Received: 21 April 2019 | Revised: 21 September 2019 | Accepted: 24 September 2019

DOI: 10.1111/ejss.12901

ORIGINAL ARTICLE

European Journal of Soil Science WILEY

Soil structure and nutrient supply drive changes in soil microbial communities during conversion of virgin desert soil to irrigated cropland

Long-Fei Chen | **Zhi-Bin He** | **Wen-Zhi Zhao** | **Ji-Liang Liu** | **Hai Zhou** | **Jing Li** | **Yang-Yang Meng** | **Li-Sha Wang**

Linze Inland River Basin Research Station, Chinese Ecosystem Research Network, Key Laboratory of Eco-hydrology of Inland River Basin, Northwest Institute of Eco-Environment and Resources, Lanzhou, China

Correspondence
Zhi-Bin He, Linze Inland River Basin Research Station, Chinese Ecosystem Research Network, Key Laboratory of Eco-hydrology of Inland River Basin, Northwest Institute of Eco-Environment and Resources, Chinese Academy of Sciences, Lanzhou 730000, China.
Email: hzbmail@lzb.ac.cn

Funding information
Key Program of the Chinese Academy of Sciences, Grant/Award Number: QYZDJ-SSW-DQC040; National Key Research and Development Program of China, Grant/Award Number: 2017YFC0504306; Strategic Priority Program of the Chinese Academy of Sciences, Grant/Award Number: XDA2003010102; General Program of the National Natural Science Foundation of China, Grant/Award Number: 41771290, 41877153; CAS "Light of West China" Program, Grant/Award Number: 29Y829861

Abstract

Soil microorganisms are critical to soil health and environmental functions; however, the dynamics of microbial communities and their response to soil variables following conversion of desert soils to oasis farmland have not been well documented. We used high-throughput pyrosequencing to investigate the dynamics of soil microbial communities along an irrigated cultivation chronosequence (cultivated for 16, 33, 45 and 60 years) and in adjacent non-cultivated soil in a desert-oasis ecotone in northwestern China. Additionally, we explored which soil variables may be responsible for shifts in microbial communities. Generally, cultivation in desert soil increased microbial community abundance and diversity; however, bacterial abundance and diversity increased along the cultivation chronosequence, whereas fungal abundance and diversity initially increased and then decreased. Continuous crop cultivation also resulted in a shift in microbial community composition, notably with a decrease in nitrogen (N)-fixing microbes (*Proteobacteria* and *Cyanobacteria*) and an increase in ammonia-oxidizing (*Nitrosomonadales*) and nitrite-oxidizing microbes (*Nitrospirae*). Redundancy analysis showed that soil organic carbon, total N, available N, available phosphorus and bulk density explained over 80% of the variation in both bacterial and fungal communities; this indicated the critical roles of nutrient supply and soil structure in shaping the composition and diversity of microbial communities during the conversion of native desert soils to irrigated croplands.

Highlights

- Cultivation in desert soil increased microbial community abundance and diversity.
- Cultivation decreased N-fixing microbes.
- Cultivation increased ammonia-oxidizing and nitrite-oxidizing microbes.
- Soil structure and nutrient supply shaped the diversity of microbial communities.

KEYWORDS

cultivation, bacterial community, fungal community, Illumina MiSeq platform, desert-oasis region

1 | INTRODUCTION

Desert soils in arid northwestern China have been cultivated for crop production since the Han Dynasty (206 B.C. – 220 A.D.) (Li et al., 2009; Zhao, Yang, Liu, Yang, & Li, 2016). Agriculture intensified in the region to accommodate the rapidly growing population and a consequent increase in food demand and included the expansion of cultivated oases during the period from the middle to the end of the last century (Huang, Wang, & Zhang, 2007; Li & Yan, 2013). The expansion of arable land into oases significantly increased grain production and altered landscape patterns (Feng et al., 2010; Li, Tang, Jia, & Li, 2015; Zhao et al., 2016). However, intensive land management poses serious environmental risks, such as water shortages, desertification and salinization (Liu, Zhao, Chang, Li, & Du, 2010; Wang, Xiao, Li, & Li, 2008). Therefore, interest in sustainable agriculture in cultivated desert soils has been steadily increasing (Li et al., 2009; Zhang, Zhao, & Fu, 2017; Zhao et al., 2016). To date, most of the studies have focused on the effects of cultivation on soil physicochemical properties and macrofauna community composition (Huang, Zeng, & Lei, 2015; Li et al., 2009; Li et al., 2013), whereas the responses of microbial communities remain poorly understood (Cheng, Chen, & Zhang, 2018; Li, Liu, Ren, & Liu, 2018; Wang et al., 2012).

Microbes are the most abundant and diverse group of soil organisms (Mcguire & Treseder, 2010). They play an essential role in driving soil biogeochemical processes, including nutrient cycling, atmospheric nitrogen (N) fixation, decomposition of organic materials and pollutants, the formation of aggregates and stabilization of soils (Bardgett & Putten, 2014; Rashid et al., 2016; Schimel & Schaeffer, 2012; Singh, Bardgett, Smith, & Reay, 2010). Because of their vast importance, microbial community composition and diversity are often used as an indicator of soil health, especially in microbially dominated desert ecosystems (Bastida, Hernández, Albaladejo, & Carlos, 2013; Fu, Zou, & Coleman, 2009; Mcguire & Treseder, 2010). Characterization of the structure and diversity of soil microbial communities, and of their relationships with environmental factors, is essential for a comprehensive evaluation of soil health and the sustainability of croplands in desert-oasis ecotones (Li et al., 2018; Wang et al., 2012).

Desert ecosystems are close to the physical limitations of life and soil microbes are generally severely constrained by available liquid water, and organic matter and nutrient supplies (Ball, Adams, Barrett, Wall, & Virginia, 2018; Crits-Christoph et al., 2013; Mccrackin, Harms, Grimm, Hall, & Kaye, 2008; Pajares, Escalante, Noguez, & García-Oliva, 2016). Conversion of virgin desert to arable land involves agricultural practices, such as tillage, fertilization and irrigation, that have large effects on soil moisture, carbon (C) cycling and nutrient availability (Li et al., 2009; Su, Yang, Liu, & Wang, 2010; Zhang et al., 2017), and thus have the potential to greatly influence the diversity and composition of soil microbial communities. For example, fertilizer application resulted in a significant increase in soil bacterial abundance in the Gurbantonggut Desert (Li, Yan, Tang, Jia, & Li, 2014); similar trends for soil bacterial abundance were also observed in the Badain Jaran Desert (Li et al., 2018). Van Horn et al. (2014) observed that increased moisture and organic resources inputs would further stimulate microbial activity and result in a shift in community composition to copiotrophic organisms in a polar desert of Antarctica. In addition, the changes in soil structure often observed following the conversion of native desert soils to irrigated croplands could also explain changes in microbial community structure (Lozano, Hortal, Armas, & Pugnaire, 2014; Cheng, Zhang et al. 2018).

The oasis area in the middle to lower reaches of the Heihe River Basin, the second largest inland river in the arid area of northwestern China, had increased from 2,412 km^2 in 1949 to 6,766 km^2 in 2010 due to the transformation of desert to oasis farmland (Zhao, 2012). Maintaining soil quality in these croplands is important for sustainable productivity and stability of the entire oasis ecosystem (Zhao et al., 2016; Cheng, Chen et al., 2018). In this study, we investigated the dynamics of soil microbial communities along a cultivation chronosequence using high-throughput pyrosequencing, and explored the role of selected soil properties in shifts in microbial communities in a desert-oasis ecotone in the Heihe River Basin, northwestern China. We hypothesized that (a) continuous cultivation resulted in a strong shift in microbial community diversity and composition; and (b) soil structure, water and nutrient supply drive changes in soil microbial communities during conversion of virgin desert soil to irrigated cropland.

2 | METHODS

2.1 | Study sites

The study was conducted in a centuries-old artificial oasis (100°07'E, 39°21'N; 1384 m a.s.l.) in the middle reaches of the Heihe River Basin. The area is situated in Linze County, Gansu Province, bordering the Badain Jaran Desert to the north. The site has a temperate, arid and continental climate, with a mean annual temperature (MAT) of about 7.6°C. Mean annual precipitation (MAP) is about 117 mm, about 80% of which occurs during the

growing season (May to September) (Li et al., 2013). Major landscape types in the study region include a peripheral desert, desert-oasis ecotone and central oasis. In the desert-oasis ecotone, the soils are generally coarse textured and are classified as Calcic Yermosol according to the WRB system. Crop production depends fully on irrigation, with water originating from the Heihe River.

