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Light grazing alleviates aeolian erosion–deposition effects on microbial communities in a semi-arid grassland

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Abstract

Background Soil erosion affects the stability of terrestrial ecosystems and ecosystem services by directly or indirectly impacting the cycling of soil materials and energy and reducing the fertility of grassland soils. However, research on microbial adaptation to grazing and soil erosion is limited, particularly in relation to grassland ecosystem restoration. Here, we assess microbial communities subjected to simulated soil erosion and grazing in a semi-arid grassland of Inner Mongolia, China.

Results No significant change was observed in soil variables. However, the structure of the soil microbial community underwent significant changes as a result of soil erosion and soil erosion plus grazing, leading to a significant increase in the relative abundance of Cyanobacteria (116.80% vs 116.38%). Wind erosion and deposition contributed to an increase in the network complexity of soil bacterial and fungal communities. However, much of this effect was alleviated by grazing. Simultaneously, aeolian processes and grazing regulate soil microbial community assembly, leading to inconsistent patterns of change in bacterial and fungal communities. Under wind erosion and deposition, the relative contribution of deterministic processes (4.44% vs 31.11%) in bacterial communities increased, while the relative contribution of stochastic processes (2.23% vs 20%) in fungal communities reduced. Grazing resulted in a decrease in the relative contribution of deterministic processes (8.89%) in the bacterial community and an increase in the relative contribution of stochastic processes (8.89%) in the fungal community.

Conclusion This study presents a comprehensive investigation of the response of soil microbial communities to aeolian erosion–deposition and grazing in a semi-arid grassland. Our findings indicate that microbial communities in the semi-arid grassland show resistance to external disturbances and that light grazing mitigates the effects of aeolian erosion–deposition on microbial communities, which is essential for maintaining the stability and biodiversity of grassland ecosystems.

Keywords Semi-arid grassland, Erosion, Grazing, Soil microbial community network, Deposition

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Introduction

Grasslands, covering ~ 32 million km² of terrestrial ecosystems, play a crucial role in maintaining ecological balance, preventing wind and sand erosion, retaining water, and providing essential ecological services (Bardgett et al. 2021). Among the various land uses in grassland ecosystems, grazing is the most prevalent and extensive, leading to alterations in vegetation community structure and an increase in bare ground area, which in turn enhances the potential for wind erosion (Wei et al. 2022). The associated activities of grazing, trampling, and excretion result in changes in the soil environment, subsequently influencing the soil microbial community (Yu et al. 2023; Wang et al. 2019). Moreover, livestock trampling can disrupt soil crusts, reducing water infiltration and soil stability (Zhou et al. 2010; Tabeni et al. 2014; Van Klink et al. 2015). Additionally, the expansion of exposed soil areas and reduction in vegetation caused by grazing can increase airflow over the soil surface, creating favorable conditions for dust events (Zhao et al. 2005; Ludwig et al. 2007; Hoffmann et al. 2008; Belnap et al. 2009; Nauman et al. 2018). The aeolian sand processes triggered by grazing, including wind erosion and dust deposition, can further impact the structure and composition of soil microbial communities (Zheng et al. 2021; Qiu et al. 2021).

Soil wind erosion processes often result in changes in the physicochemical properties of the soil. Numerous studies have demonstrated that depositional areas exhibit higher water content, greater soil organic matter, and various mineral nutrients, but lower aeration and pH compared to eroded areas (Berhe et al. 2018; Doetterl et al. 2012; Li et al. 2019). Wind erosion can remove fine sediments such as silt, clay, and fine sand, leading to a higher proportion of large particles and a lower proportion of small particles in the soil particle composition within the wind erosion area. Conversely, the grain composition in the depositional areas exhibits the opposite trend (Wei et al. 2016). Furthermore, the processes of topsoil migration and dust emission induced by wind erosion can affect the composition and structure of the soil microbial community, subsequently altering the soil nutrient pool. Previous studies have revealed the negative impact of soil erosion on soil microbial biomass, abundance, and composition (Li et al. 2015). Specifically, wind erosion has been shown to have detrimental effects on microbial characteristics (Wei et al. 2016). Therefore, it is reasonable to hypothesize that wind erosion and deposition may have contrasting effects on the composition and diversity of microbial communities, considering their opposing effects on soil nutrient pools. However, the interaction between grazing and soil erosion on soil microorganisms in typical grasslands remains poorly understood.

Investigating whether there is a coupling effect between grazing and soil erosion on soil microorganisms in the grasslands would be beneficial for accurately predicting alterations in soil microbial communities and evaluating their ecosystem functions.

Understanding the ecological processes that govern the assembly of soil microbial communities in grassland soils is crucial for predicting ecosystem responses to environmental change (Zhou and Ning 2017). Determinism and stochasticity play a role in shaping soil microbial communities (Jiang et al. 2021; Ning et al. 2019). Deterministic processes include ecological selection imposed by abiotic and biotic factors. (Tripathi et al. 2018). Stochastic processes include ecological drift, random births, deaths and probabilistic diffusion (Chase et al. 2011). Previous studies have suggested that the composition of bacterial communities in temperate grasslands is predominantly influenced by stochastic processes (Xu et al. 2021; Du et al. 2021). However, it has also been demonstrated that grassland bacterial communities are primarily controlled by deterministic processes in the topsoil (0–10 cm) (Liu et al. 2021). In areas where long-range dispersal is not constrained, deterministic processes are more likely to occur (Cottenie 2005). For instance, in Inner Mongolia's steppes, where year-round winds and dust storms can transport soil particles hundreds of kilometers, deterministic processes are expected to play a significant role (Liu et al. 2021). Wind speed and dust transport have been shown to influence the distribution of microorganisms in the near-surface atmosphere (Barberán et al. 2015). In the context of grassland restoration, previous studies have indicated that stochastic processes dominate the assembly mechanisms of soil fungal communities (Guo et al. 2023). Additionally, a combination of deterministic and stochastic processes has been found to govern the assembly mechanisms of soil fungal communities in ecosystems threatened by desertification (Gong et al. 2023). However, the relative contribution of deterministic and stochastic processes to soil microbial communities in semi-arid temperate grasslands remains unclear. Quantifying the extent to which deterministic and stochastic processes influence soil microbial communities is crucial for understanding the adaptive capacity of soil microbes in the face of environmental change.

To further investigate the effects of aeolian processes and grazing on soil microbial communities, this study aimed to achieve the following objectives: (i) exploring how aeolian processes and grazing affect the composition, diversity, and stability of soil microbial communities, (ii) understanding the patterns of co-occurrence networks within microbial communities in response to aeolian processes and grazing, and identifying key taxa involved, and (iii) determining the relative importance of

soil microbial community assembly processes in eroded, deposited, and grazed plots. The effects of wind erosion and grazing on the availability of soil resources and soil structure have been shown in previous studies (Ma et al. 2019, Kong et al. 2022, Hao et al. 2022, Xu et al. 2023). Furthermore, our previous observations at the study site indicated that wind erosion did not affect plant species richness, deposition decreased species richness, and grazing increased species richness (Zheng et al. 2021). Therefore, we hypothesize that (H1) wind erosion will reduce soil microbial diversity and network complexity, while deposition, by enhancing soil nutrients, will increase them; (H2) soil erosion and grazing would increase the relative contribution of deterministic processes and decrease the relative contribution of stochastic processes in bacterial communities, deposition would decrease the relative contribution of deterministic processes in bacterial communities and the relative contribution of stochastic processes in fungal communities. To test these hypotheses, this study examined the responses of soil microbial communities to aeolian processes and grazing in a semi-arid grassland subjected to simulated soil wind erosion, deposition, and grazing for a period of seven years in Inner Mongolia, China.

