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Changes in soil fertility and microbial communities following cultivation of native grassland in Horqin Sandy Land, China: a 60-year chronosequence

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Abstract

Background Grassland conversion to cropland is a prevailing change of land use in traditionally nomadic areas, especially in the Mongolian Plateau. We investigated the effects of grassland conversion followed by continuous cultivation on soil properties and microbial community characteristics in Horqin Sandy Land, a typical agro-pastoral transition zone of Northern China. Soil samples were collected from the topsoil (upper 20 cm) across a 60-year cultivation chronosequence (5, 15, 25, 35 and 60 years) and unconverted native grassland. Soil physico-chemical properties were determined and high-throughput sequencing was used to assess microbial community diversity and composition.

Results Grassland cultivation resulted in changes to soil properties in both the short and longer term. Initially, it significantly increased soil bulk density (BD), electrical conductivity (EC), soil total nitrogen (TN), available phosphorus (AP) and available potassium (AK) concentrations, while reducing soil water content (SWC) and soil organic carbon content (SOC). Over the next 35–55 years of continuous cultivation, the trend for most of these characteristics was of reversion towards values nearer to those of native grassland, except for SOC which remained highly depleted. Cultivation of grassland substantially altered soil microbial communities at phylum level but there was no significant difference in microbial α -diversity between native grassland and any cropland. However, soil bacterial and fungal community structures at phylum level in the croplands of all cultivation years were different from those in the native grasslands. Heatmaps further revealed that bacterial and fungal structures in cropland tended to become more similar to native grassland after 15 and 25 years of cultivation, respectively. Redundancy analysis indicated that SOC, EC and BD were primary determinants of microbial community composition and diversity.

Conclusions These findings suggest that agricultural cultivation of grassland has considerable effects on soil fertility and microbial characteristics of Horqin Sandy Land. Intensive high-yield forage grass production is proposed as an alternative to avoid further native grassland reclamation, while meeting the grazing development needs in the ethnic minority settlements of eco-fragile regions.

Keywords Grassland–cropland conversion, Reclamation, Soil properties, Microbe, Horqin Sandy Land

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Background

Grasslands occupy more than 40% of the world's land surface and are highly susceptible to anthropogenic activity and climate change (Yang et al. 2022). In addition to supplying dairy products and meat for human consumption, as a major biome in terrestrial ecosystem, they have a role in resisting desertification, regulating the climate change, and maintaining biodiversity (White et al. 2000; Wang et al. 2021). In China, 313 million hectares of grasslands, accounting for 78% of the total area, are distributed across the northern arid and semi-arid temperate zone (He et al. 2017). Conversion of grassland to cropland has become one of the most common land-use changes, due to rapid population growth, and is a crucial strategy to relieve the shortage of arable land (Ding et al. 2013; Tang et al. 2019; Zhao et al. 2020). Around 20% of natural grasslands in Mongolia, Russia, and China have been converted to croplands (White et al. 2000). On the Mongolian Plateau, in particular, agricultural cultivation has gradually replaced native grassland to meet food demand and alleviate shortages of forage in winter, as traditional nomadic ways have given way to settlement.

When grasslands are converted to croplands, the removal of the natural vegetation and subsequent cultivation management may decrease surface vegetation cover, destabilize the soils, and subsequently modify their characteristics (Zucca et al. 2010; Qiao et al. 2015; Tang et al. 2019; Okolo et al. 2020). He et al. (2017) has shown that transition of grassland to spring wheat in the Xilin River Basin of China increased aboveground plant biomass by 48%, but it decreased belowground biomass by 98%, and almost all of the aboveground crop biomass was harvested and removed. Qiao et al. (2015) reported that the upper 30 cm of topsoil lost 10% of its carbon storage when it was converted from pasture to farmland in Tibetan grasslands. A meta-analysis that compiled data from 81 studies around the world suggested that grassland conversion significantly decreased soil silt and clay contents, pH and available potassium (AK) contents, but increased soil sand contents, bulk density (BD), available phosphorus (AP) and moisture contents (Tang et al. 2019). Numerous other investigations have also confirmed that unmanaged grasslands have lower BD and electrical conductivity (EC), and higher pH, than farmlands (Wang et al. 2021; Zhang et al. 2022). However, there is little consensus regarding the effects on soil characteristics, despite an abundance of documented evidence, because differences will have arisen from diverse initial soil properties, climatic and environmental factors, agricultural managements including cropping systems, fertilization, irrigation and duration of cultivation.

Soil microbes are integral to the ecosystem functions that maintain plant productivity and soil fertility (Hu

et al. 2021; Zhang et al. 2022), and they are sensitive to changes in their environment (Maron et al. 2018; Ren et al. 2019). Therefore, changes in soil physico-chemical properties resulting from land use and management can have an impact on the composition and structure of the microbial communities (Ferreira et al. 2016; Hu et al. 2021). Emerging studies on the impact of cropping have revealed that conversion to arable crops could alter the proportion of copiotrophs and oligotrophs and generally increase soil microbial diversity, as a result of fertilization, irrigation and tillage (Fierer et al. 2012; He et al. 2017; Dos Santos et al. 2019; Wang et al. 2019). On the other hand, tillage and continual fertilization in barren drylands may have opposite effects on the species composition of soil microbes (Wang et al. 2010b; Zhou et al. 2016). Even though much previous work has focused on the impacts of human activities on semi-arid ecosystems with harsh environmental conditions around the world (Li et al. 2020b; Hu et al. 2021; Wang et al. 2021; Zhang et al. 2022), there are limited taxonomically based data to help understand changes in soil microbial community structures in response to grassland cultivation, or their underlying drivers.

The Horqin Sandy Land, the largest sandy land in China with an area of 5.23×10^6 ha, is located in the southeast of the Mongolian Plateau. It belongs to the semi-arid, agro-pastoral transition zone and an ecologically fragile area of Northern China (Tang et al. 2016). Livestock production based on vast grasslands has historically been the primary source of income for local pastoralists (Miao et al. 2022). Some of these grasslands have potential for cultivation, with flat terrain, a shallow water table, and relatively high fertility—in contrast to the mobile and semi-mobile sandy areas in the same region. An increasing area of grassland has been cultivated, primarily near nomad settlements to obtain more grain and forage, since animal husbandry cooperatives and the household contract responsibility system, were successively established (Gongbuzeren et al. 2015). The area of cultivated land has increased from 6.3×10^5 ha in 1960 to 2.1×10^6 ha in 2019, with 5.8×10^5 hectares of grassland having been reclaimed between 2010 and 2019 (Du 2019). As a result, farmlands with different cultivation histories widely distributed in this region provide unique opportunities to examine chronosequences that can reveal long-term trends resulting from anthropogenic activities.

We investigated such a chronosequence using sites ranging from an uncultivated control of native grassland to some areas that had been cultivated continuously for 60 years in a representative region of Horqin Sandy Land. Basic soil physico-chemical properties were measured and soil microbial communities were assessed using Illumina MiSeq sequencing. We hypothesized that (1)

the conversion of natural grassland to cropland would degrade soil properties and modify microbial composition, and the extent of change would depend on the duration of continuous cultivation; (2) soil microbial changes were closely related to alterations of soil properties; and (3) soil organic carbon would be an important driver in shaping microbial community structure. This information is aimed at evaluating current changes in grassland conversion to cropland of arid and semi-arid regions and informing development of sustainable management strategies for the ethnic minority settlements of eco-fragile regions.

Materials and methods

Research site and soil sampling

The study was carried out in Ulanadu village, Wengniute County, near the Desertification Ecological Experimental Station of the Institute of Applied Ecology, Chinese Academy of Sciences, located in the Inner Mongolia Autonomous Region (43°02' N, 119°39'E, 480 m a.s.l.). The experimental area is situated at the southwestern fringe of Horqin Sandy Land, in an ecotone between typical cultivation and husbandry in China. It has a temperate continental climate, with a mean annual temperature (1980–2017) of 7.3 °C, representing a brief hot summer but a long cold winter. The average annual precipitation is 318 mm, with nearly 70% falling between June and August during the growing season. The annual potential evaporation is c. 2200 mm. The average wind velocity is 3.6 m s⁻¹, with the prevailing direction northwest in the spring and winter, and southwest in the summer and autumn. The soil is classified as an aeolian sandy soil according to the soil taxonomy system of China and as an Orthi-sandic Entisol according to the FAO–UNESCO classification. It is characterized by susceptibility to wind erosion due to its coarse texture (Cao et al. 2008). The undulating landscape supports native grassland with sparsely distributed trees of *Ulmus pumila*. The indigenous vegetation comprises a typical Mongolian flora of relatively high diversity. Dominant species include the shrubs *Caragana microphylla* and *Salix flavida*, and annual and perennial herbs, such as *Chenopodium acuminatum*, *Artemisia scoparia*, *Artemisia wudanica* and *Bassia dasyphylla*. The vegetation cover is 40–85% with 150–250 g m⁻² average standing dry biomass.