Since the 1950s, desert soils have been gradually converted to farmland to mitigate the pressure of population growth (Zhao, 2012). Major crops grown in the area are maize (*Zea mays L.*) and spring wheat (*Triticum aestivum L.*), with one harvest per year. Before the year 2000, spring wheat-maize strip intercropping was the main cultivation pattern. Since then, seed maize monoculture has become widely practised in the area. Fertilization rates in maize in the last 20 years reached 250–350 kg CH_4N_2O ha^{-1}, 90–150 kg P_2O_5 ha^{-1} and 60–90 kg K_2O ha^{-1} per year. Farmyard manure is also applied annually at about 3,000 to 6,000 kg ha^{-1}. Fields are irrigated six to eight times during the maize-growing season using flood irrigation.

2.2 | Experimental design and soil sampling

Our study site was located at the desert-oasis ecotone, near the Linze Inland River Basin Research Station, Chinese Academy of Sciences. We selected four sites to represent a cultivation chronosequence, with sites cultivated in natural sandy lands for 16, 33, 45 and 60 years; additionally, one adjacent, non-cultivated virgin sandy-land site served as a reference (control). The period of cultivation of each cropland was determined from the records at the station or by interviewing farm owners. Previous studies at this site showed that soil properties in the croplands before cultivation were similar to those in the adjacent non-cultivated sandy areas (Su et al., 2010; Zhang et al., 2017).

In September 2017, about 20 days after the latest irrigation, three 30 m × 30 m plots were established in each cropland site and in the control, giving a total of 15 sample plots. Within each plot, 12 samples of topsoil (0–20 cm) were collected along an S-shaped pattern from each plot after removal of the litter layer and then mixed to form one soil sample. Subsequently, visible roots and litter debris were removed from each soil sample, which was then sieved through a 2-mm soil sieve. Then, samples were divided into two subsamples. One subsample was immediately stored at −80 °C for later DNA analysis and the other subsample was air-dried for physicochemical analysis. In addition, five undisturbed soil cores were obtained from each plot for the measurements of soil moisture content (SM) and bulk density (BD) using a standard container with a volume of 100 cm^3.

2.3 | Analysis of soil physical and chemical properties

Soil pH was determined with a pH meter (PHS-3C pH acidometer, Shanghai Puchun Measure Instrument Co., Ltd., Shanghai, China) in a soil:water ratio of 1:5. Soil salinity was measured with inoLab® Cond 7310 (WTW, Munich, Germany) in 1:5 soil:water suspensions (Cao, Ding, & Yu, 2016). Soil organic carbon (SOC) was determined with the $K_2Cr_2O_7$-H_2SO_4 oxidation method of Walkley-Black (Nelson, Sommers, Page, Miller, & Keeney, 1982). Total nitrogen (TN) was measured with the Kjeldahl method (Jackson, 1973). Total phosphorus (TP) was determined colorimetrically after wet digestion with H_2SO_4-$HClO_4$ (Parkinson & Allen, 1975). The easily oxidizable organic carbon (EOC) was determined with the $KMnO_4$ (33 mmol L^{-1}) oxidation method described by Blair, Lefroy, and Lisle (1995). Ammonium-N (NH_4^+-N) and nitrate-N (NO_3^--N) were determined with an AA3 Continuous Flow Analytical System (Bran+Luebbe, Norderstedt, Germany) following extractions of fresh soil with 1 mol L^{-1} KCl. Available phosphorus (AP) was measured with the Olsen method (Olsen & Sommers, 1982).

2.4 | DNA extraction and sequencing

Deoxyribonucleic acid (DNA) was extracted directly from 0.5 g of the soil samples (fresh weight) using a Fast DNA Spin Kit (MP Biomedicals, Santa Ana, CA, USA) according to the manufacturer's instructions. The DNA extracts were quantified with 1% agarose gel electrophoresis and a spectrophotometer (NanoDrop ND-1000, NanoDrop Technologies, Wilmington, MA, USA). Soil bacterial community composition was evaluated by amplifying the V4-V5 region of the 16S rRNA gene using PCR primers 515F (5′-GTGCCAGCMGCCGCGG-3′) and 907R (5′-CCGTCAATTCMTTTRAGTTT-3′) (Biddle, Fitzgibbon, Schuster, Brenchley, & House, 2008; Jing et al., 2015). Soil fungal community composition was assessed by sequencing the internal transcribed spacer (ITS) rRNA gene using primers ITS1F (5′-CTTGGTC ATTTAGAGGAAGTA A-3′) and ITS2R (5′-GCTGCGTT CTT CATCGATGC-3′) (Tedersoo, Kõljalg, Hallenberg, & Larsson, 2003).

Polymerase chain reactions (PCR) were performed in triplicate in 20 μL mixtures containing 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 and 10 ng Template DNA. The amplification procedure was as follows: 95°C

for 5 min; 27 cycles of 95°C for 30 s, 55°C for 30 s and 72°C for 45 s; and 72°C for 10 min. The PCR amplicons were detected with 2% agarose gel electrophoresis. The triplicate amplicons were pooled and purified using an AxyPrep DNA Gel Extraction Kit (Axygen Biosciences, Union City, CA, USA) and quantified using a QuantiFluor™ -ST Handheld Fluorometer (Promega, Madison, WI, USA). The concentration of purified PCR amplicons was determined and the purified PCR amplicons were then mixed at equimolar ratios for sequencing analysis. Sequencing was conducted on the Miseq PE250 platform (Illumina, San Diego, CA, USA).

2.5 | Processing of sequencing data

Raw sequence data were quality filtered and chimera checked using the QIIME software (version 1.17) with the inclusion criteria of mean quality score ≥20 and length ≥200 bp. Sequences with the same barcode were sorted into the same sample and then potential chimeric sequences were identified and removed with the UCHIME algorithm in the Usearch program. Operational taxonomic units (OTUs) were clustered at the 97%-similarity level using the Usearch program (http://drive5.com/usearch/). Taxonomic assignment of 16S rRNA sequences and ITS sequences was determined with the bacterial SILVA reference database (http://www.arb-silva.de) and the Unite reference database (http://un ite.ut.ee/index.php) using the RDP naïve Bayesian classifier at 97% level.

2.6 | Statistical analysis

Alpha diversity indices including Good's coverage, Chao1 and Shannon's index were obtained using MOTHUR (http://www.mothur.org/). One-way analysis of variance (ANOVA) and the least significant difference (LSD) multiple comparison ($p < .05$) were performed to detect the effect of cultivation period on soil properties and microbial community composition and diversity using SPSS version 17.0 (SPSS Inc., Chicago, IL, USA). Principal coordinate analysis (PCoA) was used to evaluate differences in microbial communities among cultivation periods, based on Bray-Curtis distances. Pearson correlation analysis was used to assess the relationships between dominant microbial communities and soil physicochemical properties. Redundancy analysis (RDA) using Monte Carlo permutation (999 repetitions) was used to determine the main environmental factors influencing microbial communities. The PCoA, Pearson correlation analysis and RDA were conducted using the R software package v.3.2.3.

3 | RESULTS

3.1 | Changes in soil physicochemical properties

Soil BD decreased significantly ($p < .001$), but soil salinity did not change with cultivation time (Table 1). Although soil pH did not significantly vary in the early stages of cultivation (16 and 33 years), a significant decrease was observed in the 45-year and 60-year sites compared to the non-cultivated site ($p < .01$) (Table 1). Soil moisture increased dramatically in 16-year, 33-year, 45-year and 60-year sites compared to the non-cultivated site ($p < .001$), whereas no significant differences were observed among 16-year, 33-year, 45-year and 60-year sites. Concentrations of SOC, TN, EOC, NH_4^+-N, NO_3^--N and AP increased dramatically ($p < .001$) after 16 years of cultivation compared to the non-cultivated site. Subsequently, contents of TN and NO_3^--N increased significantly with cultivation time, reaching the highest values at the 60-year site, concentrations of SOC, NH_4^+-N and AP increased initially and then decreased, with the highest values observed at the 45-year site, whereas concentrations of EOC varied little with cultivation time, with the highest values observed at the 60-year site (Table 1). No significant difference was observed in TP along the cultivation chronosequence (Table 1).

3.2 | Diversity and composition of the soil bacterial community

A total of 1,113,898 bacterial sequences were obtained from the complete dataset and a total of 8,667 OTUs were identified. The Good's coverage values for all samples were above 97% (Figure 2), indicating that the number of bacterial sequences obtained represented bacterial communities well.