Materials and methods

Study site and experimental design

The experimental site was in a semi-arid, temperate steppe in Duolun County (42° 02' N, 116° 16' E, 1324 m a.s.l.), Inner Mongolia, China (Zheng et al. 2022). This region experiences a mid-temperate monsoonal climate characterized by semi-aridity. The average annual temperature is 2.1 °C, with an evaporation rate of 1748 mm and an annual precipitation of 379.1 mm, primarily concentrated in the months of June to August, accounting for ~ 67% of the total annual precipitation (Chen et al. 2014). The mean and maximum annual wind speeds are recorded as 3.46 m/s and 9.11 m/s, respectively, with gusts reaching up to 25.5 m/s. The spring season is often characterized by dryness, leading to the presence of dry sand and wind, creating favorable conditions for the occurrence of blowing sand or dust storms. The study site, located in the Xilin River basin, has been subjected to extensive inappropriate land use practices, including overgrazing, leading to moderate to severe aeolian soil erosion (Hoffmann, et al. 2011; Hoffmann et al. 2008). In 1999, the steppe area within the basin was estimated to have a total degraded area of 7689.3 km², which accounted for 72% of the total basin (Ma et al. 2017; Tong et al. 2004). The soil types in the study area are classified as chestnut soil (according to Chinese classification) and ordinary calcareous soil (according to FAO classification). The dominant grass species at the site include *Artemisia*

frigida, *Stipa krylovii*, *Agropyron cristatum*, *Leymus chinensis*, *Potentilla tanacetifolia*, and *Cleistogenes squarrosa* (Sagar et al. 2019).

The experiment, consisting of six treatments, was established in 2009 and commenced in April 2010. A complete random block design was employed, with a total of thirty 4 × 4 m plots and arranged in six rows and five columns, with a 2.5-m buffer plot was maintained between each plot, then six treatment combinations are control (C), grazing (G), soil erosion (SE), soil erosion plus grazing (SE + G), soil deposition (SD), soil deposition plus grazing (SD + G). To minimize the influence of natural winds and soil deposition from adjacent plots, polyvinyl chloride (PVC) boards were positioned 10 cm above ground level in each plot. Starting from 2010 to 2016, aeolian processes were simulated annually in early May. In the soil erosion plots, a wind extinguisher (Taining Machinery Ltd. Co., Taizhou, Jiangsu, China) was employed to blow off 1.5–3 cm of topsoil (Ma et al. 2019; Ma et al. 2017). The soil blown into the five soil erosion plots was collected using a cloth bag, thoroughly mixed, and divided into five equal parts. Subsequently, the soil was evenly spread on the surface of the soil deposition plots using rubber gloves. The estimated levels of soil erosion and deposition in the Inner Mongolian grasslands were of moderate intensity. Grazing activities were conducted from June to September, for a duration of 4 h per month, using 1-year-old sheep. This grazing intensity was determined based on previous studies conducted in the region, indicating light grazing in the area (Qian et al. 2017).

Soil sampling and measurements of soil chemical properties

In mid-August 2017, three soil cores (diameter 5 cm, depth 10 cm) were randomly collected from each plot and mixed in a sterile bag, for a total of 30 soil samples. Fresh soil samples were kept on ice during transport to the laboratory and were divided into two parts after sieving through a 2-mm sieve and removal of visible roots and stones by hand. One sub-sample was stored at – 80 °C for DNA extraction, while the other sub-sample was air-dried to determine soil chemical properties. Soil total carbon (TC) and total nitrogen (TN) were determined using a Vario MAX CNS elemental analyzer (Elementar Analysensysteme GmbH, Hanau, Germany), and soil total phosphorus (TP) was determined by molybdate colorimetry after digestion with H₂SO₄-HClO₄ (Kuo 1996); soil available phosphorus (AP) was extracted with NaHCO₃ and determined using a UV photometer (UV-1900, Shimadzu, Japan). The particle size fraction of the soil (volumetric fractions) was measured using the Mastersizer 3000 (Malvern Instruments, Malvern,

UK) based on the laser diffraction technique. Soil particle size was classified according to soil taxonomy standards developed by the US Department of Agriculture into clay (<0.002 mm), silt (0.002–0.05 mm), and sand (0.05–2 mm) fractions.

Amplicon sequencing

Total DNA was extracted from three 0.5 g subsamples from each soil samples by using E.Z.N.A.[®] Soil DNA Kit (Omega Bio-tek, Inc. Norcross, GA, USA) according to the manufacturer's instructions. The primers 338F (5'-ACTCCTACGGGAGGCAGCA-3') and 806R (5'-GGA CTACHVGGGTWTCTAAT-3') were used for bacteria 16S rRNA gene amplification, and the primer pairs ITS3F (5'-GCATCGATGAAGAACGCAGC-3') and ITS4 (5'-TCCTCCGCTTATTGATATGC-3') were used for the fungal ITS gene (Pires et al. 2012; Zhao et al. 2020; Zou et al. 2020). In brief, PCR was performed in triplicate under the following conditions: 95 °C for 5 min, followed by 40 cycles of 95 °C for 15 s, 60 °C for 30 s, and 72 °C for 30 s, followed by a final extension of 5 min at 72 °C. The Illumina Nextera kit was used to prepare the sequencing libraries. Paired-end sequencing (2×300 bp) was done by using an Illumina HiSeq platform at Shanghai Personal Biotechnology Co., Ltd (Shanghai, China). Data were deposited in the China National Microbiology Data Center (NMDC) with accession numbers NMDC10018265 (<https://nmdc.cn/resource/genomics/project/detail/NMDC10018265>). The raw DNA sequencing reads were processed using QIIME v1.8.0, USEARCH, and UPARSE. USEARCH was used to further denoise, dereplicate, and compress the trimmed sequence reads. The high-quality sequence reads were aligned to the SILVA v132 database (<http://www.arb-silva.de>) (Quast et al. 2012) and the UNITE database (Kõljalg et al. 2013) to obtain OTUs with 97% similarity by using UCLUST. More than 99.9% of our sequence reads were mapped against the database.

Data analysis and statistics

Correlation analysis and analysis of variance were conducted using R version 4.1.2. Graphs were generated using Origin (OriginLab, Northampton, MA, USA). Two-way ANOVAs were employed to examine the impact of different treatments on soil chemistry, relative abundances of bacteria and fungi at the phyla and genus levels, as well as potential major taxa. Pearson correlations were used to assess the relationships between the relative abundance of major microbial phyla and soil properties. To assess the variation in soil microbial communities between treatments, a non-metric multidimensional scaling (NMDS) analysis based on pairwise Bray–Curtis and Unifrac dissimilarity was performed using 'metaMDS' in

the Vegan package (R version 4.1.2). The relationships between soil microbial communities and soil properties were analyzed using redundancy analysis (RDA) with Canoco 5 software.

Co-occurrence networks were constructed for the bacterial and fungal communities in different treatments. We classified SE and SE+G treatments as erosion and other treatments as non-erosion; SD and SD+G treatments as deposition and other treatments as non-deposition; G, SE+G and SD+G treatments as grazing and other treatments as non-grazing. Only keep OTUs detected in more than half of samples (bacteria, fungi). Co-occurrence networks were constructed using Spearman correlation coefficients (r)>0.6 and p -values<0.05. The p -values were adjusted using the Benjamini–Hochberg method. To describe the overall topological characteristics of the networks, several indicators were calculated (number of edges and nodes, clustering coefficient, graph density, network diameter, modularity, average degree and average path length). Statistical analysis and visualising the networks resulting from the different treatments were performed using Gephi (Bastian et al. 2009).

To predict putative bacterial functional profiles, the FAPROTAX (v1.1) database (<http://www.loucalab.com/archive/FAPROTAX/>) was employed, using OTU-level data to map prokaryotic evolution to defined metabolic or other ecologically related functions based on current literature on cultured lineages. Fungal functional prediction was performed using the FUNGUILD (v1.0) database (Nguyen et al. 2016), assigning putative life strategies to taxonomically defined OTUs (Nguyen et al. 2016).

We assessed the assembly process of soil bacterial and fungal communities using null model analysis (Stegen et al. 2013). This method can be used to identify the assembly processes of communities by estimating the standard deviation of observed ecological patterns and comparing them to the randomly shuffled ecological patterns generated by null models (Chase 2010; Chase et al. 2011). To measure changes in phylogenetic and taxonomic diversity, we used null-model-based measures of phylogenetic and taxonomic β -diversity metrics (beta-NTI and Raup–Crick matrix based on Bray–Curtis distance, RC_{bray}). The β NTI quantifies the magnitude and direction of the deviation between the observed value of β MNTD and the null distribution of β MNTD. It is also an estimate of the phylogenetic turnover of a given stochastic and deterministic ecological process (Stegen et al. 2012; Wang et al. 2013; Dini-Andreote et al. 2015). Values of $|\beta$ NTI|>2 indicate that the observed turnover between the two communities is mainly controlled by selection processes; β NTI > +2 is consistent with variable selection, whereas β NTI < -2 indicates homogeneous

selection. Therefore, $|\beta\text{NTI}| < 2$ means that the replacement of a group of communities is controlled by dispersal limitation, homogenizing dispersal, or undominated processes. To clarify these processes, the Raup–Crick (RC_{bray}) matrix was constructed based on the standard Bray–Curtis matrix of the community. The RC_{bray} matrix provides information on whether the observed levels of mobility deviate significantly from expectations. This value is equal to the observed deviation between the Bray–Curtis distance and zero distributions, ranging from -1 to $+1$. Within this range, $|RC_{\text{bray}}| < 0.95$ can be interpreted as the effect of an undominated process. Conversely, dispersal limitation plus drift resulted in a greater than expected turnover rate ($RC_{\text{bray}} > +0.95$), while $RC_{\text{bray}} < -0.95$ indicated that the turnover rate of community composition was mainly controlled by homogenizing dispersal (Zhou and Ning 2017; Tripathi et al. 2018).