Maize (*Zea mays* L.) most commonly has been cultivated as a monoculture since native grassland was converted to cropland. Seeds have been generally sown in early May using a mechanical drill, with plants spaced at 0.50 m between rows and 0.30 m between plants. Chemical fertilizer and water irrigation have been applied during the growing season since 1990. Between 1990 and

2005, annual fertilizer application included 150 kg ha⁻¹ of urea, 75 kg ha⁻¹ of diammonium phosphate and 35 t ha⁻¹ of sheep and cattle manure; after 2005, 350 kg ha⁻¹ compound fertilizer (N 18% - P₂O₅ 6% - K₂O 6%) and 75 kg ha⁻¹ of urea and 20 t ha⁻¹ of manure were employed. Before 1990, extensive cultivation with no chemical fertilizer or manure as well as irrigation had been adopted. Fertilizers were applied simultaneously with maize sowing. Annual irrigation of 1800 m³ ha⁻¹, pumped from groundwater, was applied to alleviate drought at the seedling, tasseling and spinning stages. Herbicide and pesticide applications were required for the control of weeds and pests. Maize cobs were harvested and nearly all of the stalks were removed for fodder at the beginning of October every year. In the control native grasslands, grazing was not permitted during the growing season from May to September, and around 70% of the aboveground biomass was harvested at the end of October each year for hay feed. No fertilizers, pesticides or irrigation were employed there. More details of the annual agricultural management in grassland and farmlands are shown in Table 1.

Historically, the land of Ulanadu village was 700 ha of intact native grassland with uniform soil conditions. Due to the farmland expansion around this village, grassland has been converted and subsequently cultivated continuously. A mosaic of areas with different cultivation histories was chosen for space-for-time substitution analysis. Areas with specific cultivation durations of farmlands 5, 15, 25, 35 and 60 years, respectively (CUL5, CUL15, CUL25, CUL35 and CUL60) were identified by fieldwork and consultation with local pastoralists and staff from adjacent experimental station. Precise reclamation and continuity of cultivation history had been meticulously recorded by annual survey since the station establishment and the organization of local desertification combating. Areas of native grassland (CUL0) were also taken as controls. Six areas were identified to represent each cultivation duration treatment, and a 1 ha plot was located randomly within each. In order to be representative as possible, the distance between replicates within a landscape mosaic of 300 ha farmland was at least 500 m. Thus, there were 36 plots (6 treatments × 6 replicates) in total in the experiment.

Soil samples were collected from each plot at a depth of 0–20 cm in late October 2020. Six soil cores were obtained using a spade at randomly selected locations at least 50 m apart and 20 m from the boundary (to prevent edge effects) in each plot. After manually removing surface debris, they were combined into one bulk sample. Subsequently samples were separated into two parts. The first was stored and transported

Table 1 Management history of native grassland and cropland plots of different periods of continuous cultivation in Horqin Sandy Land

Treatment	Cultivation duration (years)	Fertilization (kg ha ⁻¹ year ⁻¹)	Managements
CUL0	0	No fertilization	Native grassland without grazing No irrigation and no tillage No herbicide and pesticide application 70% of the aboveground biomass was mowed once a year for hay feed
CUL5	5	Compound fertilizer (350) and Urea (75)	<i>Zea mays</i> monoculture Irrigation with 1800 m ³ ha ⁻¹ Conventional tillage within 25 cm and rotation with 15 cm Herbicide and pesticide application No maize stalk aboveground was left in the farmland
CUL15	15	The same as above	The same as above
CUL25	25	Urea (150) and diammonium phosphate (75) before 2005 Compound fertilizer (350) and Urea (75) after 2005	The same as above
CUL35	35	No fertilizer application before 1990 Urea (150) and diammonium phosphate (75) and 25 t ha ⁻¹ of manure between 1990 and 2005 and compound fertilizer (350) and urea (75) after 2005	The same as above
CUL60	60	The same as above	The same as above except no herbicide and pesticide application before 1990

in a sterile polyvinyl chloride pipe on ice, for high-throughput sequencing. The remainder was transported in a zip-top plastic bag to the lab, where it was air dried, visible roots and litter were removed, and then it was passed through a 2-mm sieve before chemical analysis. Twelve additional undisturbed bulk soil samples were taken from the same depth in each treatment using customized stainless-steel cutting rings. Half of these samples were used to determine bulk density, while the remainder were used to measure soil water content.

Measurements of soil characteristics

Soil bulk density was measured using the cores of known volume (Blake and Hartage 1986). Soil water content was determined by oven drying at 105 °C. Soil pH and electrical conductivity (EC) were measured in a soil–water aqueous extract (1:2.5 by mass) after 30 min shaking at low speed (Orion Star 310p, Thermo, USA). Soil organic carbon was determined by an external heating method using potassium dichromate (Carter and Gregorich 2007). The total N was determined by titration of distillates after Kjeldahl digestion (Lu 1999). The molybdenum–antimony anti-colorimetric method and flame atomic absorption

spectrophotometry, respectively, were used to determine soil available phosphorus (AP) and potassium (AK) (Lu 1999).

Soil DNA extraction and microbial high-throughput sequencing

Soil DNA extraction, purification and labeling were performed as described by Zhang et al. (2022). DNA from soil samples was extracted using an OMEGA Soil DNA Kit (Omega Bio-Tek, Norcross, GA, USA) in accordance with the manufacturer's instructions and then stored at – 20 °C. A spectrophotometer (NanoDrop NC2000, Thermo Fisher Scientific, Waltham, MA, USA) and 1 percent agarose gel electrophoresis were used to measure the extracted DNAs. All DNA samples were stored at – 80 °C prior to PCR amplification and sequencing. The bacterial V3–V4 region of 16S rRNA was amplified with forward primer 338F (5'-ACTCCTACGGGAGGCAGC A-3') and reverse primer 806R (5'-GGACTACHVGGG TWTCTAAT-3'). PCR amplification targeting the fungal ITS-V1 region was carried out using the forward primer ITS5 (5'-GGAAGTAAAAGTCGTAACAAGG-3') and the reverse primer ITS2 (5'-GCTGCGTTCTTCATC GATGC-3') (Tang et al. 2022).

The amplicons were analyzed by paired-end sequencing based on the Illumina platform by the Personal Biotechnology Company, Shanghai, China. With minor modifications, microbiome bioinformatics were carried out using QIIME 2 2019.4 in accordance with the official tutorials (<https://docs.qiime2.org/2019.4/tutorials>). The quality of raw high-throughput sequences was evaluated. Trim-paired primer sequence fragments and mismatched primer sequences were eliminated using cutadapt. Selected sequences were quality-filtered, denoised, merged, and chimeras were eliminated through the use of Divisive Amplicon Denoising Algorithm 2 (DADA2) techniques (Callahan et al. 2016). DADA2 deduces the sequences and produces amplicon sequence variations (ASVs) that are identical. Only de-replication or grouping based on 100% similarity was performed for DADA2. At that sequencing depth, each sample and its relative abundance would predict ASVs. The SILVA Release 132 (<http://www.arb-silva.de>) and UNITE Release 8.0 (<https://unite.ut.ee>) databases were used to classify ASVs as bacteria or fungi (Bokulich et al. 2018). Sequences were rarefied for data analyses. Raw sequencing files were deposited in the National Centre for Biotechnology Information Sequence Read Archive (SRA) with the accession number “PRJNA885802”.

Statistical analysis

The ASV table in QIIME 2 was used to calculate the microbial alpha-diversity parameters including Chao1 richness, Observed species, Shannon diversity index, and Simpson index. Nonmetric multidimensional scaling (NMDS), based on Bray–Curtis distance and hierarchical clustering, was carried out using the Vegan package within the statistical software R 3.6.1 to examine the similarity and variation of community composition across different treatments. Soil properties and microbial community characteristics were tested for significant differences by one-way ANOVA with the Holm–Bonferroni test, or by the nonparametric Kruskal–Wallis test, depending on whether data were normally distributed or not. Redundancy analysis was employed to assess the relationships between soil properties and microbial characteristics using Canoco 5.0 software. Additional statistical tests were performed and graphs visualized using OriginPro 2019b (Origin Lab Inc., Northampton, MA, USA).

Results

Changes in soil properties after cultivation

The chronosequence showed that cultivation of the grassland considerably changed soil properties, in both the short and longer terms (Table 2). The initially low bulk density (BD) in native grassland (CUL0) increased

Table 2 Main soil physico-chemical properties in response to different periods of continuous cultivation

Treatments	BD (g cm ⁻³)	SWC (%)	pH	EC (mS cm ⁻¹)
CUL0	1.36 (0.05)d	2.94 (0.42)c	7.93 (0.16)ab	335 (26.0)d
CUL5	1.67 (0.07)a	0.97 (0.06)f	8.06 (0.19)a	773 (73.8)b
CUL15	1.63 (0.07)a	1.78 (0.15)e	7.73 (0.10)b	902 (59.9)a
CUL25	1.53 (0.05)b	2.34 (0.13)d	7.91 (0.11)ab	500 (46.9)c
CUL35	1.46 (0.05)bc	3.92 (0.64)b	7.88 (0.09)ab	328 (35.5)d
CUL60	1.42 (0.03)cd	4.87 (0.26)a	8.04 (0.13)b	353 (32.4)d

BD represents bulk density, SWC represents soil water content and EC represents electrical conductivity. Values represent means of six replicates, with standard errors shown in parentheses. Different lowercase letters indicate significant differences at $p < 0.05$

significantly after the first 5 years of cultivation and then declined steadily to become not significantly different from its original value after 60 years. Electrical conductivity (EC) peaked after 15 years, but it had also returned to near its initial value after 60 years. Soil water content (SWC) showed the inverse trend, dropping rapidly after 5 years and then progressively increasing again. Soil pH varied little ranged from 7.73 to 8.06, with no obvious trend over time.