The soil bacteria belonged to 44 phyla, 132 classes, 275 orders, 526 families and 1006 genera. The dominant phyla (relative abundance >1%) were *Proteobacteria* (25.16–37.14%), *Actinobacteria* (16.57–19.22%), *Acidobacteria* (9.56–13.89%), *Chloroflexi* (8.24–11.63%), *Firmicutes* (4.80–12.83%), *Planctomycetes* (4.53–6.03%), *Gemmatimonadetes* (3.76–5.47%), *Bacteroidetes* (2.33–3.09%), *Verrucomicrobia* (1.55–2.17%), *unclassified_k_norank* (1.10–1.76%), *Nitrospirae* (0.67–1.19%) and *Cyanobacteria* (0.32–1.74%), together accounting for more than 97% of bacterial sequences across all samples (Figure 1a). Notably, the relative abundance of *Proteobacteria*

TABLE 1 Soil physicochemical properties along a cultivation chronosequence from non-cultivated (ck) to cultivated for 60 years. Values (±SD) followed by different lowercase letters within rows are significantly different at $p < .05$

	BD (g cm^{-3})	SM (%)	pH	Salinity (g kg^{-1})	SOC (g kg^{-1})	TN (g kg^{-1})	TP (g kg^{-1})	NH_4^+-N (mg kg^{-1})	NO_3^-N (mg kg^{-1})	EOC (g kg^{-1})	AP (mg kg^{-1})
ck	1.56 ± 0.02 a	2.21 ± 0.32 b	8.66 ± 0.09 ab	1.02 ± 0.09 a	0.69 ± 0.14 d	0.13 ± 0.03 c	0.89 ± 0.02 a	0.53 ± 0.13 c	2.48 ± 0.66 c	0.03 ± 0.02 b	2.51 ± 0.49 d
16 years	1.52 ± 0.02 ab	11.27 ± 0.44 a	8.68 ± 0.10 a	1.05 ± 0.09 a	3.66 ± 0.86 c	0.41 ± 0.07 b	0.90 ± 0.03 a	2.10 ± 0.38 b	37.64 ± 3.23 b	0.27 ± 0.04 a	8.49 ± 0.65 c
33 years	1.49 ± 0.03 bc	9.53 ± 0.32 a	8.55 ± 0.08 abc	0.98 ± 0.08 a	5.68 ± 0.76 b	0.42 ± 0.06 b	0.86 ± 0.04 a	3.68 ± 0.45 a	69.02 ± 6.52 a	0.25 ± 0.03 a	9.08 ± 0.34 bc
45 years	1.47 ± 0.02 c	10.39 ± 0.64 a	8.42 ± 0.07 c	1.07 ± 0.13 a	7.24 ± 0.40 ab	0.55 ± 0.12 ab	0.91 ± 0.02 a	4.68 ± 0.62 a	69.48 ± 5.87 a	0.26 ± 0.04 a	11.02 ± 1.14 a
60 years	1.46 ± 0.01 c	11.85 ± 0.47 a	8.46 ± 0.04 c	1.04 ± 0.10 a	7.04 ± 0.34 a	0.75 ± 0.11 a	0.93 ± 0.06 a	4.02 ± 0.59 a	75.70 ± 11.98 a	0.28 ± 0.05 a	10.46 ± 0.67 ab
F	23.859	29.354	6.494	0.449	69.548	21.506	1.912	38.803	61.740	28.120	68.446
P	<.001	<.001	.008	NS	<.001	<.001	NS	<.001	<.001	<.001	<.001

Abbreviations: AP, available phosphorus; BD, soil bulk density; EOC, easily oxidizable organic carbon; NH_4^+-N, ammonia nitrogen; NO_3^--N, nitrate nitrogen; NS, not significant; SM, soil moisture; SOC, soil organic carbon; TN, total nitrogen; TP, total phosphorus.

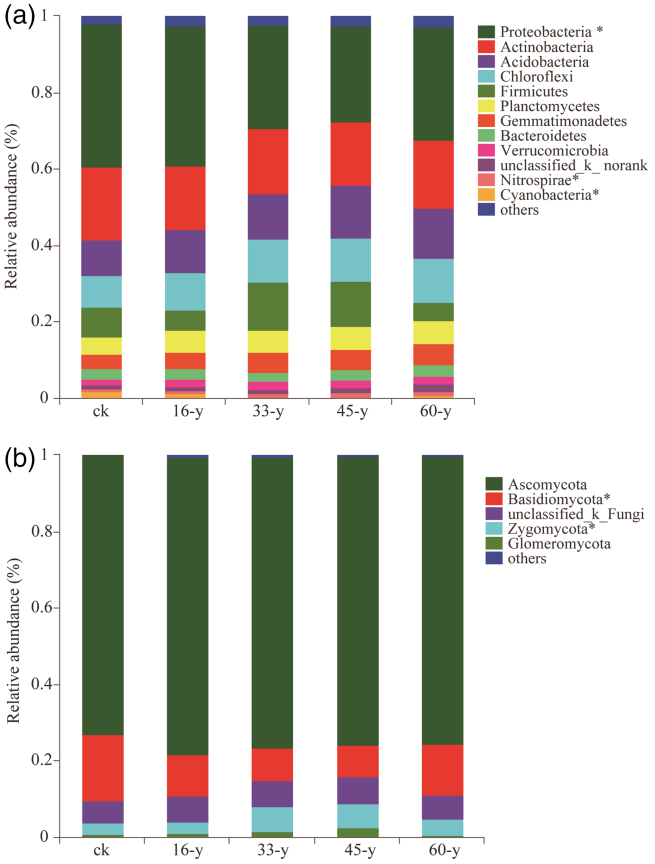

FIGURE 1 Relative abundances of the dominant bacterial (a) and fungal (b) groups at the phylum level (relative abundance >1%) along a cultivation chronosequence from non-cultivated (ck) to cultivated for 60 years (60-y). *Significant difference ($p < .05$) along cultivation chronosequence [Color figure can be viewed at wileyonlinelibrary.com]

and *Cyanobacteria* initially decreased with cultivation time ($p < .05$) and then increased at the 60-year site, with the lowest values observed at the 45-year site. The relative abundance of *Nitrospirae* increased significantly ($p < .05$) with cultivation time (Figure 1a).

Among the top 10 dominant orders, *Pseudomonadales* (1.31–12.46%), *Norank_c_Acidobacteria* (4.20–7.42%), *Anaerolineales* (1.97–3.43%) and *Nitrosomonadales* (1.40–2.73%) exhibited significant differences in relative abundance along cultivation chronosequences (Table S1). The relative abundance of *Anaerolineales* and *Nitrosomonadales* increased with cultivation time; the relative abundance of *Norank_c_Acidobacteria* initially increased with cultivation time and then decreased at the 60-year site. The relative abundance of *Pseudomonadales* decreased significantly with cultivation time ($p < .05$) and increased at the 60-year site (Table S1).

The Chao and Shannon indices indicated that the species richness and diversity of the soil bacterial community increased with cultivation time (Figure 2); specifically, the Chao index at the 45-year and 60-year sites and the Shannon index at the 60-year site were significantly higher than