Results

Soil properties

There were some effects of the two-way interaction between ED and G on TC (Additional file 1: Table S1). Soil erosion seemed to increase the content of TN and AP by 1.92% and 1.59%, respectively, and decreased the content of TC and TP by 0.80% and 1.67%, respectively. Under SE+G, the contents of TN, TC, TP, and AP tended to decrease by 12.64%, 19.83%, 18.33%, and 0.45%, respectively (Fig. 1). Although there were no significant differences in soil clay, silt and sand from the five treatments compared with those from the control, they were significantly reduced in SE and SE+G compared with grazing (Fig. 1, Additional file 1: Fig. S1).

Bacterial and fungal diversity

There were some main effects of ED on the ACE indices of bacterial communities and Shannon indices of the fungal communities, as well as some main effects of G on the Chao1 indices of bacterial communities (Table 1). The Chao1 and ACE indices of bacterial communities tended to decrease under the SD, SE, G, SD+G, and SE+G treatments, especially under the SD and G treatment (Fig. 2a, b). The results showed that wind erosion significantly reduced the Shannon index of the fungal community (Fig. 2f).

The bacterial and fungal community structures were assessed using NMDS to determine differences, and the obtained results were deemed reliable ($\text{Stress} < 0.2$, Fig. 3). Bacterial community composition was significantly different between eroded and non-erosion or between depositional and non-deposition but not significantly differed between grazing and non-grazing based on unweighted Unifrac distances (Fig. 3). However, there was no interaction between grazing and aeolian

processes on bacterial and fungal community structure (Additional file 1: Fig. S2), suggesting that light grazing had little effect on microbial community structure.

Bacterial and fungal community composition

The bacterial community was mainly composed of Actinomycetes, Proteobacteria, Acidobacteria, Chlorobacteria, and Gemmatimonadetes, accounting for $\sim 90\%$ of the relative abundance of all the identified phyla (Fig. 4a). The relative abundance of Cyanobacteria greatly increased in the SE and SE+G plots by 116.80% and 116.38%, respectively; it increased by 87.18% in the grazing plots, but decreased by 5.47% in the SD plots (Fig. 4a). There were some main effects of ED on Actinobacteria and Acidobacteria, as well as some main effects of G on Actinobacteria and Gemmatimonadetes (Table 2). The relative abundance of Actinobacteria was higher in the C, SD, G, and SD+G plots than that in the SE and SE+G plots (Additional file 1: Fig. S3a). All soil samples shared 1594 OTUs (Additional file 1: Fig. S4a).

The fungal community was mainly composed of Ascomycota, Basidiomycota, Glomeromycota, Ciliophora, and Chytridiomycota, accounting for $\sim 85\%$ of the relative abundance of all the identified phyla (Fig. 4b). The relative abundance of Ascomycota tended to increase only under the grazing treatment and was lower under all other treatments, especially under the SD and SE+G treatments. However, the relative abundance of Basidiomycetes declined in the SE+G treatment and increased in the other treatments compared to the control (Additional file 1: Fig. S3b). All soil samples shared 609 OTUs (Additional file 1: Fig. S4b).

Bacterial and fungal co-occurrence network

The network of soil microbial communities demonstrated similar co-occurrence patterns (Fig. 5). The network topology parameters used were the number of nodes and edges, and the average path length (GD), to assess the complexity of soil microbial networks, with higher numbers of edges and nodes and smaller average path distances representing greater network complexity. In both the bacterial and fungal networks, the GD was found to be lower in the eroded plots, which had a higher number of nodes and edges, compared to the non-eroded plots; similarly, the GD was observed to be lower in the deposition plots, which had a higher number of nodes and edges, compared to the non-deposition plots (Fig. 5). Thus, the erosion and deposition had a positive effect on the networks of soil microbial communities. However, the GD was found to be higher in grazed samples with a low number of nodes and edges compared to non-grazed samples. This suggests that grazing has a detrimental effect on the complexity of the bacterial and fungal

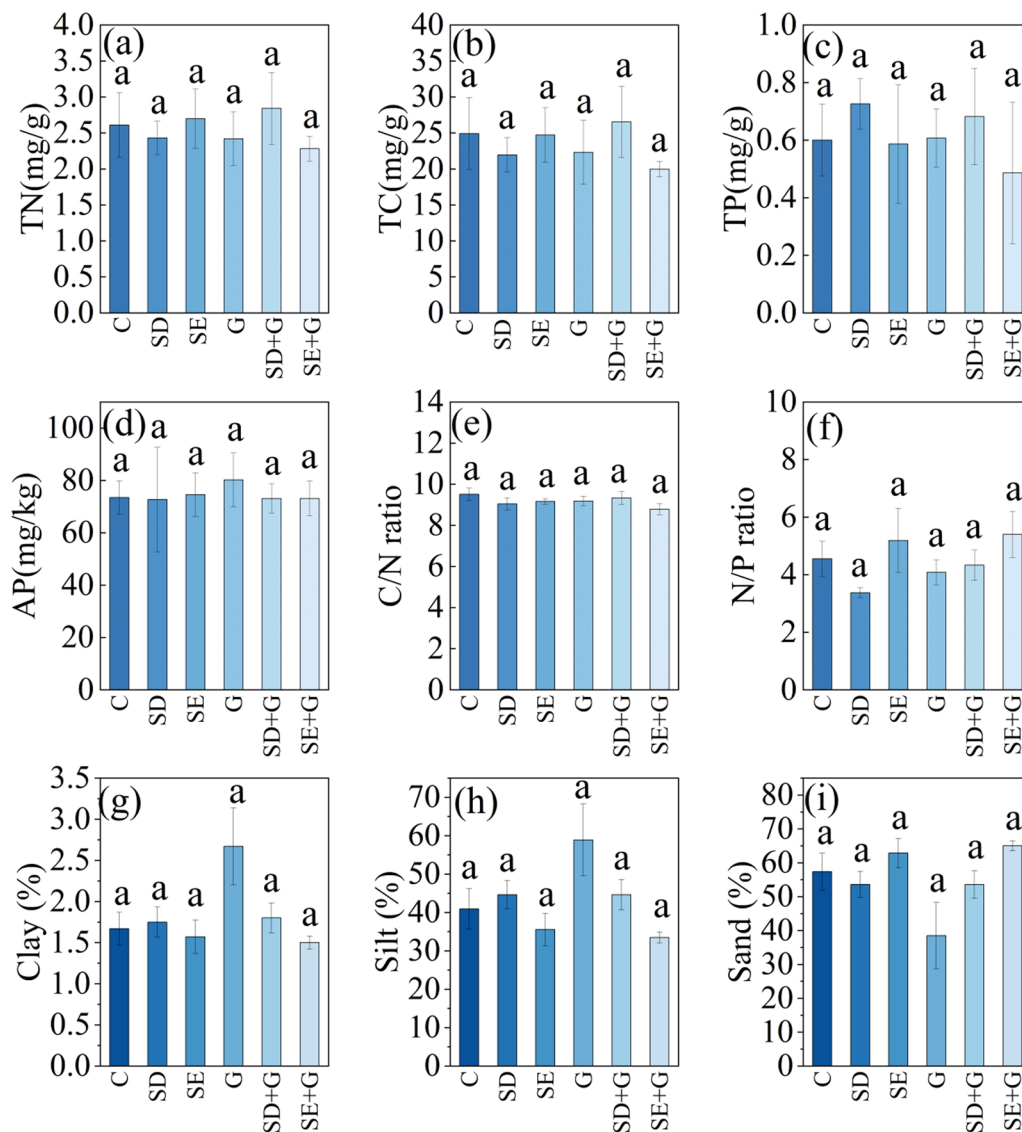


Fig. 1 Soil properties of collected soil substrates (mean \pm SE, $n=5$). **a** TN, (total nitrogen), **b** TC, (total carbon), **c** TP, (total phosphorous), **d** AP, (available phosphorous), **e** C/N ratio (Total carbon to total nitrogen ratio), **f** N/P ratio (Total nitrogen to total phosphorous ratio), **g** clay ($< 2 \mu\text{m}$), **h** silt ($2-50 \mu\text{m}$), and **i** sand ($50-2000 \mu\text{m}$). Treatment: control (C), soil deposition (SD), soil erosion (SE), grazing (G), soil deposition plus grazing (SD+G), soil erosion plus grazing (SE+G). Different lowercase letters indicate significant differences at $p < 0.05$ among the different treatments