The most striking effect on nutrient status was a reduction in soil organic carbon (SOC) by 60% after 5 years of cultivation (Fig. 1A). It reached a minimum after 25 years and subsequently showed a trend of slow recovery. In contrast, total nitrogen (TN), available phosphorus (AP) and available potassium (AK) contents had increased after 5 years, dramatically by 179% in the case of AK (Fig. 1B–D). The content of all three of these essential nutrients had dropped again sharply after 15 years of cultivation; subsequently there was another slow increase with cultivation period, which resulted in TN and AP approaching the values in uncultivated grassland again after 60 years. However, the content of AK with 60 years of cultivation was about twice the value in uncultivated native grassland (Fig. 1D).

Changes in microbial community after cultivation

Across all soil samples, bacterial communities at phylum level were dominated by Actinobacteria, which accounted for 28–45% of relative abundance, followed by Proteobacteria and Acidobacteria (Fig. 2A and Additional file 1: Table S1). When grasslands were transformed into croplands, the mean relative abundances of Actinobacteria and Acidobacteria significantly decreased. After 5 years of cultivation, they were reduced by 23% and 19%, respectively. Actinobacteria and Acidobacteria reached a minimum after 35 years and 15 years, respectively. There were no appreciable changes in the mean relative

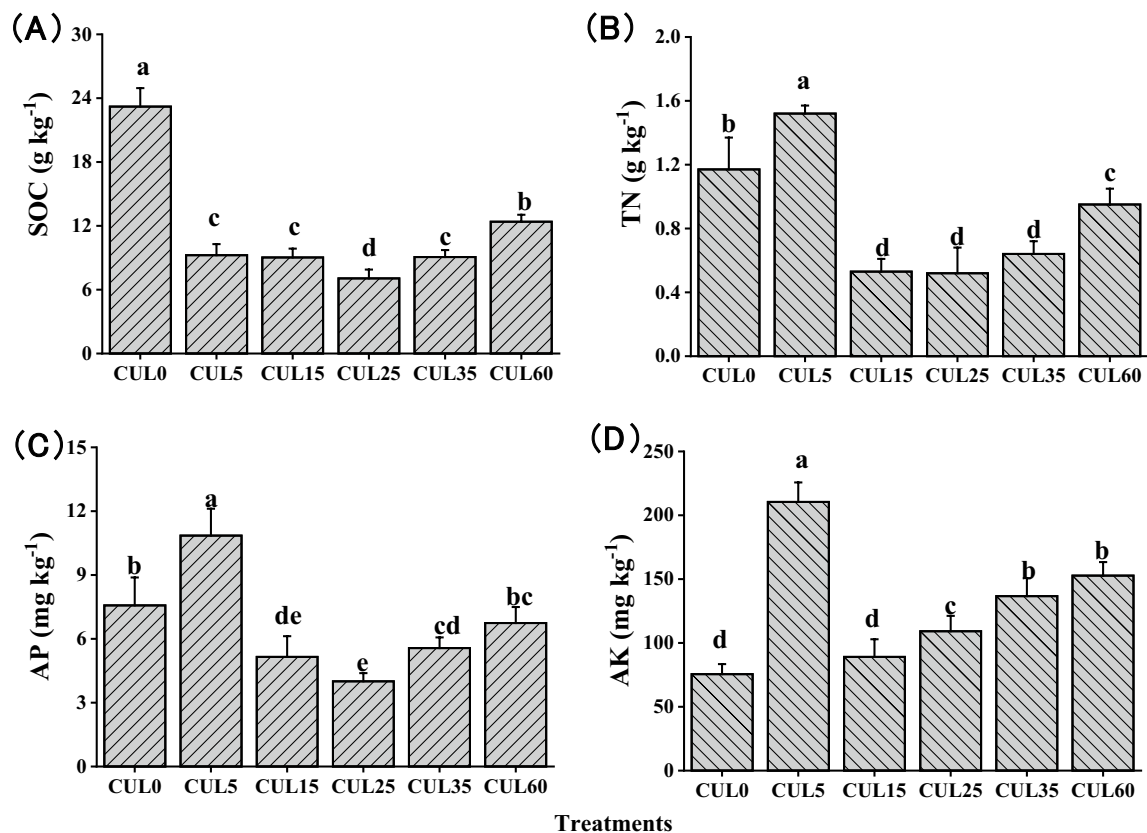


Fig. 1 Soil nutrient contents in response to different periods of continuous cultivation: **A** soil organic carbon (SOC); **B** total nitrogen (TN); **C** available phosphorus (AP); **D** available potassium (AK). Bars sharing lower case letters are not significantly different at $p < 0.05$

abundance of Proteobacteria in the chronosequence. Native grassland (CUL0) had the lowest representations of Chloroflexi, Firmicutes, Gemmatimonadetes and Bacteroidetes, at 7.6%, 1.7%, 2.9% and 2.0%, respectively. All cultivation treatments increased the proportions of these phyla to varying degrees. The treatment with 60 years of cultivation yielded the highest values of Chloroflexi and Gemmatimonadetes, significantly higher than CUL0 and CUL5, whereas Firmicutes and Bacteroidetes were greatest after 15 years, only significantly higher than CUL0.

The phylum Ascomycota dominated the fungal community in the soil samples, accounting for 70–88% of relative abundance across all cultivation periods, with Basidiomycota the next most abundant (Fig. 2B and Additional file 2: Table S2). The relative abundance of Ascomycota was significantly increased by cultivation, with abundances after 5 and 60 years greater by 26% and 19%, respectively. The mean relative abundance of Mortierellomycota also increased significantly as a result of cultivation, reaching a maximum of 4.1% after 60 years. Cultivation decreased the relative abundance of

Basidiomycota, although there was no significant difference among treatments with various cultivation years.

There was no statistically significant difference among any index of alpha diversity along the chronosequence for either bacteria or fungi (Table 2). However, nearly all of the diversity indices tended to be lower after cultivation than in the native grassland soils. Fungi were more sensitive to the effects of grassland cultivation than bacteria. For fungi, the Shannon and Chao1 indices in the CUL5 treatment were lower by 15.8% and 6.4%, respectively, than for native grassland (CUL0). The lowest Pielou index value for fungi was obtained after 35 years of cultivation, whereas the minimum Simpson index value was after 5 years of cultivation (Table 3).

The beta diversity of bacteria and fungi was represented in NMDS ordinations, with stress values of 0.0955 and 0.112, respectively (Fig. 3). For both groups, the first axis clearly differentiated the communities observed in native grassland from those of various cultivation periods. Plots with the same cultivation period tended to cluster together, but there was no clear trend