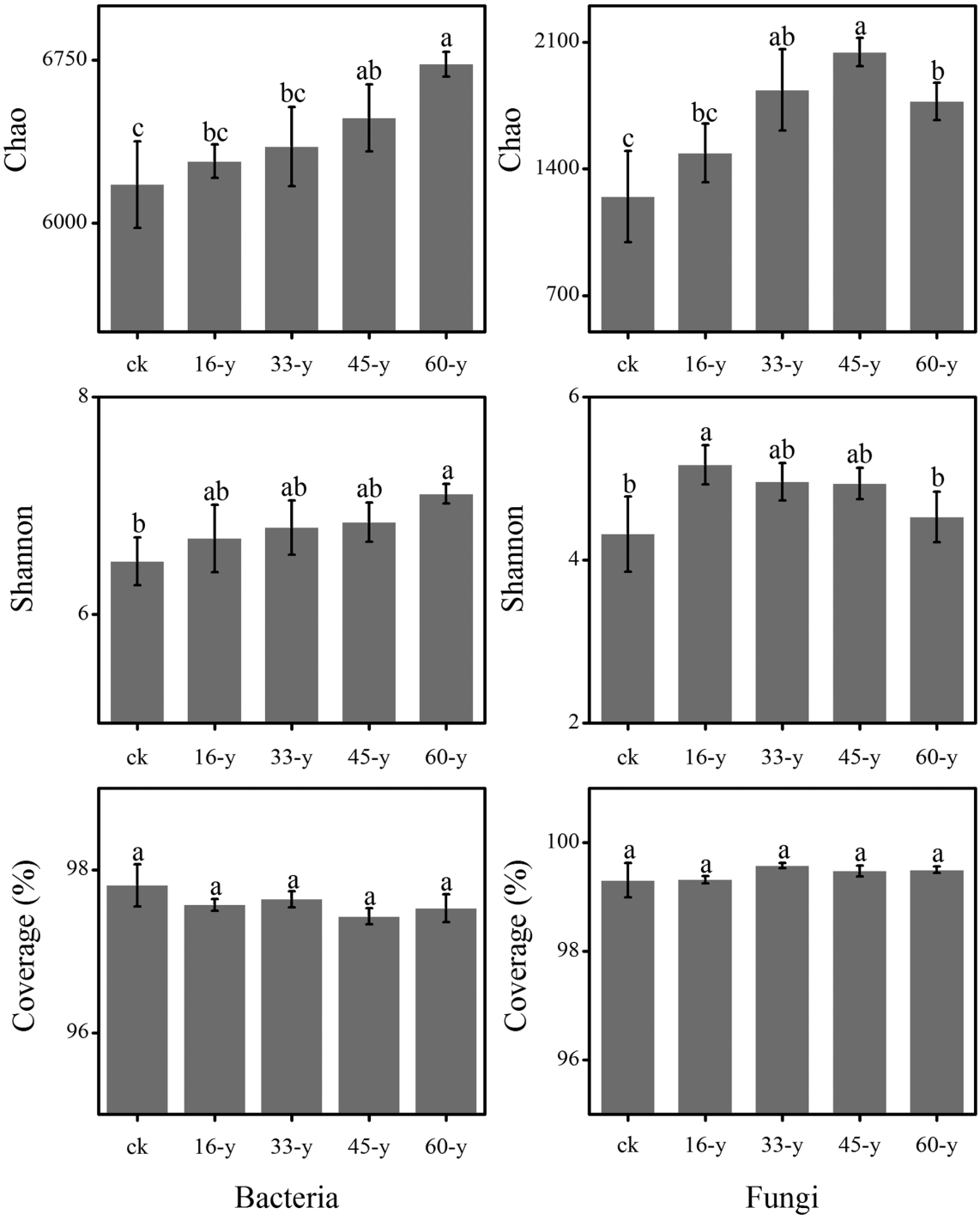

FIGURE 2 Richness and diversity indices of bacterial and fungal communities along a cultivation chronosequence from non-cultivated (ck) to cultivated for 60 years (60-y). Values are means ± standard error. Different letters indicate significant differences ($p < .05$) along the cultivation chronosequence

at the non-cultivated site. The plot of PCoA suggested clear differences along coordinate 1 in the compositions of bacterial communities in different cultivation periods. The PCoA revealed that bacterial communities at the 33-year and 45-year sites tended to group together, but were clearly separated from those at the 16-year, 60-year and non-cultivated sites, also separated from each other (Figure 3a).

3.3 | Soil fungal community diversity and composition

A total of 1,033,384 fungal sequences were obtained from the complete dataset and a total of 3,292 OTUs were identified. The Good's coverage values of all samples were above 99% (Figure 2), indicating that the number of

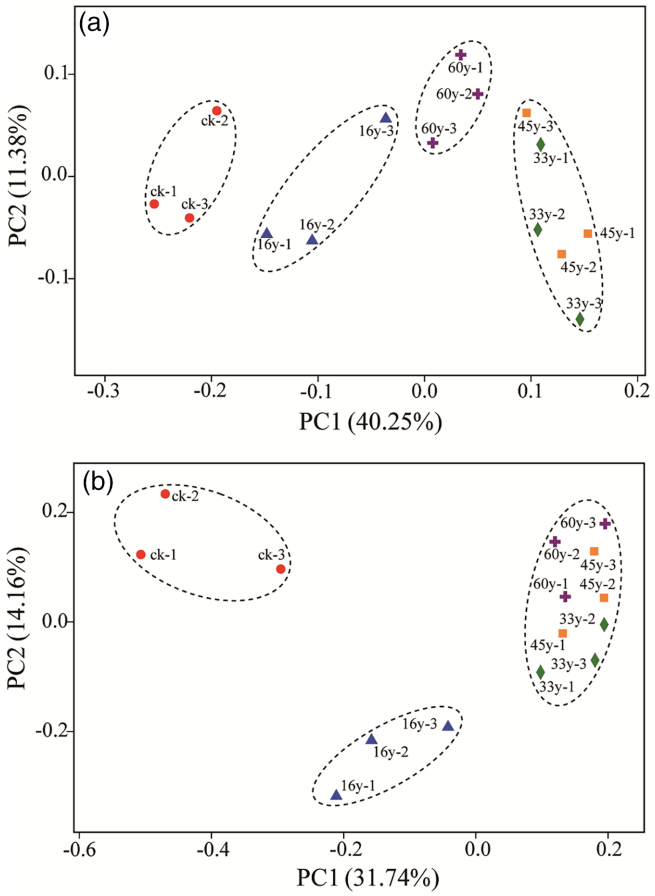

FIGURE 3 Principal coordinates analysis (PCoA) of bacterial (a) and fungal (b) community composition based on Bray-Curtis distances. Values at axes 1 and 2 are the percentages that can be explained by the corresponding axis [Color figure can be viewed at wileyonlinelibrary.com]

fungal sequences obtained represented the fungal communities well.

The fungi belonged to nine phyla, 35 classes, 102 orders, 228 families and 526 genera. The dominant phyla (relative abundance >1%) were *Ascomycota* (66.49–77.87%), *Basidiomycota* (8.26–23.70%), *unclassified_k_Fungi* (6.02–7.15%), *Zygomycota* (3.00–6.55%) and *Glomeromycota* (0.45–2.35%), together accounting for more than 99% of fungal sequences across all samples (Figure 1b). Notably, the relative abundance of *Basidiomycota* decreased with cultivation time ($p < .05$) and then increased at the 60-year site, whereas that of *Zygomycota* increased and then decreased at the 60-year site, with the highest values observed at the 45-year site (Figure 1b).

Among the top 10 dominant orders, *Hypocreales* (11.70–20.45%), *Sordariales* (8.03–15.13%), *Capnodiales* (2.09–15.41%), *Mortierellales* (3.00–6.54%), *Pezizales* (0.90–10.80%) and *Unclassified_p_Ascomycota* (2.43–4.12%) exhibited significant differences along the cultivation chronosequence (Table S1). The relative abundance of *Hypocreales*, *Sordariales*, *Mortierellales*, *Pezizales* and *Unclassified_p_ Ascomycota* initially increased and then decreased with cultivation time, with the highest values observed at the 16-year or 33-year sites; the relative abundance of *Capnodiales* decreased and then increased with cultivation time, with the highest values observed at the 60-year site (Table S1).

Based on the Shannon index, diversity of soil fungal community increased dramatically after 16 years of cultivation and then decreased with cultivation time (Figure 2). The Chao index indicated that the species richness of the soil fungal community increased significantly with cultivation time and then decreased at the 60-year site, with the highest values observed at the 45-year site (Figure 2). The plot of PCoA suggested clear differences along coordinate 1 in the compositions of fungal communities in different cultivation periods. The analysis revealed that fungal communities at the 33-year, 45-year and 60-year sites tended to group together and were clearly separated from those at the 16-year and non-cultivated sites, which were also separated from each other (Figure 3b).

3.4 | Relationships between the soil microbial community and soil properties

Together, the analysed edaphic variables explained 83.29% of the variance in the bacterial community based on RDA, with axis 1 explaining 61.34% of the variance and axis 2 explaining 12.44% (Figure 4a). The major soil physicochemical properties driving the bacterial community composition were SOC ($r^2 = 0.68$, $p = .002$), NH_4^+-N ($r^2 = .61$, $p = .004$), NO_3^--N ($r^2 = 0.58$, $p = .008$), BD ($r^2 = 0.57$, $p = .009$), AP ($r^2 = .43$, $p = .035$) and TN ($r^2 = 0.43$, $p = .039$) (Table S2).

Together, the analysed edaphic variables explained 85.43% of the variance in the fungal community based on RDA, with axis 1 explaining 26.82% of the variance and axis 2 explaining 18.69% (Figure 4b). The major soil physicochemical properties driving the fungal community composition were NO_3^--N ($r^2 = 0.77$, $p = .002$), SOC ($r^2 = 0.69$, $p = .002$), TN ($r^2 = 0.59$, $p = .005$), BD ($r^2 = 0.57$, $p = .005$), NH_4^+-N ($r^2 = 0.51$, $p = .011$) and AP ($r^2 = 0.44$, $p = .034$) (Table S2).