Table 1 Results of two-way ANOVA for testing the effects of treatment (aeolian processes (ED) and grazing (G)) on bacterial and fungal α -diversity including Chao1, ACE, and Shannon

Treatment	Bacteria						Fungi						
	Chao1		ACE		Shannon		Chao1		ACE		Shannon		
	df	F	p	F	p	F	p	F	p	F	p		
ED	2	1.31	0.07	3.51	0.03	0.91	0.42	0.98	0.39	1.21	0.32	5.32	0.01
G	1	3.46	0.04	1.73	0.05	0.4	0.53	1.43	0.24	1.43	0.24	3.02	0.1
ED \times G	2	3.19	0.81	0.28	0.76	1.03	0.37	0.01	0.99	0.02	0.98	1.13	0.34

The bold numerals highlight the significance at $p < 0.05$ for bacterial and fungal α -diversity, respectively

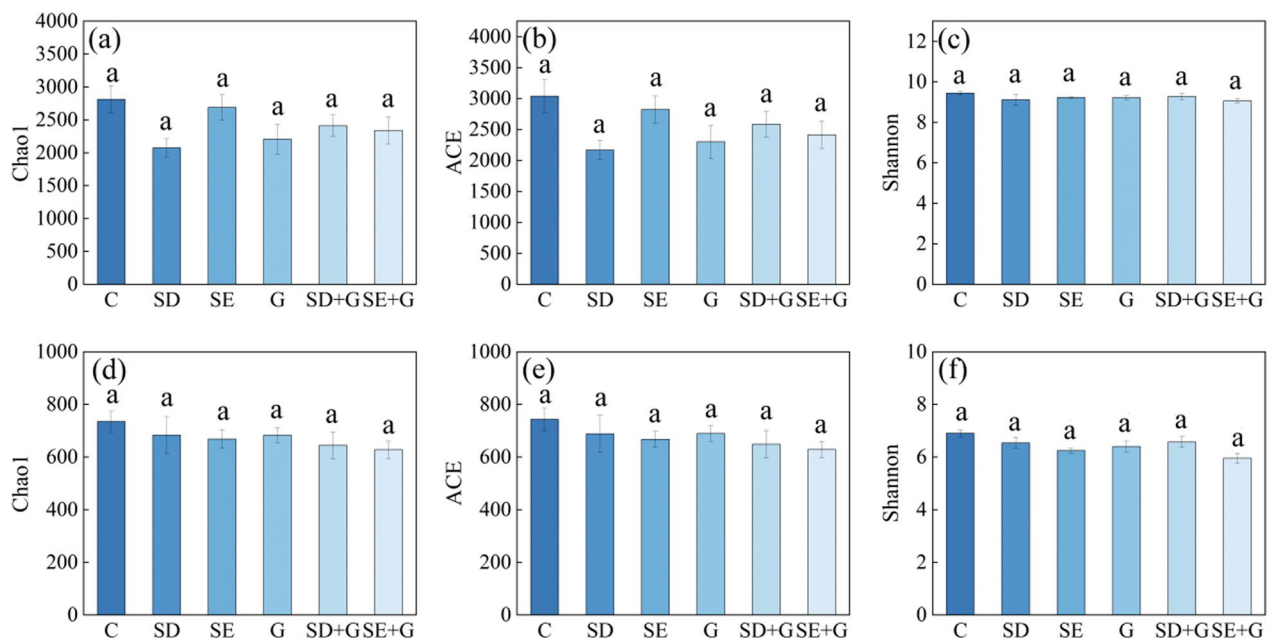


Fig. 2 Alpha-diversity of bacterial and fungal communities. Panels **a–c** represent bacterial alpha-diversity, and panels **d–f** represent fungal alpha-diversity. Different lowercase letters indicate significant differences at $p < 0.05$ among the different treatments

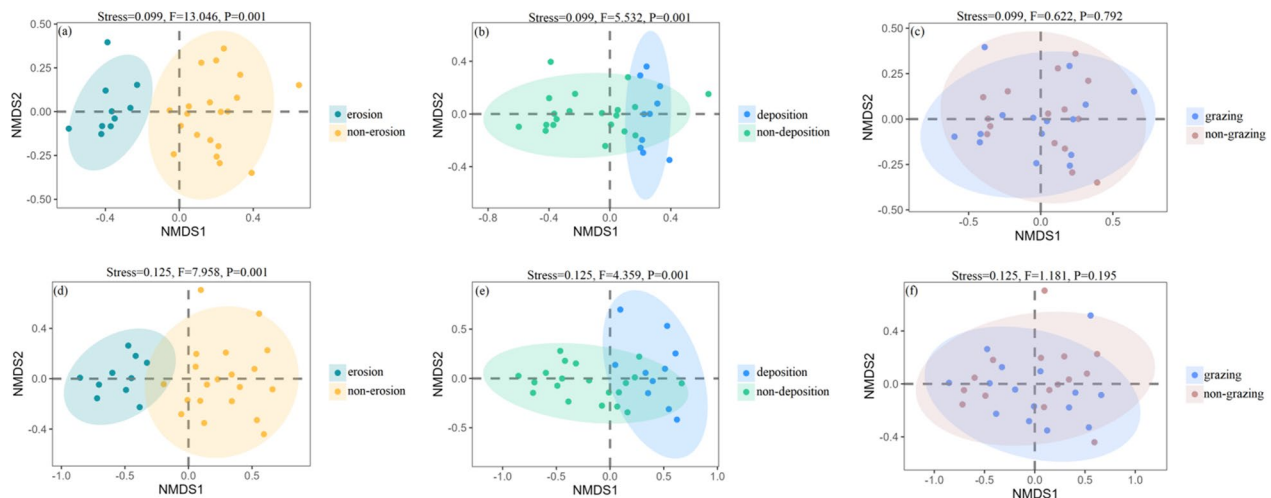


Fig. 3 The NMDS plots for bacterial (**a–c**) and fungal (**d–f**) community structures based on the Bray–Curtis distance

community network (Additional file 1: Figs. S5, S6). In erosion and deposition plots, Actinobacteria, Proteobacteria, Acidobacteria, and Chloroflexi were the keystone taxa (Fig. 5). Ascomycota, Basidiomycota, and Glomeromycota were also considered keystone taxa in erosion and deposition plots (Fig. 5). At erosion sites, Armatimonadetes, Bacteroidetes and Firmicutes were more connected, while at deposition plots, Acidobacteria, Bacteroidetes, and Verrucomicrobia were more connected (Fig. 6a).

Environmental factors related to microbial community composition

The redundancy analysis showed that TP, AP, and N/P ratio contributed significantly to the variation of the bacterial community, accounting for 83.5% of the variance, while the TP and AP contributed more to the fungal community variations, with contribution rates of 21% and 35.5%, respectively (Additional file 1: Table S2, Fig. S7).