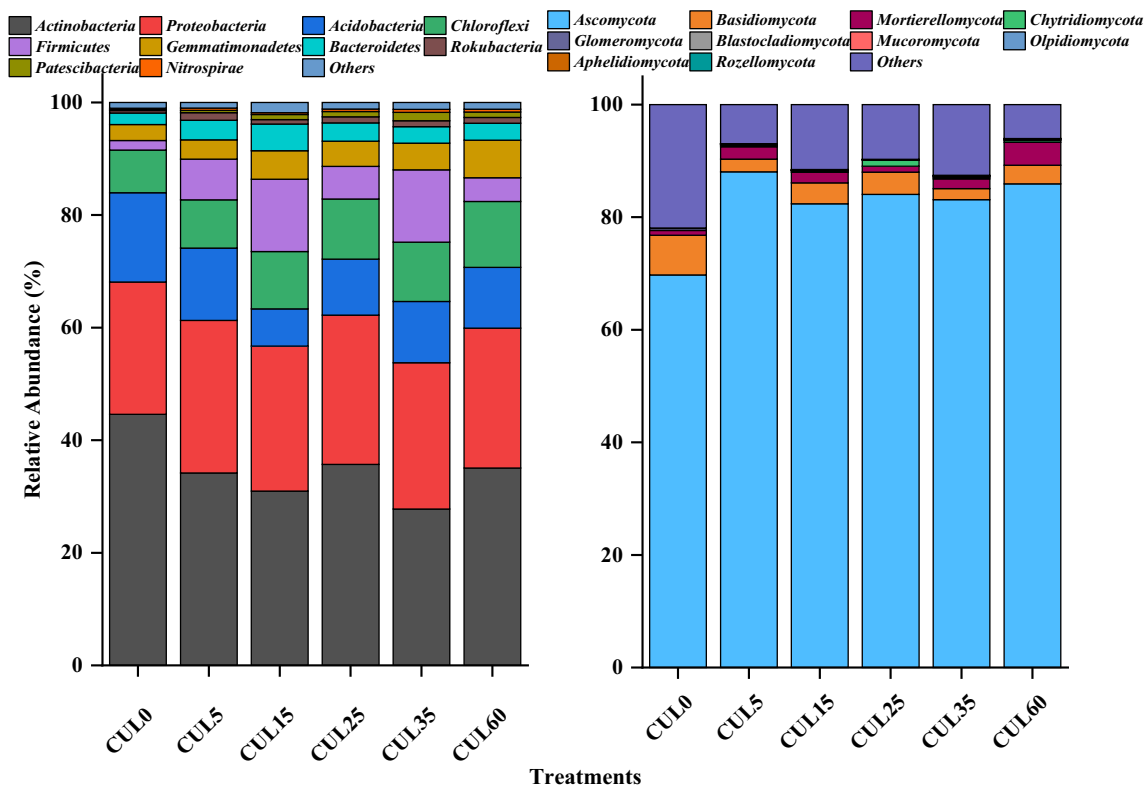


Fig. 2 The relative abundances of primary bacterial (A) and fungal (B) communities at phylum level in response to different periods of continuous cultivation

Table 3 Microbial alpha diversity indices in response to different periods of continuous cultivation

Treatments	Chao1	Shannon	Simpson	Pielou
Bacteria				
CUL0	3699 (473.6)	10.59 (0.29)	0.9987 (0.0002)	0.9096 (0.0006)
CUL5	3364 (555.9)	10.48 (0.18)	0.9987 (0.0001)	0.9061 (0.0003)
CUL15	2887 (327.0)	10.22 (0.28)	0.9980 (0.0007)	0.8989 (0.0013)
CUL25	3534 (303.4)	10.47 (0.15)	0.9984 (0.0009)	0.9008 (0.0009)
CUL35	3283 (394.7)	10.33 (0.35)	0.9975 (0.0024)	0.8922 (0.0025)
CUL60	3473 (413.9)	10.53 (0.12)	0.9978 (0.0001)	0.9058 (0.0031)
Fungi				
CUL0	500.3 (63.11)	5.82 (0.65)	0.9288 (0.0424)	0.6496 (0.0064)
CUL5	468.8 (130.5)	4.90 (1.25)	0.8461 (0.1201)	0.5512 (0.0118)
CUL15	499.4 (58.95)	5.97 (0.55)	0.9508 (0.0241)	0.6664 (0.0054)
CUL25	392.7 (90.62)	4.92 (0.98)	0.8674 (0.0875)	0.5705 (0.0926)
CUL35	396.3 (54.80)	4.60 (0.35)	0.8684 (0.0384)	0.5331 (0.0333)
CUL60	399.5 (57.28)	5.47 (0.55)	0.9190 (0.0356)	0.6331 (0.0052)

with cultivation duration. Heatmaps further revealed that soil bacterial structures at phylum level in the uncultivated grassland were most similar to those after 15 years of cultivation and least similar to those after

25 years of cultivation (Fig. 4A). For fungal community structures, uncultivated grassland was most similar to those after 25 years and least similar to those after 60 years of cultivation (Fig. 4B).

Relationships between soil properties and microbial characteristics

Redundancy analysis revealed that the composition of the soil bacterial community at phylum level and all the alpha diversity indices were strongly linked with SOC ($p=0.002$), EC ($p=0.006$), and BD ($p=0.01$), accounting for 19.7%, 7.8%, and 8.8% of the total community variation, respectively (Fig. 5A). The first and second ordination axes explained 26.7% and 15.4% of the overall variation, respectively. SOC and AK were significantly and positively related to the abundance of Actinobacteria and Pielou index, while BD and EC were significantly and positively correlated with Proteobacteria and Simpson index. Fungal alpha diversity indices and main community composition at the phylum level were closely linked to BD and SOC, accounting for 13.0% and 10.1% of variation, respectively. The first and second axes, respectively, described 29.7% and 11.5% of the entire variation in the fungal community, collectively accounting for 41.2% of

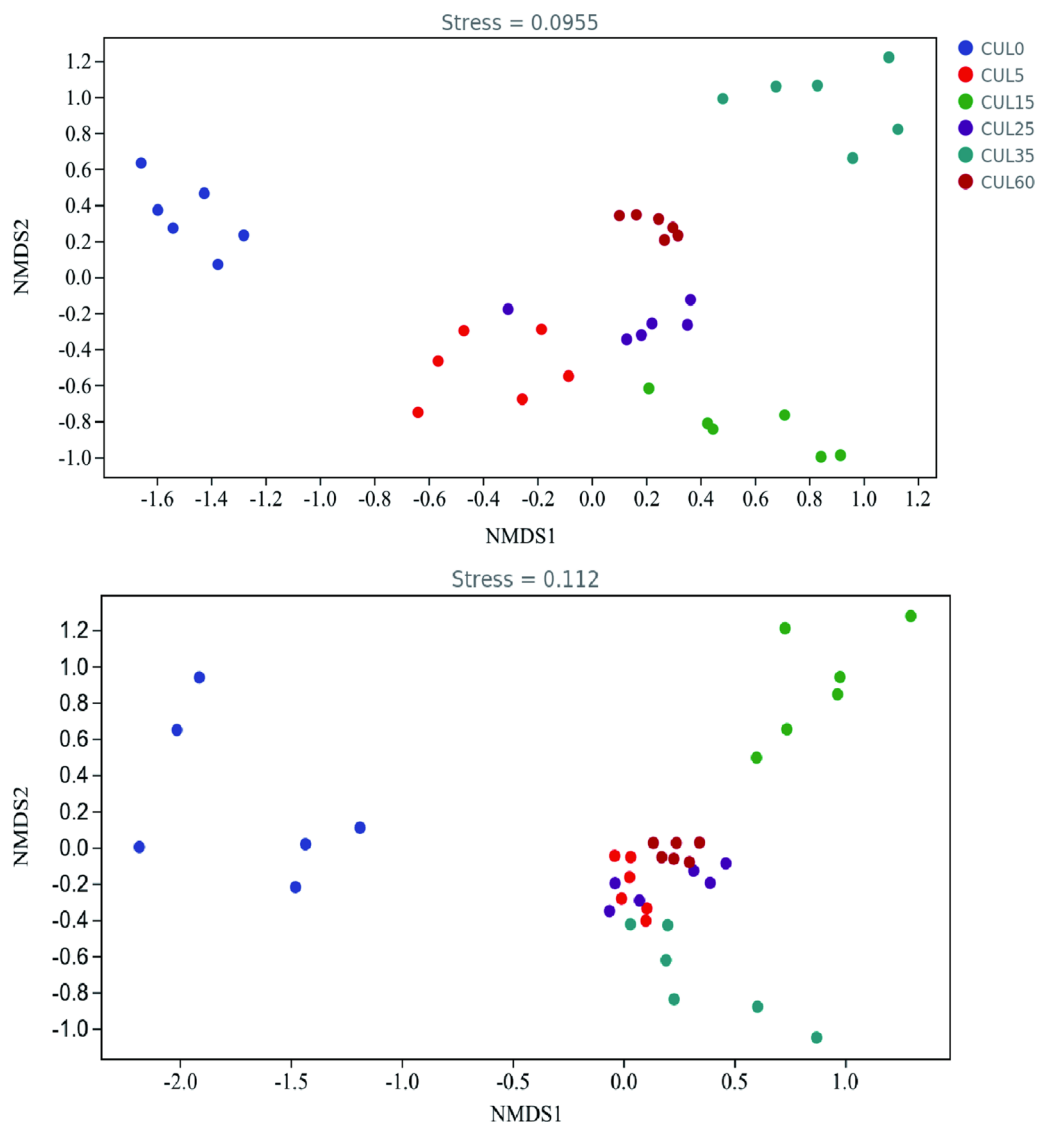


Fig. 3 Dissimilarity of soil microbial communities shown by nonmetric multidimensional scaling (NMDS): **A** bacteria and **B** fungi

it (Fig. 5B). SOC and AK were significantly, positively related to the abundance of Basidiomycota, whereas BD and SWC were similarly associated with Ascomycota, and EC with Mortierellomycota.

Discussion

Soil properties in response to grassland conversion

An increasing number of farmers and nomads have chosen to reclaim grasslands, woodlands, bare lands and even desert lands to expand crop production areas and meet their food demands, worldwide (Szoboszlai et al. 2017; Wang et al. 2021; Zhang et al. 2022). Conversion of grassland for agricultural cultivation involves changes to both plant species composition and land management

practices (Wang et al. 2021). In our experiment, indigenous perennial plants were replaced by an annual grass crop (maize), and agricultural practices such as irrigation, fertilizer and tillage were implemented during cultivation. Our hypothesis that these changes would be linked to significant alterations in soil properties was amply supported by the results, even though the interpretation of the chronosequence might be confounded to an extent by the evolving management of cultivated plots over the 60 years (cf. Table 1). The management had been consistent across plots of all cultivation ages for the last 20 years (since 2005) and effects on current measurements are likely to have been minor.