The Pearson correlation analysis showed that SOC, TN, NH_4^+-N, NO_3^--N, AP and BD were significantly correlated with the abundance of most bacterial phyla; however, the abundance of dominant fungal phyla was significantly correlated with SOC, NH_4^+-N, NO_3^--N and BD (Table 2).

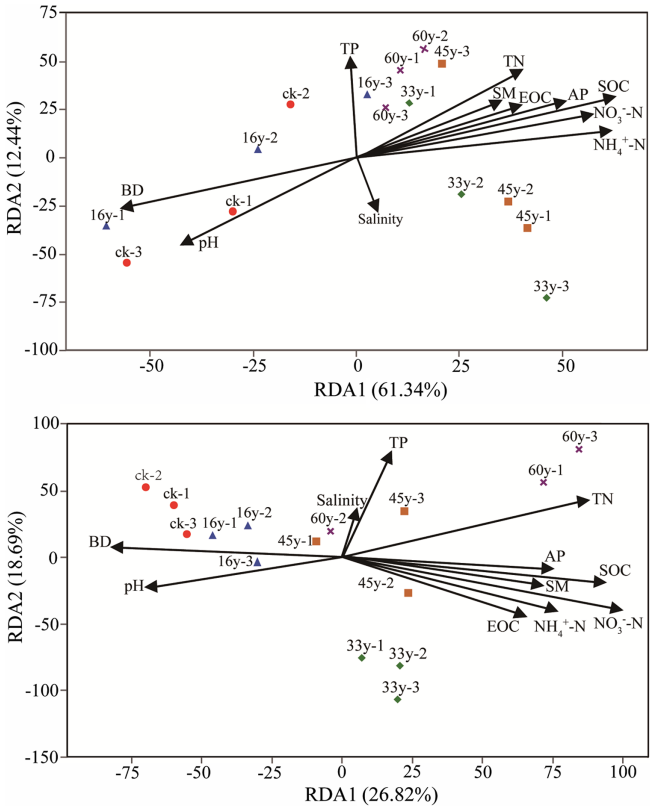

FIGURE 4 Redundancy analysis identifying the relationships between bacterial (a) and fungal (b) communities and soil physicochemical properties. Values at axes 1 and 2 are the percentages explained by the corresponding axis. AP, available phosphorus; BD, soil bulk density; EOC, easily oxidizable organic carbon; NH_4^+-N, ammonia nitrogen; NO_3^--N, nitrate nitrogen; SM, soil moisture; SOC, soil organic carbon; TN, total nitrogen; TP, total phosphorus [Color figure can be viewed at wileyonlinelibrary.com]

4 | DISCUSSION

4.1 | Effects of cultivation on soil physicochemical properties

Non-cultivated desert soils often evolve slowly due to the extremely dry environment; they exhibit loose structure and very low SOC and nutrient concentrations (Lal, 2004; Li et al., 2009). The conversion of virgin desert to croplands with irrigation, tillage and fertilization dramatically alters soil-forming processes (Su et al., 2010) and is expected to have large effects on soil properties (Li et al., 2014). In the present study, concentrations of SOC, TN, EOC, NH_4^+-N, NO_3^--N and AP increased dramatically 16 years following cultivation of natural sandy land; this indicated a significant increase in soil C and nutrient pools resulting from cultivation. Our results confirmed those of Su et al. (2010), Li et al. (2009) and Zhang et al. (2017), who also observed significant increases in the soil C pool and nutrient contents of desert soils after more than 10 years of cultivation in northwestern Chinese oases. This favourable trend in soil fertility after conversion of desert soil to arable lands was largely attributed to the increased C and nutrient inputs from manure and chemical fertilizers, and from crop residues (Su et al., 2010). In addition, irrigation and fertilization improve plant production, which in turn increases organic C and nutrient inputs to soils via litter and root production (Zhang et al., 2017).

Cultivation also had a significant effect on soil bulk density, soil moisture and pH. Generally, a lower soil bulk density, observed following the conversion of native desert soils to irrigated croplands, was attributed to a higher content of soil organic matter and the development of soil aggregates (Cheng, Zhang et al., 2018; Li et al., 2009; Zhang et al., 2017). Our results confirmed those of previous research, and a significant decrease in soil bulk density was observed with cultivation time, indicating an improvement in soil structure. In addition, the decline in soil bulk density and increase in SOC should increase the water holding capacity, which would have promoted the increase in soil moisture to some extent (Zhang, Zhao et al., 2018). Cultivation in our study also resulted in a decrease in soil pH, especially at the 45-year and 60-year sites. These results confirmed those of Su et al. (2010) and Li et al. (2018), who observed similar patterns in soil pH following the conversion of native desert soils to irrigated croplands in oases of northwestern China. The decrease in soil pH may be due to accumulation of organic acids excreted by crop roots and to the microbial decomposition of organic matter (Cheng, Chen et al., 2018; Franco-Otero, Soler-Rovira, Hernández, López-de-Sá, & Plaza, 2012). In addition, continuous flood irrigation can result in leaching of base cations in strong alkaline soils (Li et al., 2015), and thus contribute to a decrease in soil pH.

4.2 | Effects of cultivation on diversity and composition of the soil microbial community

Increasing evidence suggests that the diversity of soil microbial communities is sensitive to agricultural practices such as tillage, fertilization and irrigation (Chen et al., 2016; Lazcano, Gómez-Brandón, Revilla, & Domínguez, 2013; Li et al., 2014), and agricultural use of natural soils in non-arid climates (e.g., unmanaged forest and meadow) in particular can modify or reduce soil microbial abundance and diversity (Gómez-Acata, Valencia-Becerril, Valenzuela-Encinas, Navarro-Noya, & Dendooven, 2016; Li et al., 2015). However, the results in this study demonstrated that

TABLE 2 Pearson correlation matrix between relative abundances of the dominant bacterial and fungal groups (relative abundance >1%) at the phylum level, and soil properties

	Species name	BD	SM	pH	Salinity	SOC	TN	TP	NH_4^+-N	NO_3^--N	EOC	AP
Bacteria	*Proteobacteria*	**0.68****	−0.47	0.48	−0.11	**−0.72****	−0.44	−0.09	**−0.73****	**−0.62***	−0.51	**−0.61***
	Actinobacteria	0.31	−0.42	0.10	−0.41	−0.31	−0.22	−0.23	−0.46	−0.25	−0.53	−0.44
	Acidobacteria	**−0.61***	0.46	**−0.58***	0.13	**0.71****	**0.58***	0.06	**0.60***	**0.63***	0.48	**0.62***
	Chloroflexi	**−0.62***	0.48	−0.51	−0.07	**0.70****	**0.60***	−0.05	**0.60***	**0.73****	0.51	**0.59***
	Firmicutes	−0.12	−0.16	0.14	0.17	0.13	−0.16	−0.42	0.26	0.13	−0.05	0.01
	Planctomycetes	**−0.66****	**0.69****	−0.42	−0.07	**0.76****	**0.77****	0.21	**0.64***	**0.79*****	**0.60***	**0.67****
	Gemmatimonadetes	**−0.66****	**0.54***	**−0.55***	0.02	**0.74****	**0.58****	−0.09	**0.65****	**0.73****	**0.53***	**0.63***
	Bacteroidetes	0.05	−0.13	−0.02	0.08	−0.15	0.18	0.44	−0.22	−0.11	−0.26	−0.24
	Verrucomicrobia	−0.50	**0.56***	−0.50	−0.19	**0.58***	**0.61***	0.18	0.50	**0.66****	0.42	0.45
	Unclassified_k_norank	−0.24	0.18	−0.42	0.07	0.31	0.34	0.01	0.12	0.30	0.21	0.25
	Nitrospirae	**−0.68****	0.45	**−0.73****	0.44	**0.70****	**0.59***	0.14	**0.66****	**0.61***	**0.53***	**0.62***
	Cyanobacteria	**0.71****	**−0.53***	0.49	0.04	**−0.82*****	**−0.55***	−0.01	**−0.78****	**−0.77****	**−0.63***	**−0.70****
Fungi	*Ascomycota*	**−0.53***	0.10	−0.51	−0.31	**0.66****	0.40	−0.17	**0.54***	**0.71****	0.03	0.28
	Basidiomycota	0.16	−0.45	−0.14	−0.24	0.03	−0.19	−0.30	−0.24	0.09	−0.37	−0.17
	Unclassified_k_Fungi	**−0.56***	0.11	−0.51	−0.01	0.51	0.35	0.02	0.71	0.40	0.22	0.29
	Zygomycota	**−0.53***	0.07	**−0.56***	−0.20	**0.69****	0.35	−0.17	**0.68****	**0.56***	0.23	0.34
	Glomeromycota	−0.37	−0.10	−0.45	−0.15	**0.66****	0.22	−0.33	**0.55***	0.48	0.15	0.38

***$p < .001$.; **$p < .01$.; *$p < .05$.; Significant correlations are in bold.

Abbreviations: AP, available phosphorus; BD, soil bulk density; EOC, easily oxidizable organic carbon; NH_4^+-N, ammonia nitrogen; NO_3^--N, nitrate nitrogen; SM, soil moisture; SOC, soil organic carbon; TN, total nitrogen; TP, total phosphorus.

continuous cultivation in desert soil increased the abundance and diversity of the soil microbial community, confirming our basic hypothesis. Generally, soil bacterial communities in sandy desert soils became more abundant and more diverse with cultivation time. This was consistent with the results of Li et al. (2018), who observed a significant increase in soil bacterial abundance 36 years following conversion of native desert soils to irrigated croplands. Wang et al. (2012) also reported similar results in oasis farmlands 27 years after conversion from virgin desert. Soil microbial communities in desert ecosystems are constrained by available liquid water, as well as the availability of organic matter and the soil nutrient status (Ball et al., 2018; Crits-Christoph et al., 2013; Pajares et al., 2016).