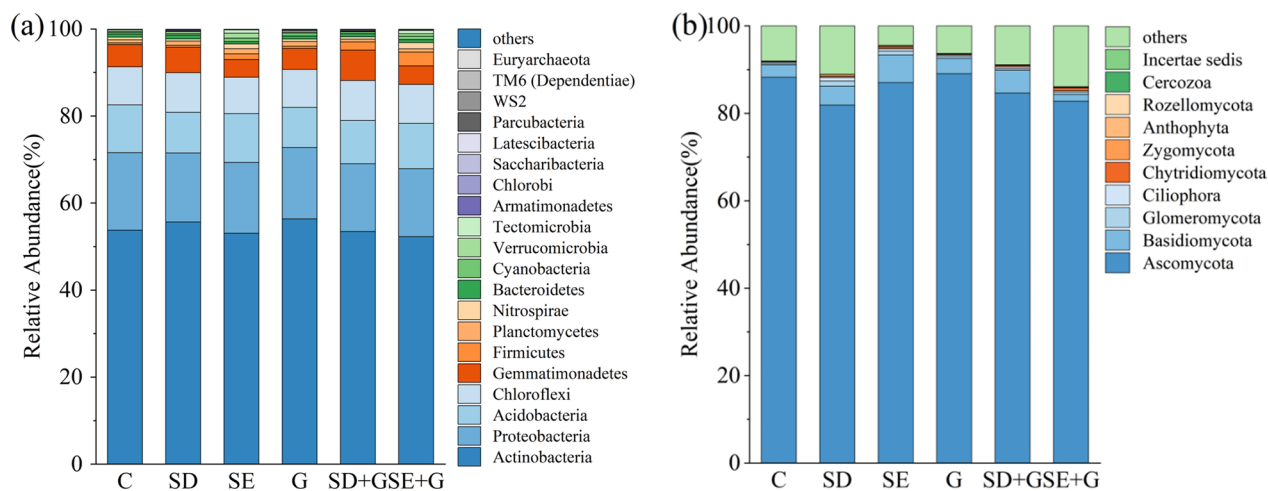


Fig. 4 Relative abundances (%) of major phyla of (a) bacteria and (b) fungi affected by aeolian processes and grazing

Based on the analysis of the FAPROTAX program, we classified specific bacterial branches into functional taxa. Particular attention was paid to groups associated with soil N cycling, which is important for grassland soils. SE+G and SE significantly increased the relative abundance of nitrate reduction and aerobic nitrite oxidation, and both also significantly increased the relative abundance of nitrification functional groups (Additional file 1: Fig. S8a, Table S3). Nitrate reduction exhibited a significant positive correlation with C/N and was negatively correlated with TP, endophyte insert pathogen exhibited a significant positive correlation with N/P and was negatively correlated with TP (Fig. 7a, b). Fungal OTUs assigned to symbiotrophs significantly increased in the SE and SE+G plots and significantly decreased in SD+G plots (Additional file 1: Fig. S8b, Table S4); while OTUs assigned to saprotrophs increased in the SD and SD+G plots and decreased in the SE and grazing plots. Finally, the OTUs assigned to pathotrophs increased in the SD plots, but decreased in the grazing and SE plots (Additional file 1: Table S4).

Assembly processes and coexistence of soil microbes

The average relative importance of variable selection and homogenizing dispersal processes during bacterial community construction was 68.89% and 28.89% in SD and 44.44% and 55.56% in SE (Fig. 8a; Additional file 1: Fig. S9 showed the phylogenetic signals). Deposition and erosion increased the relative importance of variable selection by 34.11% and 6.66%, respectively (Fig. 8a). SD decreased the relative importance of homogenizing dispersal by 15.55% and SE increased the relative importance of homogenizing dispersal by 11.12% (Fig. 8a). Under wind erosion and deposition, the relative contribution of

deterministic processes (4.44% vs 31.11%) in bacterial communities increased (Fig. 8a). The results showed that the variable selection process contributed the most to the construction of bacterial communities, with the relative importance of variable selection being greater for non-grazing (80%) than for grazing (73.33%), further noting that the relative importance of the undominated process on bacterial communities in grazed areas was six times greater than non-grazed (Fig. 8b). These results suggest that grazing reduced the relative contribution of deterministic processes (8.89%) to bacterial communities.

The contribution of the dispersal limitation process to fungal community assembly was 68.89% and 82.22% under depositional and erosion conditions, respectively (Fig. 8d). However, dispersal limitation was reduced by 13.34% (deposition) and 26.67% (erosion), when compared to non-erosion conditions (Fig. 8d). Under wind erosion and sedimentation, the relative contribution of stochastic processes (2.23% vs 20%) in fungal communities reduced (Fig. 8d). The relative importance of variable selection processes on fungal communities in soil erosion samples (24.44%) was 3.6 times greater than their effect on fungal communities in erosion samples (6.67%), while the relative importance of undominated processes on fungal communities in soil erosion samples (11.11%) was 1.6 times greater than their effect on fungal communities in deposition samples (6.67%) (Fig. 8d). The contribution of the dispersal limitation process on fungal communities in grazed areas (93.33%) was greater than in non-grazed areas (82.22%) (Fig. 8e). The relative importance of variable selection processes on fungal communities was twice as high in non-grazed sites than in grazed sites, suggesting that grazing increased the relative contribution of stochastic processes (8.89%) to fungal communities (Fig. 8e).

Table 2 Results of two-way ANOVA for testing the effects of treatments (aeolian processes (ED) and grazing (G)) on bacterial and fungal phyla

Treatment	Bacteria						Fungi					
	Actinobacteria	Proteobacteria	Acidobacteria	Chloroflexi	Gemmatimonadetes		Ascomycota	Basidiomycota	Glomeromycota	Ciliophora	Chytridiomycota	
	df	F	p	F	p	F	F	p	F	p	F	p
ED	2	5.32	0.01	0.23	0.8	0.8	1.13	0.34	0.29	0.75	0.37	0.7
G	1	3.51	0.03	0.21	0.65	0.68	0.01	0.94	0.4	0.53	0.89	0.35
ED×G	2	0.32	0.73	0.03	0.97	0.2	0.49	0.62	1.15	0.33	0.6	0.56

The bold numerals highlight the significance for bacterial and fungal phyla, $p < 0.1$ or $p < 0.05$

0.06
0.18
0.36

3.24
1.94
1.07

1.11
1.15
0.32

0.35
0.3
0.73

0.7
0.35
0.56

0.37
0.89
0.6

1.13
0.01
0.49

0.34
0.94
0.62

0.29
0.4
1.15

0.75
0.53
0.33

0.09
0.01
0.78

2.65
5.32
0.25

0.15
0.08
0.06

0.86
0.78
0.94

0.86
0.78
0.94

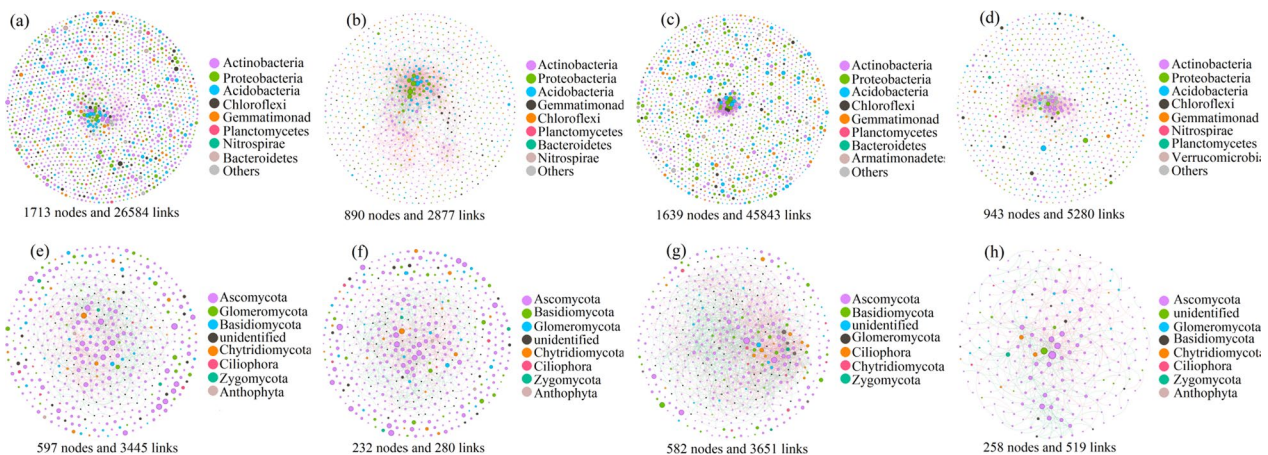


Fig. 5 Co-occurrence patterns in soil microbial communities as affected by soil erosion and deposition. Co-occurrence network of soil bacterial communities as affected by (a) soil erosion, b non-erosion, c deposition, and d non-deposition. Soil fungal community co-occurrence network as affected by (e) soil erosion, (f) non-erosion, (g) deposition, and (h) non-deposition. OTU size is proportional to number of connections. Only significantly correlated nodes (OTUs) (Spearman's $r > 0.84$; Benjamini–Hochberg FDR adjustment, $p < 0.05$) were connected (edges)