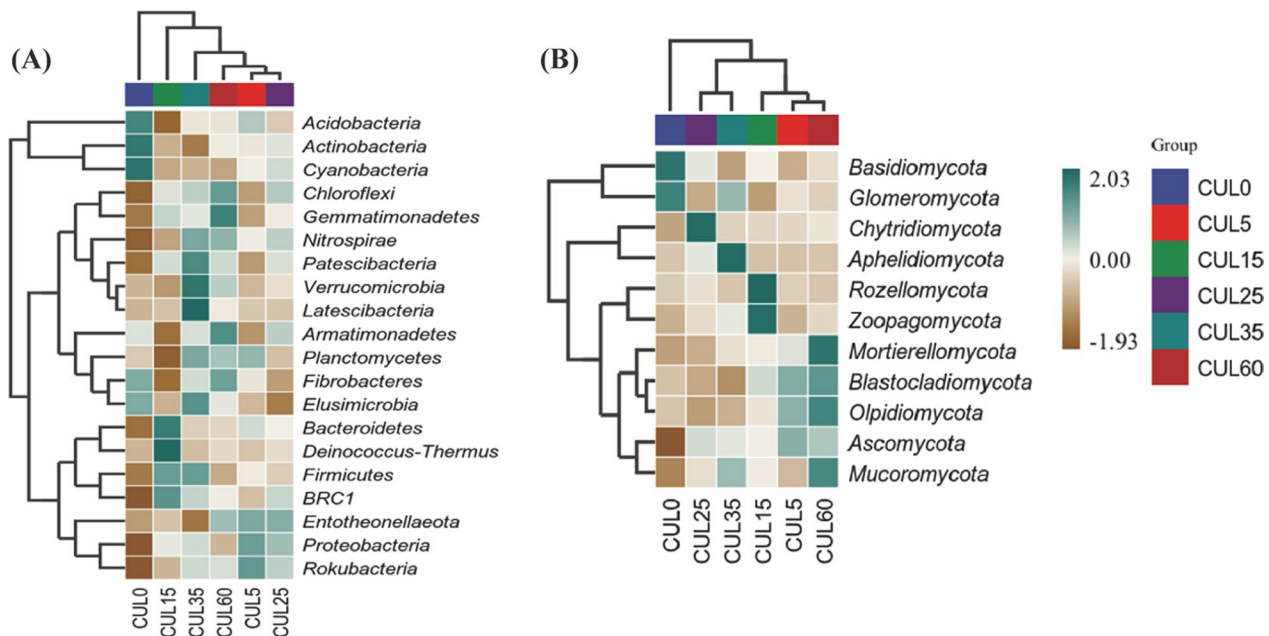


Fig. 4 Cluster heatmaps of bacterial and fungal communities at phylum level: **A** bacteria; **B** fungi. Only the 20 phyla with highest average abundance in any soil sample are shown

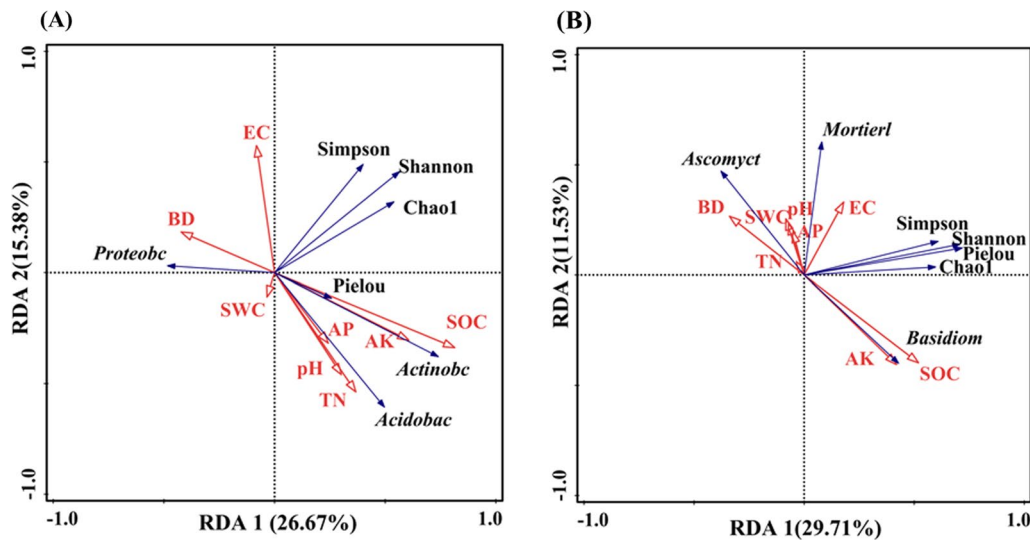


Fig. 5 Redundancy analysis (RDA) of the relationships between soil microbial community composition, alpha diversity indices at the phylum level and physicochemical properties. **A** Bacteria; **B** fungi

The chronosequence certainly demonstrated differences between different cultivation history treatments that implied substantial changes over varied timescales, some of which were highly persistent. For most soil characteristics, there were significant changes within the first 5 years, followed by a slow return to conditions more similar to those of undisturbed grassland over the next 30–55 years. Previous work has demonstrated

that long-term cultivation could lead to a considerable increase in soil bulk density (Wang et al. 2021) and such increases in Chernozem soils might result from compaction by agricultural operations (Wang et al. 2010a). The initial increase in BD and loss of SWC in the current experiment might involve a similar cause but the concomitant loss of soil organic carbon (SOC) was probably more important, as it would reduce carbon sequestration

in topsoil and influence carbon recycling processes. In contrast, no significant difference was found in the topsoil BD of Mollisols and Entisols in Northeast China after pasture had been reclaimed for cultivation (Ding et al. 2013). However, comparisons are complicated by differences in soil type, soil texture, and tillage frequency between research areas. Irrigation and fertilization are necessary to sustain good crop yield in dry and relatively barren soils (Hu et al. 2021). In the long term, grassland conversion tends to enhance topsoil moisture because croplands generally receive irrigation by pumping ground water, unlike the rain-fed grassland in this region (Guo and Gifford 2002; Tang et al. 2019). Large-scale crop farming has resulted in a major decline in groundwater levels and a depletion of water resources due to plant evapotranspiration, exacerbating environmental problems in arid and semi-arid land. In addition, alkaline materials could accumulate in the topsoil as a result of high irrigation, causing the pH to rise after cultivation (Rozema and Flowers 2008). However, we found no variation in pH between native grasslands and croplands, suggesting little impact in buffered, alkaline soil settings. The application of chemical fertilizers would have enhanced concentrations of exchangeable base cations in the soil, explaining the large, persistent increase in EC (Luneberg et al. 2018; Hu et al. 2021). After long-term cultivation (CUL35 and CUL60), however, an equilibrium appears to have been reestablished, with EC similar to that of native grassland.

As noted previously, there was a dramatic loss of SOC in the early years after cultivation, and only small signs of recovery after 60 years. Anthropogenic disturbances typically are detrimental to the organic carbon in topsoil (Chen et al. 2020). Recurrent ploughing and harrowing disrupt the aggregate structure of soil, leading to mineralization and decomposition of organic matter, a process only aggravated by fertilization and irrigation (Six et al. 1998; Dos Santos et al. 2019). Looser structure also allows significant losses of SOC by wind erosion in dry sandy soils, especially in windy winter and spring without effective vegetation cover due to nearly all of the stalks harvested for fodder (Li et al. 2009). Guo and Gifford (2002) also found that the greatest SOC depletion occurred shortly after crops were planted and Ding et al. (2013) suggested that cultivation was detrimental to SOC accumulation. We confirmed that long-term cultivation could not compensate for irreversible SOC losses from the land-use change represented by clearing grassland even though continuous sheep and cattle manure inputs after 1990. On the other hand, this implies that the agroecosystem that developed on sandy soil has a significant potential for carbon sequestration and plays a key role in

the regional carbon cycle process if appropriate managements were to be applied (Yang et al. 2022).

The total nitrogen (TN), available phosphorus (AP) and available potassium (AK) contents in topsoil were much higher after 5 years of cultivation than that in native grassland. These findings could again be attributed to greatly stimulated mineralization of organic matter and residues in native grassland, as a result of disturbance, in combination with the use of chemical fertilizers (Wang et al. 2010a). In the longer term, the persistent removal of maize cobs and stalks would restrict inputs of organic matter but could instead promote wind erosion, leading to more topsoil nutrient losses (Abegaz et al. 2016). Additionally, the diversity of residues incorporated into the soil would be reduced after monoculture maize replaced native vegetation (Wang et al. 2010a). There is evidence that steppes maintain higher root biomass than croplands (Hu et al. 2021; Wang et al. 2021) and according to Whalen et al. (2003), the plant community of the steppe absorb more nitrogen than crops, due to its dense and abundant fibrous root systems. However, we did not discriminate between the specific agricultural management effects of fertilizer, tillage, irrigation, and changing plant species on soil parameters; further studies would be required to understand their separate roles and possibly synergistic effects.