Soil fungal abundance and diversity also responded positively to cultivation. However, we did not observe a continuous increase along the cultivation chronosequence; instead, the species richness and diversity of the fungal community increased and then decreased with cultivation time (Figure 2). These results confirmed those of Wang, Li, and Ma (2017), who used phospholipid fatty acid analysis and observed similar patterns in a fungal community following the conversion of native desert soils to irrigated croplands in oases of northwestern China. Bacterial and fungal communities may have different adaptive trajectories because bacteria have a broader range of physiologies than do fungi and are, thus, more likely to successfully colonize oligotrophic soils (Brown & Jumpponen, 2015). The finding of a discontinuous increase in the fungal abundance and diversity suggests that fungi may not have as many available niches in oligotrophic soils and develop more slowly than bacteria following cultivation (Zhang, Liu et al., 2018).

The dominant flora in bacterial and fungal communities in this study was generally consistent along the cultivation chronosequence. Further, bacterial phyla of *Proteobacteria*, *Actinobacteria*, *Acidobacteria*, *Chloroflexi*, *Firmicutes*, *Planctomycetes*, *Gemmatimonadete*, *Bacteroidetes*, *Verrucomicrobia*, *Nitrospirae* and *Cyanobacteria*, and fungal phyla of *Ascomycota*, *Basidiomycota*, *Zygomycota*and *Glomeromycota* (Figure 1) found in this study, were also documented in other arid environments; for example, in the Gurbantonggut Desert, northwest China, the Atacama Desert, Chile, and arid soils from Cuatro Cienegas, Mexico (Crits-Christoph et al., 2013; Li et al., 2014; Pajares et al., 2016). However, their relative abundance was different along cultivation chronosequences. Notably, cultivation significantly decreased the relative abundance of *Proteobacteria* and *Cyanobacteria* and significantly increased that of *Nitrospirae* and *Nitrosomonadales* within *β-proteobacteria*, supporting our basic hypothesis that continuous cultivation in desert soil resulted in a strong shift in soil microbial community composition.

The diazotrophs within *Proteobacteria* and *Cyanobacteria* can fix atmospheric N_2 (Belnap, 2002; Rashid et al., 2016) and play important functional roles in N nutrition in nutrient-poor desert environments (Li et al., 2015). The decline in the relative abundance of diazotrophs observed in our study suggests a negative effect of cultivation on the N-fixation ability of microbial communities in oasis soil. Li et al. (2015) also reported a decrease in the abundance of *Cyanobacteria* following fertilizer applications in the Gurbantonggut Desert; López-Lozano, Heidelberg, Nelson, and García-Oliva (2013) reported similar findings in arid soils from Cuatro Cienegas. The *Cyanobacteria* are in general autotrophic and prefer nutrient-poor environments (López-Lozano et al., 2013; Zhang, Liu, Xue, & Wang, 2016). Thus, the decline in the relative abundance of *Cyanobacteria* may be attributed to the increased nutrient resources following cultivation.

Nitrospirae and *Nitrosomonadales* are key functional players in soil nitrification (Daims et al., 2015; Shun et al., 2018). Previous studies showed that both *Nitrospirae* and *Nitrosomonadales* were sensitive to fertilization; generally, *Nitrosomonadales* responded positively to N fertilizers, whereas the response of *Nitrospirae* was not consistent (Shun et al., 2018; Wang et al., 2012; Wertz, Leigh, & Grayston, 2011). Wertz et al. (2011) found that fertilization increased the abundance of *Nitrobacter* but not *Nitrospira* in acidic forest soils. Shun et al. (2018) also showed that fertilization led to a decrease in the abundance of *Nitrospira* in acidic Red soils. However, Freitag, Chang, Clegg, and Prosser (2005) reported that richness of a *Nitrospira* community was greater with fertilization than without. Generally, both *Nitrospirae* and *Nitrosomonadales* prefer nutrient-rich environments (Wagner et al., 2002; Han et al., 2018); the abundance of *Nitrospirae* and *Nitrosomonadales* increased significantly in response to cultivation (this study; Wang et al., 2012; Li et al., 2015), suggesting that fertilization had the potential to promote soil nitrification and thus increase N availability for crops in nutrient-poor desert soils of northwestern China.

Basidiomycota grow well mostly in natural soils and were often inhibited by frequent tillage. For example, Ciccolini, Bonari, and Pellegrino (2015) observed that tillage with high intensity had significantly reduced the abundances of Basidiomycota in Mediterranean peaty soils, and Zhang, Zhang, Meng, Li, and Mu (2018) observed similar patterns in forest soils following cultivation. In this study, cultivation was associated with lower abundances of Basidiomycota, suggesting that cultivation can also depress Basidiomycota in desert soils. Generally, Zygomycota were mainly found in farmland soils and are sensitive to changes in soil carbon content (Liu et al., 2015; Rúa, Becky, Nicole, Lily, & Colin, 2015; Zhang,

Zhang et al., 2018). For example, Liu et al. (2015) found that Zygomycota showed significant positive correlations with SOC in arable land of northeast China. The results of the present study showed that cultivation was associated with higher abundances of Zygomycota, and that Zygomycota exhibited significant positive correlations with SOC along the cultivation chronosequence, confirming the results of previous research. Currently, relatively few studies have focused on the changes in soil fungal community compositions following conversion of virgin desert to arable land. Our results provide evidence that the compositions of the soil fungal community are also sensitive to cultivation in desert ecosystems.

4.3 | Responses of the microbial community to soil properties

Soil physicochemical properties explained over 80% of the shift in microbial communities, and soil C, N, P and bulk density had significant influences on the community structure of both bacteria and fungi. These data support our hypothesis (2) that soil structure and nutrient supply drive changes in soil microbial communities during the conversion of virgin desert soil to irrigated cropland; however, we did not observe significant effects of soil moisture on soil bacterial and fungal community structure. Bacteria and fungi are known to improve soil structure by promoting the formation of soil aggregates and pores (Rashid et al., 2016). Bacteria and fungi release mucilaginous exudates and exopolysaccharides, which are mainly composed of extracellular polysaccharides; extracellular polysaccharides are mainly responsible for the formation and stabilization of aggregates and are beneficial for improving porosity and aeration in soil (Lozano et al., 2014; Rashid et al., 2016). Experimentally significant relationships were often observed between soil structure and microbial communities, especially in degraded and barren soils (Cheng, Zhang et al., 2018; Daynes, Field, Saleeba, Cole, & McGee, 2013; Lozano et al., 2014). For example, Cheng, Zhang et al. (2018) observed strong correlations between the soil microbial population and bulk density during the reclamation of abandoned salinized farmland in arid northwest China; Lozano et al. (2014) found that soil bacterial community composition and biomass were significantly affected by soil structure, especially particle size, during the secondary succession of abandoned farmland in a dry environment; and Daynes et al. (2013) developed a model for soil aggregation formation where their simulated results indicated that soil structure could explain changes in bacterial community structure. Our results confirmed those of previous research and supported the importance of soil structure and nutrient levels in the formation of microbial communities in desert soils.