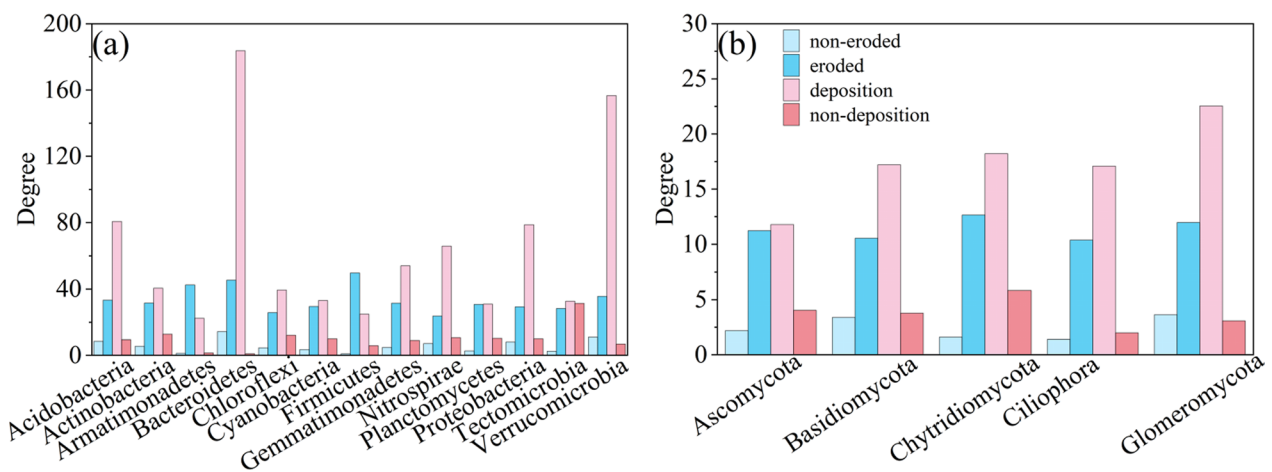


Fig. 6 Effects of different treatments on taxonomic-level connectivity distributions of (a) bacteria and (b) fungi

For the fungal community, the relative contribution of dispersal limitation (80%, 20%) and undominated (70%, 10%) processes were lower in the SD+G compared to the SE + G communities, and variable selection processes contributed 20% to the SD+G communities (Fig. 8f).

Discussion

This study provides valuable insights into the impacts of aeolian processes and grazing on soil microbial communities in semi-arid grasslands, offering important information for the development of sustainable soil management practices and the restoration of degraded land in eroding environments. Our findings indicate that both aeolian processes and grazing had negative

effects on bacterial and fungal diversity in the soil. Specifically, aeolian processes were found to enhance the complexity of soil bacterial and fungal community networks, while grazing reduced their complexity. Moreover, aeolian processes were found to enhance the relative contribution of deterministic processes (i.e., variable selection) to bacterial communities, while reducing the relative contribution of stochastic processes (i.e., homogenizing dispersal) to fungal communities. On the other hand, grazing was found to have contrasting effects, reducing the relative contribution of deterministic processes to bacterial communities, while increasing the relative contribution of stochastic processes to fungal communities.

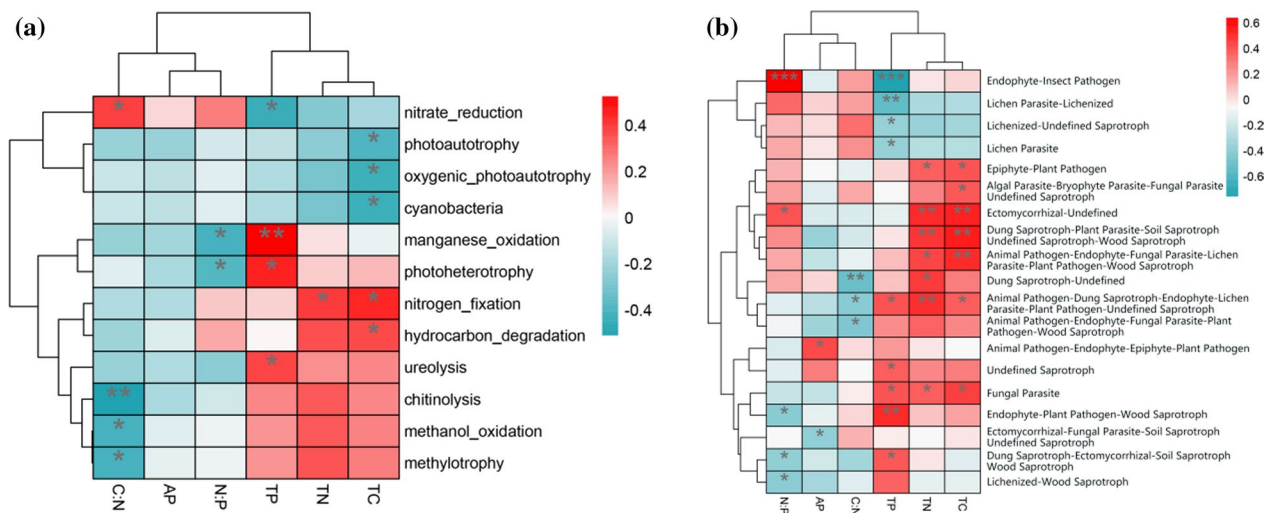


Fig. 7 Function prediction of soil bacteria (a), fungi (b) and physicochemical factors. Red indicates positive correlations and blue-green indicates negative correlations. * and ** stand for Spearman rank correlation coefficient significant levels, $p < 0.05$ or $p < 0.01$

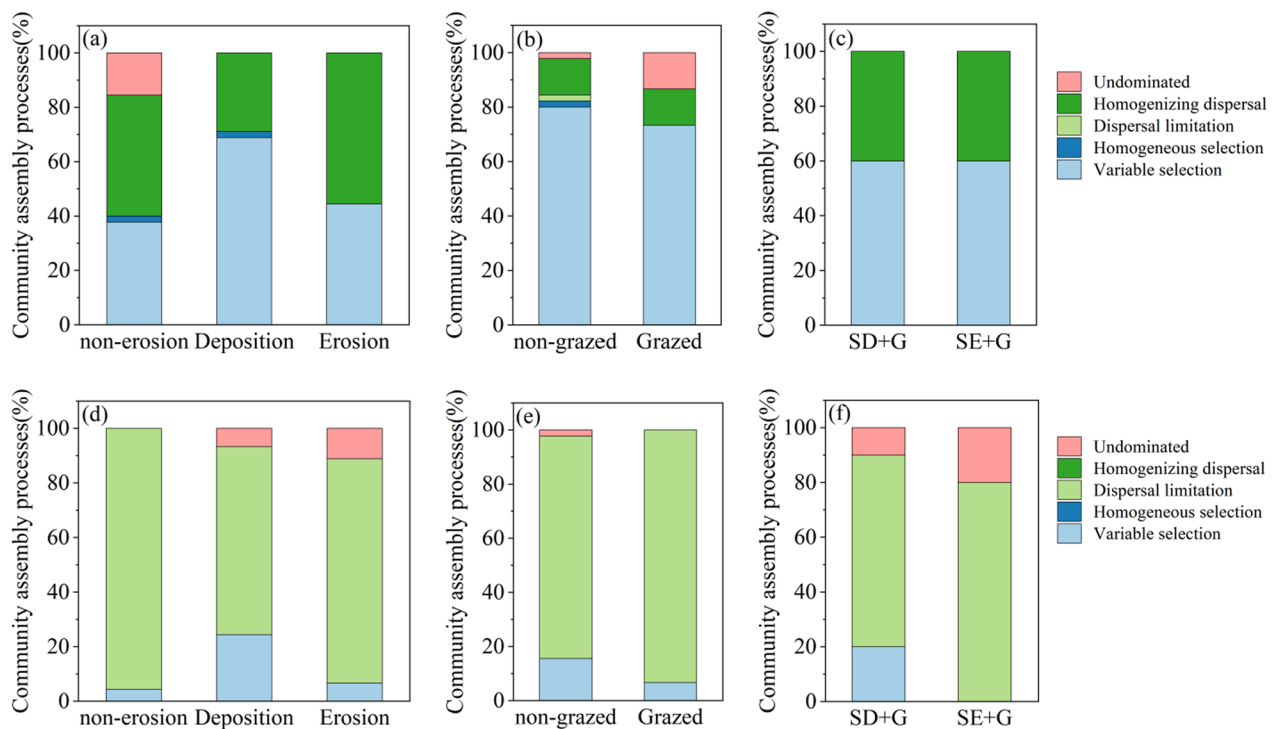


Fig. 8 The percentage of turnover in the community assembly of bacteria (a–c) and fungi (d–f) dominated by different deterministic (including variable selection and homogeneous) and stochastic processes, including homogeneous dispersal and dispersal limitation and the percentage not dominated by any single process ('undominated') in soils