Microbial community characteristics

Soil microorganisms play key roles in regulating matter and energy flow (Li et al. 2019), and can be highly sensitive to changes in soil properties (Szoboszlay et al. 2017; Hu et al. 2021). Conversion of native grassland to cropland and continuing cultivation clearly altered microhabitats to affect the microbial community composition, which supported our hypothesis. Actinobacteria and Proteobacteria are the typically predominant bacterial phyla found in grassland and farmland, respectively (Luneberg et al. 2018; Zhang et al. 2022). They colonize nutrient-rich habitats and are responsible for nitrogen fixation as well as cellulose and lignin breakdown (Bao et al. 2021). Our results revealed that grassland cultivation facilitated soil organic matter depletion and nutrient loss, and led to relatively low Actinobacteria abundances, but no discernible variation in proportions of Proteobacteria was identified across the chronosequence. These results contrasted with findings for vineyard reclamation in deserted land of Ningxia, China, where Actinobacteria and Proteobacteria abundances were markedly enhanced (Zhang et al. 2022). The difference may be due to initial soil nutrient contents, plant species and environmental factors. Acidobacteria perform great adaptability to environments that have a wide range of carbon sources

(Xu et al. 2016) and so an increase in soil organic carbon benefits Acidobacteria abundance (Navarrete et al. 2013).

Ascomycota can adapt to harsh conditions and become the dominating phylum because of their rapid proliferation (Francioli et al. 2016). They are significant decomposers of lignocellulose in the fungal community (Wang et al. 2015). Ascomycota was found to be the prevalent phylum, comprising up 70–88% of the total abundance in plots of all cultivation periods. Mortierellomycota are capable of decomposing polysaccharides and other carbohydrates in the soil (Li et al. 2020a). Agricultural conversion of grassland promoted the proportions of Ascomycota and Mortierellomycota, which suggested that this land-use change provided soil organic matter and nutrient availability for specific microbial species. Pathogenic fungal species that cause crop disease are typically found among Basidiomycota (Li et al. 2014; Hu et al. 2021). Compared to natural grassland, cultivation decreased the abundance of Basidiomycota. Possible explanations for this include the changes of C/N ratio and SOC.

Microbial community composition and its proportional representation determine microbial diversity (Ferreira et al. 2016; Francioli et al. 2016), and more stable ecosystems are frequently associated with higher levels of microbial diversity (Maron et al. 2018). Our results suggested that grassland cultivation merely altered microbial community composition but had little effect on alpha diversity. Li et al. (2018) found that farming in the desert did not always lead to an increase in the diversity of the microbial community but did cause changes in the abundant species, which was similar to our findings. Earlier research had indicated that long-term farming might affect soil microbial community structure (Li et al. 2014, 2020b; Hu et al. 2021). NMDS and hierarchical clustering revealed a considerable difference in bacterial and fungal community structures between native grassland and cultivated soils. Additionally, with the increase of cultivation duration, bacterial composition tended to resemble that of native grassland soil, whereas fungi displayed the reverse trend. Possibly, bacteria had an advantage over many fungi in severe environments when it came to acquiring nutrients (Schmidt et al. 2014), but fungi were more responsive to changes in land use than bacteria in semi-arid grassland (Hu et al. 2021). Replacement of diverse, native vegetation by monospecific maize and frequent tillage could have generated a relatively homogeneous soil environment, which is thought to play a major role in determining the architecture of microbial communities (Mendes et al. 2011). This also suggested that microbial structure might be used as a potential indicator to evaluate the stability of agricultural ecosystem in grassland.

Prior studies have demonstrated conclusively that differential responses of bacterial and fungal properties depended on the changes in soil structure and nutrients (Francioli et al. 2016; Ren et al. 2019). We found that after grassland conversion for maize, alterations in microbial communities were linked to those of soil organic carbon and bulk density, which supports our hypothesis. For the majority of terrestrial microbial communities, SOC is a critical source of carbon and energy (Sarathchandra et al. 2001). Cheng et al. (2019) demonstrated that SOC controlled the composition of the bacterial population in semi-arid agricultural ecosystems. Moreover, BD was significantly positively correlated with Proteobacteria and Ascomycota, while negatively with Actinobacteria. This might be accounted for by the fact that tillage and irrigation altered soil macro-aggregation and compaction, which in turn might have affected dominant bacterial proliferation by modulating soil oxygen availability (Kihara et al. 2012; Lu et al. 2019). The dominant microbial phyla and alpha diversity indices were shown to be significantly correlated, and their correlations with SOC and BD further demonstrated the significance of these soil factors as key determinants in shaping microbial community structure.

Implications of grassland reclamation in traditional pastoral regions

Intensive agricultural practices yield relatively high aboveground biomass for feeding livestock and human food demands when grassland is converted to arable land, albeit at the expense of massive inputs of water, chemical fertilizer, and pesticides. SOC and other nutrient changes were expected to occur primarily during the initial decade following grassland cultivation (Tang et al. 2019; Wang et al. 2021). Even though SOC depletion and soil nutrient loss were partially restored by decadal-scale periods of grassland cultivation, they did not recover to their original conditions, meaning that grassland cultivation for crop production had an irreversible impact on soil characteristics in Horqin Sandy Land. In addition, some negative effects of cultivation, such as reduced litter biomass inputs, and frequent tillage after harvest and an potential increase in soil wind erosion and soil degradation, need to be taken into account from the perspective of sustainable development in these ethnic minority settlements of ecologically fragile regions (He et al. 2017; Hu et al. 2021). For sustainable development of this artificial ecosystem, appropriate agricultural management strategies, such as organic material inputs (manure or harvest residue), fallowing, or even acceptable amounts of abandonment may be proposed if cultivation is necessary. Moreover, patterns of intensive, high-yield, forage grass production should be explored as an alternative to

further cultivation, to reconcile minimizing the grassland area reclaimed with supporting the traditional livelihood of local ethnic minorities.

Although no discernible differences in microbial diversity were discovered between native grassland and cultivated land, there were very clear differences in the bacterial and fungal community structures. These findings suggested that the microbial community had a degree of resilience in its capacity to maintain diversity in response to grassland conversion to cropland (Lu et al. 2019). On the other hand, it was established that differences in soil characteristics between grassland and cultivated land affected the structure of the microbial communities, and that ongoing cultivation weakened community heterogeneity. It is likely that, this could involve irreversible loss of ecological functions. Consequently, a thorough evaluation of how this delicate ecosystem responds to anthropogenic disturbances is indispensable to understanding the structure of microbial communities. Furthermore, the main limitation in our experiment is that soil samples for each treatment were collected only once. There might be seasonal changes in the soil microbial community and soil properties (Gilbert et al. 2010). Therefore, additional evaluation of soil microbial communities from multi-seasonal sampling that reflected soil changes more comprehensively would be valuable.

Conclusion

Conversion of native grassland to cropland and its continuous cultivation for 60 years had profound effects on soil fertility and microbial characteristics in Horqin Sandy Land. Initially, cultivation of grassland changed soil nutrient contents rapidly (AP, AK, TN and SOC), and similarly influenced soil physical properties (BD, EC and SWC). The most persistent effect was the depletion of SOC, which only recovered partially in 60 years of cultivation, whereas other available nutrients tended to show better recovery in the long term (albeit still at lower concentrations than in native grassland), mostly as a result of agricultural management practices. This indicates that further grassland cultivation would disturb nutrient cycling on a greater scale and exacerbate soil degradation. There were discrepancies in microbial composition at phylum level and their community structures between native grassland and croplands of all ages, but the fact that there were no significant differences in their α -diversity indices suggests a degree of microbial resilience and stability. SOC and BD were demonstrated to be of fundamental importance in determining microbial community composition and diversity. In consequence, appropriate agricultural strategies to increase organic

material inputs after cultivation are recommended. In addition, the intensification of forage grass production is proposed as an alternative cultivation to expanding the area of the cultivation, in order to minimize the cultivated grassland area and better coordinate cropping and animal husbandry in dry agro-pasture ecotones.

Supplementary Information

The online version contains supplementary material available at <https://doi.org/10.1186/s13717-023-00431-2>.

Additional file 1: Table S1. Mean abundances of measured soil bacterial communities at phylum level in response to different periods of continuous cultivation.

Additional file 2: Table S2. Mean abundances of measured soil fungal communities at phylum level in response to different periods of continuous cultivation.

Acknowledgements

Special thanks are given to Yongming Luo, Hongmei Wang for their valuable help in field soil sampling. Sequencing service was provided by Personal Biotechnology Co., Ltd Shanghai, China.