The close relationship between soil properties and microbial communities was confirmed by Pearson correlation analysis. For example, SOC, TN, NH_4^+-N, NO_3^--N, AP and BD were significantly correlated with the abundance of most bacterial phyla; the abundance of dominant fungal phyla was also significantly correlated with SOC, NH_4^+-N, NO_3^--N and BD. A negative correlation between soil C, N, P and *Proteobacteria* and *Cyanobacteria* indicated that the decline in abundance of N-fixing microbes observed following cultivation may be due to C, N and P enrichment from manure and chemical fertilizers. However, *Nitrospirae*, known as key nitrite oxidizers (Daims et al., 2015; Shun et al., 2018), were significantly positively correlated with soil C, N and P, indicating that fertilization may promote soil nitrification in oases of northwestern China.

5 | CONCLUSIONS

Our results indicated that cultivation in a desert soil increased microbial community abundance and diversity, but that bacterial and fungal communities responded differently along a cultivation chronosequence. Continuous cultivation also resulted in a strong shift in microbial community composition, notably with a negative impact on N-fixing microbes and a positive impact on ammonia-oxidizing and nitrite-oxidizing microbes. Changes in soil structure and nutrient enhancement due to applications of manure and chemical fertilizers reshaped the composition and diversity of microbial communities during the conversion of native desert soils to irrigated croplands. This study increased the understanding of the evolution of soil microbial communities during conversion of desert to arable land and highlighted the need to focus on the dynamics of microbes involved in the soil N cycle.

ACKNOWLEDGEMENTS

This work was supported by the Key Program of the Chinese Academy of Sciences (Grant No. QYZDJ-SSW-DQC040), the National Key Research and Development Programme of China (Grant No. 2017YFC0504306), the Strategic Priority Programme of the Chinese Academy of Sciences (Grant No. XDA2003010102), the National Natural Science Foundation of China (Grant No. 41771290 and 41877153) and the CAS "Light of West China" Programme (Grant No. 29Y829861).

DATA AVAILABILITY STATEMENT

The data used to support the findings of this study are available from the corresponding author upon request.

ORCID

Long-Fei Chen https://orcid.org/0000-0003-1027-8172

REFERENCES

Ball, B. A., Adams, B. J., Barrett, J. E., Wall, D. H., & Virginia, R. A. (2018). Soil biological responses to C, N and P fertilization in a polar desert of Antarctica. *Soil Biology and Biochemistry*, *122*, 7–18.

Bardgett, R. D., & Putten, W. H. V. D. (2014). Belowground biodiversity and ecosystem functioning. *Nature*, *515*(7528), 505–511.

Bastida, F., Hernández, T., Albaladejo, J., & Carlos, G. (2013). Phylogenetic and functional changes in the microbial community of long-term restored soils under semiarid climate. *Soil Biology and Biochemistry*, *65*(65), 12–21.

Belnap, J. (2002). Nitrogen fixation in biological soil crusts from southeast Utah, USA. *Biology and Fertility of Soils*, *35*(2), 128–135.

Biddle, J. F., Fitzgibbon, S., Schuster, S. C., Brenchley, J. E., & House, C. H. (2008). Metagenomic signatures of the Peru margin subseafloor biosphere show a genetically distinct environment. *PNAS*, *105*(30), 10583–10588.

Blair, G. J., Lefroy, R., & Lisle, L. (1995). Soil carbon fractions based on their degree of oxidation, and the development of a carbon management index for agricultural systems. *Australian Journal of Agricultural Research*, *46*(7), 1459–1466.

Brown, S. P., & Jumpponen, A. (2015). Phylogenetic diversity analyses reveal disparity between fungal and bacterial communities during microbial primary succession. *Soil Biology and Biochemistry*, *89*, 52–60.

Cao, L., Ding, J. L., & Yu, H. Y. (2016). Relationship between multiscale landscape pattern and salinity in Weigan and Kuqa rivers delta oasis. *Transactions of the Chinese Society of Agricultural Engineering*, *32*(3), 101–110 (in Chinese).

Chen, C., Zhang, J., Lu, M., Qin, C., Chen, Y., & Yang, L. (2016). Microbial communities of an arable soil treated for 8 years with organic and inorganic fertilizers. *Biology and Fertility of Soils*, *52*(4), 1–13.

Cheng, Z., Chen, Y., & Zhang, F. (2018). Effect of reclamation of abandoned salinized farmland on soil bacterial communities in arid northwest China. *Science of the Total Environment*, *630*, 799–808.

Cheng, Z., Zhang, F., Gale, W. J., Wang, W., Sang, W., & Yang, H. (2018). Effects of reclamation years on composition and diversity of soil bacterial communities in northwest China. *Canadian Journal of Microbiology*, *64*(1), 28–40.

Ciccolini, V., Bonari, E., & Pellegrino, E. (2015). Land-use intensity and soil properties shape the composition of fungal communities in mediterranean peaty soils drained for agricultural purposes. *Biology and Fertility of Soils*, *51*(6), 719–731.

Crits-Christoph, A., Robinson, C. K., Barnum, T., Fricke, W., Davila, A. F., & Jedynak, B. (2013). Colonization patterns of soil microbial communities in the Atacama Desert. *Microbiome*, *1*(1), 28.

Daims, H., Lebedeva, E. V., Pjevac, P., Han, P., Herbold, C., & Albertsen, M. (2015). Complete nitrification by *Nitrospira* bacteria. *Nature*, *528*, 504–509.

Daynes, C. N., Field, D. J., Saleeba, J. A., Cole, M. A., & McGee, P. A. (2013). Development and stabilisation of soil structure via interactions between organic matter, arbuscular mycorrhizal fungi and plant roots. *Soil Biology and Biochemistry*, *57*, 683–694.

Feng, Y. X., Luo, G. P., Zhou, D. C., Han, Q. F., Lu, L., & Li, Y. Z. (2010). Effects of land use change on landscape pattern of a typical arid watershed in the recent 50 years: a case study on Manas River Watershed in Xinjiang. *Acta Ecologica Sinica*, *30*(16), 4295–4305 in Chinese.

Franco-Otero, V. G., Soler-Rovira, P., Hernández, D., López-de-Sá, E. G., & Plaza, C. (2012). Short-term effects of organic municipal wastes on wheat yield, microbial biomass, microbial activity, and chemical properties of soil. *Biology and Fertility of Soils*, *48*(2), 205–216.

Freitag, T. E., Chang, L., Clegg, C. D., & Prosser, J. I. (2005). Influence of inorganic nitrogen management regime on the diversity of nitrite-oxidizing bacteria in agricultural grassland soils. *Applied and Environmental Microbiology*, *71*, 8323–8334.

Fu, S., Zou, X., & Coleman, D. (2009). Highlights and perspectives of soil biology and ecology research in china. *Soil Biology and Biochemistry*, *41*(5), 868–876.

Gómez-Acata, E. S., Valencia-Becerril, I., Valenzuela-Encinas, C., Navarro-Noya, Y. E., & Dendooven, L. (2016). Deforestation and cultivation with maize (*Zea mays* L.) has a profound effect on the bacterial community structure in soil. *Land Degradation and Development*, *27*(4), 1122–1130.

Han, S., Xiong, X., Luo, X., Zeng, L., Wei, D., Chen, W., & Huang, Q. (2018). Fertilization rather than aggregate size fractions shape the nitrite-oxidizing microbial community in a Mollisol. *Soil Biology and Biochemistry*, *124*, 179-183.

Huang, C. B., Zeng, F. J., & Lei, J. Q. (2015). Cultivation effects on the carbon and nitrogen dynamics at depth in oasis farmlands of the southern tarim basin, China. *Soil Science and Plant Nutrition*, *61*(2), 287–294.

Huang, J., Wang, R., & Zhang, H. (2007). Analysis of patterns and ecological security trend of modern oasis landscapes in Xinjiang, China. *Environmental Monitoring and Assessment*, *134*(1-3), 411–419.

Jackson, M. L. (1973). *Soil chemical analysis*. Engewood Cliffs, NJ: Prentice-Hall.

Jing, X., Sanders, N. J., Shi, Y., Chu, H., Classen, A. T., & Zhao, K. (2015). The links between ecosystem multifunctionality and above- and belowground biodiversity are mediated by climate. *Nature Communications*, *6*(6), 8159.

Lal, R. (2004). Carbon sequestration in dryland ecosystems. *Environmental Management*, *33*(4), 528–544.

Lazcano, C., Gómez-Brandón, M., Revilla, P., & Domínguez, J. (2013). Short-term effects of organic and inorganic fertilizers on soil microbial community structure and function. *Biology and Fertility of Soils*, *49*(6), 723–733.

Li, C. H., Tang, L. S., Jia, Z. J., & Li, Y. (2015). Profile changes in the soil microbial community when desert becomes oasis. *PLoS One*, *10*(10), e0139626.

Li, C. H., Yan, K., Tang, L., Jia, Z., & Li, Y. (2014). Change in deep soil microbial communities due to long-term fertilization. *Soil Biology and Biochemistry*, *75*, 264–272.