Effects of soil aeolian processes and grazing on bacterial and fungal diversity

Soil erosion is a selective transport process that affects the physical, chemical, and biological properties of soils. In this study, erosion led to a reduction in bacterial and

fungal alpha diversity (Fig. 2). The erosion process contributes to the depletion of nutrients from the top-soil layer. Specifically, under wind erosion treatments, the upper layer of soil is destroyed and removed from the ecosystem, leading to a substantial loss of organic

matter and nutrients from the soil. Consequently, there is a noticeable decline in nutrient availability within the topsoil layer. Previous studies have demonstrated that wind erosion can degrade soil structure, reduce nutrient and water efficiency, as well as impair overall soil functionality (Li et al. 2019; Lal and Pimentel 2008; Mendonça et al. 2017; Smith et al. 2015). Soil bacteria primarily inhabit soil micropores and aggregates (Hoorman et al. 2011), where they have better access to substrates. The disruption of soil structure caused by erosion, such as the fragmentation of soil aggregates, may expose bacteria to air, thereby limiting their access to substrates. Furthermore, the reduction in nutrients resulting from wind erosion can have severe impacts on the habitats of bacteria and fungi. It is well-established that both changes in habitat and the loss of ecological niches can lead to a decline in fungal and bacterial diversity (Su et al. 2022; Zhang et al. 2018). This can be attributed to the creation of an unfavorable environment for microbial survival in areas with low plant cover due to the significant fluctuations in soil moisture and temperature caused by grazing. Additionally, the removal of canopy vegetation by grazing animals, results in a substantial reduction in litter (Luo et al. 2009; Liu et al. 2011). This reduction in litter input leads to a decrease in organic matter and nutrient availability in the soil (Song et al. 2017), disrupting the energy flow and material cycling within the ecosystem, ultimately leading to a decline in bacterial and fungal diversity. Although bacteria and fungi exhibit different responses to environmental changes, long-term erosion has consistently shown a negative impact on their diversity. Fungal communities are typically more stable but less adaptable compared to bacterial communities (Bapiri et al. 2010; Chen et al. 2020). This implies that during prolonged habitat destruction, fungi exhibit slower resilience and recovery mechanisms compared to bacteria. As a result, fungal communities may not fully recover or, in some cases, may lose their reproductive capacity even after environmental reconstruction efforts. In this study, although the interaction between grazing and wind erosion tended to reduce bacterial and fungal diversity, it is important to note that the scale of our experimental study and the size of the plots are relatively small. Future research should investigate the effects of dual stress from grazing and wind erosion on soil microorganisms at larger spatial scales to gain a more comprehensive understanding of their combined impacts.

Persistent wind erosion and deposition have been shown to hinder the colonization of dispersed spores and propagules (Kasel et al. 2008). Our findings highlight the significant impacts of soil erosion and deposition on the structure of soil microbial communities, while grazing did not have a significant effect on the structure of soil

microbial community (Fig. 3). This finding is consistent with previous studies (Helgason et al. 2014; Zhang et al. 2022; Ma et al. 2017; Patra et al. 2005). Soils affected by wind erosion are typically dominated by clay and loam soils, which are rich in organic matter and nutrients (Feller et al. 1997; Percival et al. 2000). These soils, along with their organic matter and nutrients, are carried by wind currents and deposited in various locations, resulting in significant loss of soil carbon, nitrogen, and other nutrients in the source area, while adding substantial nutrients and organic matter to the deposition area. This process leads to differences in soil microbial communities between wind-eroded and depositional plots. Grazing moderates these effects, although we did not observe a direct interaction between grazing and aeolian processes on soil microbial community structure, possibly due to the light grazing intensity modeled in this study. Future studies should consider different disturbance intensities to further assess their effects on microbial community structure.

Shifts in the composition of soil bacteria and fungi

Soil erosion can cause changes in the abundance of different microbial taxa (Fig. 4). Previous studies have linked alterations in the relative abundances of key microbiota taxa in eroded areas to soil nutrient levels (Qiu et al. 2021). Our study revealed a decrease in the relative abundance of Actinomycetes in soil erosion plots, which is consistent with the findings of Zhang et al. (2022). Soil erosion has been shown to reduce soil organic carbon levels (Zhang et al. 2022), and this decline may be attributed to the positive correlation between Actinomycetes and organic carbon. Interestingly, desert soils, which are prone to soil erosion, are often rich in Actinobacteria and Cyanobacteria (Fierer et al. 2007). Cyanobacteria have the ability to stabilize soil aggregates and enhance soil resistance to erosion (Chamizo et al. 2018a, b). In our study, we observed an increase in the relative abundance of Cyanobacteria in response to soil erosion (Additional file 1: Fig. S3a). This may be attributed to the ability of Cyanobacteria to thrive in environments characterized by extremely low levels of soil moisture and aeration (Singh et al. 2016). Furthermore, our study found that the relative abundance of Acidobacteria was highest in the SE + G plots, followed by the erosion and deposition plots. This pattern may be influenced by soil nutrient levels and pH conditions. The deposition plots exhibited the highest soil nutrient levels, while the erosion plots had the lowest levels. Acidobacteria are known to be adapted to nutrient-poor soils and are considered oligotrophic (Ward et al. 2009; Kielak et al. 2016). Additionally, soil pH has been shown to negatively affect the abundance of Acidobacteria (Wongkiew et al. 2022). Zheng et al.

(2020) demonstrated that the application of a microbial restoration substrate led to a reduction in the relative abundance of the Acidobacteria phylum (Wongkiew et al. 2022). Kong et al. (2022) also reported relatively low relative abundances of acidophilic bacteria in erosion plots characterized by higher soil pH values. Previous studies have indicated a negative correlation between the Acidobacteria phylum and soil organic matter (Fierer et al. 2007), and soil erosion has been shown to decrease soil organic carbon levels (Zhang et al. 2022), which in turn affects the abundance of the Acidobacteria phylum. Furthermore, grazing can exacerbate the effects of wind erosion on the abundance of the Acidobacteria phylum by altering the form of organic carbon input to the soil (Xun et al. 2018).

Our study revealed that the relative abundance of Ascomycota increased only under grazing treatment, which can be attributed to the increased cellulose content in the soil resulting from the mixing of plants with manure during grazing activities. The Ascomycete phylum has a wide range of substrates and can utilize organic carbon as a substrate, which can be further enhanced by the unstable carbon excreted by livestock during grazing activities (Fontaine et al. 2011). In contrast, Basidiomycetes showed a decrease in the SE+G treatment and an increase in other treatments. Basidiomycetes are oligotrophic fungi that primarily utilize lignin as a substrate and have a lower ability to withstand environmental disturbances compared to Ascomycetes (Yao et al. 2017). Ascomycete hyphae, which represent another major group of fungi in soil, possess higher porosity and a stronger ability to invade space (Carlile 1995). Although our results suggest that soil aeolian processes and grazing have significant and contrasting effects on soil bacterial and fungal community composition, this relationship needs further research based on the complexity and interrelatedness of the factors involved.

