015). Despite higher EC detected in farmland soil than the native desert, most microbial community metrics did not correlate with EC in this study. Contrary to what has been reported (Köberl et al., 2011; Pasternak et al., 2013; Lüneberg et al., 2018), we found that bacterial, archaeal and fungal communities and most microbial classes were not associated with pH, but pH was not very divergent in these soils. These findings indicate that desert soil microbial communities were more structured by significant changes in soil moisture and soil fertility rather than small changes in soil pH and salinity caused by land-use transformations. However, it is noteworthy that here and in other studies, the relationships between microbial communities and soil properties were microbial taxa-dependent (Table S3-S5), owing to differences in their life-strategies (Fierer et al., 2007; Lüneberg et al., 2018) and metabolic and physiological characteristics (Fierer et al., 2012). This finding implies that

microbial taxonomic profiles as opposed to diversity indices might constitute more meaningful ecological units with which to understand microbial responses to land-use transformations in arid deserts. In addition, tillage practice can also affect soil microbial community structure owing to changes in soil macroaggregation and compaction that can mediate soil O_2 availability (Kihara et al., 2012; Lu et al., 2019). However, our study could not disentangle the effects of cropping, fertilization, irrigation and tillage on soil microbial succession, which is an area in need of further study.

4.4. Implications of farming reclamation and abandonment on ethical land management

Contrary to forest agricultural conversions (Kaschuk et al., 2011), desert reclamation revealed increased microbial biomass of bacteria, fungal and archaeal groups, and enhanced soil C and nutrients characteristics that are frequently associated with healthy and productive soils. This indicates that desert soil microbial communities can elicit a positive response to farming reclamation and support agricultural productivity. However, the abilities of these communities to rebound to natural states are a concern if water resource limitations may force abandonment of reclaimed lands. Our chronosequence of farming abandonment provided an opportunity to investigate soil microbial community dynamics in response to a sudden halt in intensive farming in the arid desert. Soil microbial diversity is another indicator of soil quality (Schloter et al., 2003), which has been closely linked with ecosystem functions (Bernhard and Kelly, 2016). For the most part, no significant differences in microbial diversity among farmland soil and abandoned farmland soils were detected, but we found increased bacterial richness in some cases and enhanced fungal community biomass after 5 years of abandonment compared to the farmland soil. These insights indicate community resilience to land use changes and the capacity of microbial communities to sustain diversity with the loss of agricultural nutrient and water inputs. However, there are also some concerns. If these microbial communities were impacted too severely, then the functions and roles of the desert soil microbial communities may be lost. Compared to the native desert soils, soil microbial communities in abandoned reclaimed soils did not return to their unmanaged state even after 10 years, indicating some irreversible implications of land-use changes. This could impact potential essential ecosystem services of native desert soil biota. Notably, wind erosion of desert soils is typically reduced by a major complex of superficial soil microorganisms, e.g. desert soil crusts (Liu et al., 2017; Hu et al., 2019). Therefore, while desert farming may be agronomically productive, consideration of how this ecosystem will be impacted after abandonment is important if any future land conversions are to be recommended. Further work is still required to address how changes of soil microbial community structure influence desert soil ecological processes and functions.

5. Conclusions

In summary, the land-use transformation of native desert for agriculture caused profound changes in soil physicochemical characteristics and microbial community structure in response to both farming reclamation and farming abandonment. These findings imply that desert soil microbial community structures were reshaped by cropping, irrigation, fertilization and tillage for agriculture. Some changes in microbial community structure were irreversible, as communities did not return to unmanaged states after short-term abandonment. These findings provide insights into microbial responses to desert soil degradation caused by anthropogenic land-use transformation and should be considered when developing sustainable agriculture plans. Future work should test the independent effects of crop plantation, irrigation, fertilization and tillage on soil microbial communities. Additionally, changes to desert soil ecological processes and functions that parallel shifts in microbial community characteristics should be evaluated.

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 material

Supplementary data to this article can be found online at https://doi.org/10.1016/j.catena.2021.105678.

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