Li, F. R., Feng, Q., Liu, J. L., Sun, T. S., Ren, W., & Guan, Z. H. (2013). Effects of the conversion of native vegetation to farmlands on soil microarthropod biodiversity and ecosystem functioning in a desert oasis. *Ecosystems*, *16*(7), 1364–1377.

Li, F. R., Liu, J. L., Ren, W., & Liu, L. L. (2018). Land-use change alters patterns of soil biodiversity in arid lands of northwestern china. *Plant and Soil*, *428*(1–2), 1–18.

Li, S., & Yan, C. Z. (2013). Oasis evolution and human factors analysis in Hexi Corridor over the recent 20 years. *Journal of Arid Land Resources and Environment*, *27*(4), 92–98 (in Chinese).

Li, X. G., Li, Y. K., Li, F. M., Zhang, P. L., Yin, P., & Ma, Q. (2009). Changes in soil organic carbon, nutrients and aggregation after conversion of native desert soil into irrigated arable land. *Soil and Tillage Research*, *104*(2), 263–269.

Liu, B., Zhao, W. Z., Chang, X. X., Li, S. B., & Du, M. W. (2010). Water requirements and stability of oasis ecosystem in arid region, China. *Environmental Earth Sciences*, *59*, 1235.

Liu, J., Sui, Y., Yu, Z., Shi, Y., Chu, H., & Jin, J. (2015). Soil carbon content drives the biogeographical distribution of fungal communities in the black soil zone of northeast china. *Soil Biology and Biochemistry*, *83*, 29–39.

López-Lozano, N. E., Heidelberg, K. B., Nelson, W. C., & García-Oliva, F. (2013). Microbial secondary succession in soil microcosms of a desert oasis in the Cuatro Cienegas Basin, Mexico. *PeerJ*, *1*(1), e47.

Lozano, Y. M., Hortal, S., Armas, C., & Pugnaire, F. I. (2014). Interactions among soil, plants, and microorganisms drive secondary succession in a dry environment. *Soil Biology and Biochemistry*, *78*, 298–306.

Mccrackin, M. L., Harms, T. K., Grimm, N. B., Hall, S. J., & Kaye, J. P. (2008). Responses of soil microorganisms to resource availability in urban, desert soils. *Biogeochemistry*, *87*(2), 143–155.

Mcguire, K. L., & Treseder, K. K. (2010). Microbial communities and their relevance for ecosystem models: decomposition as a case study. *Soil Biology and Biochemistry*, *42*(4), 529–535.

Nelson, D.W., Sommers, L.E., Page, A.L., Miller, R.H., & Keeney, D.R. (1982) Total carbon, organic carbon, and organic matter. Methods of Soil Analysis, Part 2, Chemical and Microbial Properties. Agronomy Society of America, Agronomy Monograph 9, Madison, Wisconsin, pp. 539-552.

Olsen, S. R., & Sommers, L. E. (1982). Phosphorous. In A. L. Page, R. H. Miller, & D. R. Keeney (Eds.), *Methods of soil analysis, part 2, chemical and microbial properties* (pp. 403–430). Madison, WI: ASA-SSSA.

Pajares, S., Escalante, A. E., Noguez, A. M., & García-Oliva, F. (2016). Spatial heterogeneity of physicochemical properties explains differences in microbial composition in arid soils from Cuatro Cienegas, Mexico. *Peerj*, *4*(9), e2459.

Parkinson, J. A., & Allen, S. E. (1975). A wet oxidation procedure suitable for the determination of nitrogen and mineral nutrients in biological material. *Communications in Soil Science and Plant Analysis*, *6*, 1–11.

Rashid, M. I., Mujawar, L. H., Shahzad, T., Almeelbi, T., Ismail, I. M. I., & Oves, M. (2016). Bacteria and fungi can contribute to nutrients bioavailability and aggregate formation in degraded soils. *Microbiological Research*, *183*, 26–41.

Rúa, M. A., Becky, M., Nicole, H., Lily, V., & Colin, J. (2015). Ectomycorrhizal fungal communities and enzymatic activities vary across an ecotone between a forest and field. *Journal of Fungi*, *1*(2), 185–210.

Schimel, J. P., & Schaeffer, S. M. (2012). Microbial control over carbon cycling in soil. *Frontiers in Microbiology*, *3*, 348.

Shun, H., Zeng, L. Y., Luo, X. S., Xiong, X., Wen, S. L., Wang, B. R., & Huang, Q. Y. (2018). Shifts in Nitrobacter- and Nitrospira-like nitrite-oxidizing bacterial communities under long-term fertilization practices. *Soil Biology and Biochemistry*, *124*, 118–125.

Singh, B. K., Bardgett, R. D., Smith, P., & Reay, D. S. (2010). Microorganisms and climate change: terrestrial feedbacks and mitigation options. *Nature Reviews Microbiology*, *8*(11), 779–790.

Su, Y. Z., Yang, R., Liu, W. J., & Wang, X. F. (2010). Evolution of soil structure and fertility after conversion of native sandy desert soil to irrigated cropland in arid region, china. *Soil Science*, *175*(5), 246–254.

Tedersoo, L., Kõljalg, U., Hallenberg, N., & Larsson, K. H. (2003). Fine scale distribution of ectomycorrhizal fungi and roots across substrate layers including coarse woody debris in a mixed forest. *New Phytologist*, *159*, 153–165.

Van Horn, D. J., Okie, J. G., Buelow, H. N., Gooseff, M. N., Barrett, J. E., & Takacsvesbach, C. D. (2014). Soil microbial responses to increased moisture and organic resources along a salinity gradient in a polar desert. *Applied and Environmental Microbiology*, *80*(10), 3034–3043.

Wagner, M., Loy, A., Nogueira, R., Purkhold, U., Lee, N., & Daims, H. (2002). Microbial community composition and function in wastewater treatment plants. *Antonie van Leeuwenhoek International Journal of General and Molecular Microbiology*, *81*, 665-680.

Wang, B. Z., Zhang, C. X., Liu, J. L., Zeng, X. W., Li, F. R., & Jia, Z. J. (2012). Microbial community changes along a land-use gradient of desert soil origin. *Pedosphere*, *22*(5), 593–603.

Wang, Y., Xiao, D., Li, Y., & Li, X. (2008). Soil salinity evolution and its relationship with dynamics of groundwater in the oasis of inland river basins: case study from the fubei region of Xinjiang Province, China. *Environmental Monitoring and Assessment*, *140*(1-3), 291–302.

Wang, Y. Y., Li, C. H., & Ma, J. (2017). Effects of desert reclamation on soil microbial community and microbial diversity. *Journal of Desert Research*, *37*(3), 514–522 (in Chinese).

Wertz, S., Leigh, A. K., & Grayston, S. J. (2011). Effects of long-term fertilization of forest soils on potential nitrification and on the abundance and community structure of ammonia oxidizers and nitrite oxidizers. *FEMS Microbiology Ecology*, *79*, 142–154.

Zhang, C., Liu, G., Xue, S., & Wang, G. (2016). Soil bacterial community dynamics reflect changes in plant community and soil properties during the secondary succession of abandoned farmland in the Loess Plateau. *Soil Biology and Biochemistry*, *97*, 40–49.

Zhang, H.H., Zhang, S.Y., Meng, X.X.Y., Li, M.S, & Mu, L.Q. (2018) Conversion from natural wetlands to forestland and farmland alters the composition of soil fungal communities in Sanjiang Plain, Northeast China. *Biotechnology and Biotechnological Equipment*, *32*(4), 951–960. https://doi.org/10.1080/13102818.2018.1459208

Zhang, Y., Zhao, W., & Fu, L. (2017). Soil macropore characteristics following conversion of native desert soils to irrigated croplands in a desert-oasis ecotone, Northwest China. *Soil and Tillage Research*, *168*, 176–186.

Zhao, W. Z., Yang, R., Liu, B., Yang, Q. Y., & Li, F. (2016). Oasification of northwestern China: a review. *Journal of Desert Research*, *36*(1), 1–5 (in Chinese).

Zhao, X. J. (2012). *Study on the spatio-temporal characteristics of oasisization in the reaches of Heihe river basin from 1949 to 2009*. Lanzhou City, China: Lanzhou University (in Chinese).

SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section at the end of this article.

How to cite this article: Chen L-F, He Z-B, Zhao W-Z, et al. Soil structure and nutrient supply drive changes in soil microbial communities during conversion of virgin desert soil to irrigated cropland. *Eur J Soil Sci*. 2020;71:768–781. https://doi.org/10.1111/ejss.12901