Author contributions

JT and FP analyzed the data and wrote the original draft. JY collected soil samples and ADJ revised the original draft. RM and XH conducted the experiment, analyzed the data, and edited the manuscript. All authors read and approved the final manuscript.

Funding

This research was supported by Key Project of Chinese National Programs for Research and Development (2016YFC0500803) and Foundation of Scientific Research of Henan Institute of Science and Technology (208010617009).

Availability of data and materials

The data generated and analyzed during the present study are available from the corresponding author.

Declarations

Ethics approval and consent to participate

Not applicable.

Consent for publication

Not applicable.

Competing interests

The authors declare that they have no competing interests.

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Received: 25 December 2022 Accepted: 27 March 2023

Published online: 11 April 2023

References

- Abegaz A, Winowiecki LA, Vagen TG, Langan S, Smith JU (2016) Spatial and temporal dynamics of soil organic carbon in landscapes of the upper Blue Nile Basin of the Ethiopian Highlands. *Agric Ecosyst Environ* 218:190–208. <https://doi.org/10.1016/j.agee.2015.11.019>
- Bao YY, Jan J, Guo ZY, Chen RR, Wu M, Li ZP, Lin XG, Feng YZ (2021) Important ecophysiological roles of non-dominant *Actinobacteria* in plant residue decomposition, especially in less fertile soils. *Microbiome* 9:84. <https://doi.org/10.1186/s40168-021-01032-x>
- Blake GR, Hartage KH (1986) Bulk density. In: *Methods of Soil Analysis*. ASA and SSSA, Madison, WI
- Bokulich NA, Kaehler BD, Ram RJ, Matthew D, Evan B, Rob K, Huttley GA, Gregory CJ (2018) Optimizing taxonomic classification of marker-gene amplicon sequences with QIIME 2's q2-feature-classifier plugin. *Microbiome* 6:90. <https://doi.org/10.1186/s40168-018-0470-z>
- Callahan BJ, McMurdie PJ, Rosen MJ, Han AW, Johnson A, Holmes SP (2016) DADA2: high-resolution sample inference from Illumina amplicon data. *Nat Methods* 13:581–583. <https://doi.org/10.1038/nmeth.3869>
- Cao CY, Jiang DM, Teng XH, Jiang Y, Liang WJ, Cui ZB (2008) Soil chemical and microbiological properties along a chronosequence of *Caragana microphylla* Lam. plantations in the Horqin sandy land of Northeast China. *Appl Soil Ecol* 40:78–85. <https://doi.org/10.1016/j.apsoil.2008.03.008>
- Carter MR, Gregorich EG (2007) *Soil sampling and methods of analysis*. CRC Press, Boca Raton
- Chen HH, Dai ZM, Veach AM, Zheng JQ, Xu JM, Schadt CW (2020) Global meta-analyses show that conservation tillage practices promote soil fungal and bacterial biomass. *Agric Ecosyst Environ* 293:106841. <https://doi.org/10.1016/j.agee.2020.106841>
- Cheng ZB, Chen Y, Zhang FH (2019) Effect of cropping systems after abandoned salinized farmland reclamation on soil bacterial communities in arid northwest China. *Soil Tillage Res* 187:204–213. <https://doi.org/10.1016/j.still.2018.12.015>
- Ding F, Hu YL, Li L, Li A, Shi SW, Lian PY, Zeng DH (2013) Changes in soil organic carbon and total nitrogen stocks after conversion of meadow to cropland in Northeast China. *Plant Soil* 373:659–672. <https://doi.org/10.1007/s11104-013-1827-5>
- Dos Santos UJ, De Medeiros EV, Duda GP, Marques MC, de Souza ES, Brosard M, Hammecker C (2019) Land use changes the soil carbon stocks, microbial biomass and fatty acid methyl ester (FAME) in Brazilian semiarid area. *Arch Agron Soil Sci* 65:755–769. <https://doi.org/10.1080/03650340.2018.1523544>
- Du Y (2019) *Analysis of land cover change and driving factors in Horqin Sandy Land in recent 20 years*. Shanghai Normal University, Shanghai
- Ferreira ACC, Leite LFC, de Araujo ASF, Eisenhauer N (2016) Land-use type effects on soil organic carbon and microbial properties in a semi-arid region of Northeast Brazil. *Land Degrad Dev* 27:171–178. <https://doi.org/10.1002/ldr.2282>
- Fierer N, Lauber CL, Ramirez KS, Zaneveld J, Bradford MA, Knight R (2012) Comparative metagenomic, phylogenetic and physiological analyses of soil microbial communities across nitrogen gradients. *ISME J* 6:1007–1017. <https://doi.org/10.1038/ismej.2011.159>
- Francois D, Elke S, Guillaume L, Tesfaye W, François B, Thomas R (2016) Mineral vs. organic amendments: microbial community structure, activity and abundance of agriculturally relevant microbes are driven by long-term fertilization strategies. *Front Microbiol* 7:289. <https://doi.org/10.3389/fmicb.2016.01446>
- Gilbert JA, Field D, Swift P, Newbold L, Oliver A, Smyth T, Somerfield PJ, Huse S, Joint I (2010) The seasonal structure of microbial communities in the Western English Channel. *Environ Microbiol* 11:3132–3139. <https://doi.org/10.1111/j.1462-2920.2009.02017.x>
- Gongbuzeren LYB, Li WJ (2015) China's rangeland management policy debates: what have we learned? *Rangel Ecol Manag* 68:305–314. <https://doi.org/10.1016/j.rama.2015.05.007>
- Guo LB, Gifford RM (2002) Soil carbon stocks and land use change: a meta analysis. *Glob Chang Biol* 8:345–360. <https://doi.org/10.1046/j.1354-1013.2002.00486.x>
- He YT, Xu MG, Qi YC, Dong YS, He XH, Li JW, Liu XC, Sun LJ (2017) Differential responses of soil microbial community to four-decade long grazing and cultivation in a semi-arid grassland. *Sustainability* 9:128. <https://doi.org/10.3390/su9010128>
- Hu YG, Wang ZR, Zhang ZS, Song NP, Zhou HK, Li YK, Wang YN, Li CS, Hale L (2021) Alteration of desert soil microbial community structure in response to agricultural reclamation and abandonment. *Catena* 207:105678. <https://doi.org/10.1016/j.catena.2021.105678>
- Kihara J, Martius C, Bationo A, Thuita M, Lesueur D, Herrmann L, Amelung W, Vlek PLG (2012) Soil aggregation and total diversity of bacteria and fungi in various tillage systems of sub-humid and semi-arid Kenya. *Appl Soil Ecol* 58:12–20. <https://doi.org/10.1016/j.apsoil.2012.03.004>
- Li FR, Zhao WZ, Liu JL, Huang ZG (2009) Degraded vegetation and wind erosion influence soil carbon, nitrogen and phosphorus accumulation in sandy grasslands. *Plant Soil* 317:79–92. <https://doi.org/10.1007/s11104-008-9789-8>
- Li XG, Ding CF, Zhang TL, Wang XX (2014) Fungal pathogen accumulation at the expense of plant-beneficial fungi as a consequence of consecutive peanut monoculturing. *Soil Biol Biochem* 72:11–18. <https://doi.org/10.1016/j.soilbio.2014.01.019>
- Li FR, Liu JL, Ren W, Liu LL (2018) Land-use change alters patterns of soil biodiversity in arid lands of northwestern China. *Plant Soil* 428:371–388. <https://doi.org/10.1007/s11104-018-3673-y>
- Li XB, He HB, Zhang XD, Yan XX, Six J, Cai ZC, Barthel M, Zhang JB, Necpalova M, Ma QQ, Li ZA (2019) Distinct responses of soil fungal and bacterial nitrate immobilization to land conversion from forest to agriculture. *Soil Biol Biochem* 134:81–89. <https://doi.org/10.1016/j.soilbio.2019.03.023>
- Li F, Zhang SQ, Wang Y, Li Y, Li PP, Chen L, Jie XL, Hua DS, Feng B, Yue K, Han YL (2020a) Rare fungus, *Mortierella capitata*, promotes crop growth by stimulating primary metabolisms related genes and reshaping rhizosphere bacterial community. *Soil Biol Biochem* 151:108017. <https://doi.org/10.1016/j.soilbio.2020.108017>
- Li JB, Liu GM, Kwak JH, Chang SX, Gao HC, Wu QC, Yang JS, Chen JL (2020b) Reclamation of desert land to continuous cotton cropping affects soil properties and microbial communities in the desert-oasis ecotone of Xinjiang, China. *J Soils Sediments* 20:862–873. <https://doi.org/10.1007/s11368-019-02469-2>
- Lu RK (1999) *Soil and agro-chemical analysis methods*. China Agricultural Science and Technology Press, Beijing
- Lu J, Qiu KC, Li WX, Wu Y, Ti JS, Chen F, Wen XY (2019) Tillage systems influence the abundance and composition of autotrophic CO₂-fixing bacteria in wheat soils in North China. *Eur J Soil Biol* 93:103086. <https://doi.org/10.1016/j.ejsobi.2019.103086>
- Luneberg K, Schneider D, Siebe C, Daniel R (2018) Drylands soil bacterial community is affected by land use change and different irrigation practices in the Mezquital Valley, Mexico. *Sci Rep* 8:1413. <https://doi.org/10.1038/s41598-018-19743-x>
- Maron PA, Sarr A, Kaisermann A, Leveque J, Mathieu O, Guigue J, Karimi B, Bernard L, Dequiedt S, Terrat S, Chabbi A, Ranjard L (2018) High microbial diversity promotes soil ecosystem functioning. *Appl Environ Microbiol* 84:e02738-17. <https://doi.org/10.1128/AEM.02738-17>
- Mendes R, Kruijt M, Bruijn DJ, Dekkers E, Voort MVD, Schneider JHM, Piceno YM, DeSantis TZ, Andersen GL, Bakker PAHM, Raaijmakers JM (2011) Deciphering the rhizosphere microbiome for disease-suppressive bacteria. *Science* 332:1097–1100. <https://doi.org/10.1126/science.1203980>
- Miao RH, Liu YZ, Wu LQ, Wang D, Liu YC, Miao Y, Yang ZL, Guo MX, Ma J (2022) Effects of long-term grazing exclusion on plant and soil properties vary with position in dune systems in the Horqin Sandy Land. *Catena* 209:105860. <https://doi.org/10.1016/j.catena.2021.105860>
- Navarrete AA, Kuramae EE, de Hollander M, Pijl AS, van Veen JA, Tsai SM (2013) Acidobacterial community responses to agricultural management of soybean in Amazon forest soils. *FEMS Microbiol Ecol* 83:607–621. <https://doi.org/10.1111/1574-6941.12018>
- Okolo CC, Gebresamuel G, Zenebe A, Haile M, Eze PN (2020) Accumulation of organic carbon in various soil aggregate sizes under different land use systems in a semi-arid environment. *Agric Ecosyst Environ* 297:106924. <https://doi.org/10.1016/j.agee.2020.106924>
- Qiao N, Xu XL, Cao GM, Ouyang H, Kuzyakov Y (2015) Land use change decreases soil carbon stocks in Tibetan grasslands. *Plant Soil* 395:231–241. <https://doi.org/10.1007/s11104-015-2556-8>
- Ren CJ, Liu WC, Zhao FZ, Zhong ZK, Deng J, Han XH, Yang GH, Feng YZ, Ren GX (2019) Soil bacterial and fungal diversity and compositions respond differently to forest development. *Catena* 181:104071. <https://doi.org/10.1016/j.catena.2019.104071>

- Rozema J, Flowers T (2008) Crops for a salinized world. *Science* 322:1478–1479. <https://doi.org/10.1126/science.1168572>
- Sarathchandra SU, Ghani A, Yeates GW, Burch G, Cox NR (2001) Effect of nitrogen and phosphate fertilisers on microbial and nematode diversity in pasture soils. *Soil Biol Biochem* 33:953–964. [https://doi.org/10.1016/S0038-0717\(00\)00245-5](https://doi.org/10.1016/S0038-0717(00)00245-5)
- Schmidt SK, Nemergut DR, Darcy JL, Lynch R (2014) Do bacterial and fungal communities assemble differently during primary succession? *Mol Ecol* 23:254–258. <https://doi.org/10.1111/mec.12589>
- Six J, Elliott TE, Paustian K, Doran JW (1998) Aggregation and soil organic matter accumulation in cultivated and native grassland soils. *Soil Sci Soc Am J* 62:1367–1377. <https://doi.org/10.2136/sssaj1998.03615995006200050032x>
- Szoboszlay M, Dohrmann AB, Poeplau C, Don A, Tebbe CC (2017) Impact of land-use change and soil organic carbon quality on microbial diversity in soils across Europe. *FEMS Microbiol Ecol* 93:146. <https://doi.org/10.1093/femsec/fix146>
- Tang J, Davy AJ, Jiang DM, Musa A, Wu DF, Wang YC, Miao CP (2016) Effects of excluding grazing on the vegetation and soils of degraded sparse-elm grassland in the Horqin Sandy Land, China. *Agric Ecosyst Environ* 235:340–348. <https://doi.org/10.1016/j.agee.2016.11.005>
- Tang SM, Guo JX, Li SC, Li JH, Xie S, Zhai XJ, Wang CJ, Zhang YJ, Wang K (2019) Synthesis of soil carbon losses in response to conversion of grassland to agriculture land. *Soil Tillage Res* 185:29–35. <https://doi.org/10.1016/j.still.2018.08.011>
- Tang J, Yin JZ, Davy AJ, Pan FF, Han X, Huang SN, Wu DF (2022) Biogas slurry as an alternative to chemical fertilizer: changes in soil properties and microbial communities of fluvo-aquic soil in the North China Plain. *Sustainability* 14:15099. <https://doi.org/10.3390/su142215099>
- Wang Q, Zhang L, Li L, Bai YH, Cao J, Han XG (2010a) Changes in carbon and nitrogen of Chernozem soil along a cultivation chronosequence in a semi-arid grassland. *Eur J Soil Sci* 60:916–923. <https://doi.org/10.1111/j.1365-2389.2009.01174.x>
- Wang Y, Xu J, Shen JH, Luo YM, Scheu S, Ke X (2010b) Tillage, residue burning and crop rotation alter soil fungal community and water-stable aggregation in arable fields. *Soil Tillage Res* 107:71–79. <https://doi.org/10.1016/j.still.2010.02.008>
- Wang F, Liang YT, Jiang YJ, Yang YF, Xue K, Xiong JB, Zhou JZ, Sun B (2015) Planting increases the abundance and structure complexity of soil core functional genes relevant to carbon and nitrogen cycling. *Sci Rep* 5:14345. <https://doi.org/10.1038/srep14345>
- Wang ZR, Liu YB, Zhao LN, Zhang WL, Liu LC (2019) Change of soil microbial community under long-term fertilization in a reclaimed sandy agricultural ecosystem. *PeerJ* 7:e6497. <https://doi.org/10.7717/peerj.6497>
- Wang C, Li LH, Yan YC, Cai YR, Xu DW, Wang X, Chen JQ, Xin XP (2021) Effects of cultivation and agricultural abandonment on soil carbon, nitrogen and phosphorus in a meadow steppe in eastern Inner Mongolia. *Agric Ecosyst Environ* 309:107284. <https://doi.org/10.1016/j.agee.2020.107284>
- Whalen JK, Willms WD, Dormaar JF (2003) Soil carbon, nitrogen and phosphorus in modified rangeland communities. *J Range Manage* 56:665–672. <https://doi.org/10.2307/4003944>
- White R, Murray S, Rohweder M, Prince S, Thompson K (2000) Pilot analysis of global systems: Grassland Ecosystems. World Resources Institute, Washington, DC
- Xu N, Tan GC, Wang HY, Gai XP (2016) Effect of biochar additions to soil on nitrogen leaching, microbial biomass and bacterial community structure. *Eur J Soil Biol* 74:1–8. <https://doi.org/10.1016/j.ejsobi.2016.02.004>
- Yang Y, Shi Y, Sun WJ, Chang JF, Zhu JX, Chen LY, Wang X, Guo YP, Zhang HT, Yu LF, Zhao SQ, Xu K, Zhu JL, Sheng HH, Wang YY, Peng YF, Zhao X, Wang XP, Hu HF, Chen SP, Huang M, Wei XF, Wang SP, Zhu B, Niu SL, Tang ZY, Liu LL, Fang YT (2022) Terrestrial carbon sinks in China and around the world and their contribution to carbon neutrality. *Sci China Life Sci* 65:861–895. <https://doi.org/10.1007/s11427-021-2045-5>
- Zhang L, Xue TT, Yuan L, Gao FF, Hao XY, Yang CL, Wang L, Han YL, Li H, Wang H (2022) The effect of vineyard reclamation on soil properties and microbial communities in desertified land in Hongsibu, Ningxia. *Catena* 211:106002. <https://doi.org/10.1016/j.catena.2021.106002>
- Zhao L, Xu H, Liu JH, Li H, Men J, Yang XS (2020) Changes in soil properties and crop yields of farmland over a 20-year reclamation period from grassland in the hilly areas of Hebei, China. *Arch Agron Soil Sci* 67:594–606. <https://doi.org/10.1080/03650340.2020.1741552>
- Zhou J, Jiang X, Zhou BK, Zhao BS, Ma MC, Guan DW, Li J, Chen SF, Cao FM, Shen DL, Qin J (2016) Thirty four years of nitrogen fertilization decreases fungal diversity and alters fungal community composition in black soil in northeast China. *Soil Biol Biochem* 95:135–143. <https://doi.org/10.1016/j.soilbio.2015.12.012>
- Zucca C, Canu A, Previtali F (2010) Soil degradation by land use change in an agropastoral area in Sardinia (Italy). *Catena* 83:46–54. <https://doi.org/10.1016/j.catena.2010.07.003>

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