Soil aeolian processes and grazing effects on bacterial and fungal co-occurrence patterns

Our findings indicate that erosion and deposition contribute to increased complexity in bacteria and fungi networks, while grazing resulted in a reduction in the same. The complexity is influenced by changes in land management and disturbances, and the microbial symbiotic networks at erosion and deposition sites are primarily driven by resource availability (Yang et al. 2023; Kong et al. 2022; Hao et al. 2022). Although erosion and deposition had minimal effects on soil nutrient pools in our study, a previous study found that both erosion and deposition increased surface soil moisture (Chi 2021), creating a more favorable environment for the restoration of bacterial and fungal networks. Furthermore, our results

indicate significant differences in soil microbial community structure and composition between erosion and deposition (Table 2; Fig. 3), a series of dynamic changes between different microorganisms can be triggered. Grazed selective feeding can influence aboveground vegetation, and changes in plant community composition can release different root secretions, leading to changes in soil microbial community structure due to the close relationship between soil microorganisms and root secretions (Nettan et al. 2019; Mastný et al. 2021). In addition, climatic conditioning, grazing intensity and duration also affect soil microorganisms (Hu et al. 2019; Liang and Gornish 2019). In our study, Actinobacteria, Proteobacteria, Acidobacteria, and Chloroflexi were identified as keystone taxa of bacteria (Fig. 5), while Ascomycota, Basidiomycota, and Glomeromycota were identified as key taxa of fungi (Fig. 5), which is consistent with previous findings (Hao et al. 2022; Ling et al. 2016). Firmicutes, Bacteroidetes, Actinobacteria, and Acidobacteria were highly associated generalist bacteria in erosion plots. Firmicutes and Bacteroidetes are involved in organic matter decomposition and polysaccharide metabolism (Huang and Liu 2020; Martens et al. 2009). The Actinobacteria phylum plays a crucial role in soil restoration, while the Acidobacteria phylum, being oligotrophic, is well-adapted to the relatively nutrient-poor soils of erosion plots. Bacteroidetes, Verrucomicrobia, and Proteobacteria were highly associated generalists in deposition sites (Fig. 6a). Proteobacteria, being eutrophic, benefitted from the buried and enriched nutrients in the deposition plots, providing the necessary resources for their growth and reproduction. Chytridiomycota, Ascomycetes, and Basidiomycota were highly connected generalists in erosion sites (Fig. 6b). This suggests that Ascomycetes and Basidiomycota are well-adapted to environments where soil structure is disrupted and nutrients are lost.

Different assembly processes of bacterial and fungal communities

Erosion and the combination of soil erosion and grazing (SE+G) significantly increased the relative abundance of nitrate reduction and aerobic nitrite oxidation groups. This increase may be attributed to the enhanced relative abundance of bacterial phyla involved in nitrogen cycling, such as Proteobacteria (Vesela et al. 2010). To advance our understanding of ecosystem diversity and multifunctionality, it is crucial to unravel the processes governing microbial community assembly (Singh et al. 2020). In grassland ecosystems, changes in soil microbial community assembly may be influenced by plant species richness and disturbance intensity. Reduced plant diversity has been shown to promote environmental homogeneity by diminishing the complexity of plant-soil interactions

and facilitating community convergence (Fukami and Nakajima 2013; Shoemaker et al. 2020), thereby increasing stochasticity. However, in our study sites, grazing increased the diversity of aboveground plant species (Chi 2021) and the relative contribution of stochastic processes to the fungal community. This suggests that the relationship between aboveground plant diversity and soil microbial community assembly processes may not follow a simple linear pattern. Under low disturbance conditions, increased stochasticity has been reported due to reduced ecological pressure, which dampens the influence of environmental filtering (Chen et al. 2023; Zhou and Ning 2017). In our study, light grazing reduced the relative contribution of deterministic processes to the bacterial community. This could be attributed to the complex nature of soil microbial community assembly, which is influenced by multiple factors, and the non-linear relationship between grazing intensity and soil microbial community assembly. Therefore, future studies should consider different disturbance intensities to better evaluate the processes driving microbial community assembly, given the inherent variability of soil microbial communities.

Our findings demonstrate that soil deposition and erosion increased the relative contribution of deterministic processes (i.e., variable selection) to bacterial communities, while decreasing the relative contribution of stochastic processes (i.e., homogenizing dispersal) to fungal communities. Conversely, grazing decreased the relative contribution of deterministic processes to bacterial communities and increased the relative contribution of stochastic processes to fungal communities. These observations may be attributed to soil nutrient loss. Previous studies have indicated that in moderate or relatively stable soil environments, where stochastic processes play a prominent role, bacterial communities are more likely to undergo changes resulting from random birth and death events and probability diffusion (Trivedi et al. 2017; Huang et al. 2022). However, in extreme or highly disturbed soils, where specific environmental factors shape microbial community composition, deterministic processes assume greater importance. In our study, we observed that variable selection dominated the assembly of bacterial communities in soil deposition and erosion plots, where nutrient loss occurred due to soil erosion. Soil erosion can lead to soil structure deterioration, nutrient loss, and reduced nutrient availability, thereby intensifying its regulatory effect on microbial community dynamics (Xiao et al. 2018; Wei et al. 2016), consequently diminishing the contribution of stochastic processes to bacterial community composition. In contrast, stochastic processes, particularly dispersal limitation, exerted a significant influence on the assembly of soil fungal

communities compared to deterministic processes. The relatively weak selection effect on fungal communities may be explained by the high adaptability of fungi to nutrient-poor environments (Graham et al. 2017). Fungal hyphal networks are better suited for disturbed and nutrient-poor soil environments compared to bacterial communities, as they facilitate water and nutrient uptake, and some fungi can enhance their viability by utilizing multiple nutrients simultaneously (Wang et al. 2020; Yuste et al. 2011). Studies have demonstrated that bacteria primarily degrade simple amino acids, organic acids, and carbohydrates, whereas fungi are primarily involved in the degradation and transformation of recalcitrant soil carbon, such as lignin (Barnard et al. 2013; Courty et al. 2010; Xiao et al. 2018). Taken together, our findings highlight the combined effects of deterministic and stochastic processes on the response of bacteria and fungi to aeolian processes and grazing. This sheds light on the intricate nature of microbial diversity and enhances our comprehension of microbial communities in grassland ecosystems.

Conclusion

The present study aimed to investigate the impacts of wind erosion, deposition, and grazing on the composition of bacterial and fungal communities in a semi-arid grassland. Our findings revealed that wind erosion, deposition, and grazing exerted distinct effects on different aspects of bacterial and fungal communities. Nonetheless, the analysis of community structure and assembly indicated that these microbial communities possessed a certain degree of resistance against wind erosion disturbances. It is important to highlight that the plot sizes in this study were relatively limited, and only light grazing was considered in the study. Therefore, further research is necessary to investigate the impacts of both grazing intensity and wind erosion on soil microorganisms at larger spatial scales, in order to achieve a more comprehensive understanding of the combined effects of these factors. A thorough comprehension of the alterations in soil microbiological profiles in degraded areas holds great promise for enhancing our capacity to efficiently manage soil erosion and restore degraded landscapes.

Supplementary Information

The online version contains supplementary material available at <https://doi.org/10.1186/s13717-024-00510-y>.

Additional file 1: Table S1. Results of two-way ANOVA for testing the effects of treatment (aeolian processes (ED) and grazing (G)) on soil properties. **Table S2.** Redundancy analysis of (a) bacterial and (b) fungal genus and soil properties. **Table S3.** Effects of soil erosion and deposition on the relative abundance of bacteria function. **Table S4.** Effects of soil erosion and deposition on the relative abundance of fungal function.

The different lowercase letters within the same row indicate significant differences among treatments at $p < 0.05$. **Fig. S1.** Particle size distribution of the surficial soil. **Fig. S2.** The NMDS plots for bacterial (a) and fungal (b) community structures based on the Bray-Curtis distance. **Fig. S3.** Soil bacterial and fungal composition as affected by soil erosion. The relative abundance of the dominant bacterial and fungal phyla (a: bacterial; b: fungus) levels that were significantly affected by soil erosion. Error bars are standard errors of the mean. Means with the same lowercase letter were not significant at $p < 0.05$ among erosion levels. **Fig. S4.** Venn diagram of ASV distribution in (a) soil bacteria and (b) fungi. **Fig. S5.** Co-occurrence network patterns in soil microbial communities as affected by soil erosion and deposition. Co-occurrence networks of soil bacteria as affected by (a) grazing and (b) non-grazing. Co-occurrence network of soil fungi as affected by (c) grazing and (d) non-grazing. The sizes of the nodes (OTUs) are proportional to the number of connections. Only nodes (OTUs) that were significantly correlated to each other (Spearman's $r > 0.84$; after Benjamini and Hochberg FDR adjust, $p < 0.05$) were connected (edges). **Fig. S6.** Effects of different treatments on taxonomic-level connectivity distributions of (a) bacteria and (b) fungi. **Fig. S7.** Redundancy analysis of (a) bacterial and (b) fungal genus and soil properties. **Fig. S8.** Function prediction of (a) soil bacteria and (b) fungi.

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Author contributions

Shijie Han, Junqiang Zheng and Shiqiang Wan conceived the presented idea and received important feedback from all co-authors. Field management was carried out by Shiqiang Wan. Sampling collections and DNA preparation were carried out by Junqiang Zheng, Mingming Cui, and Biqi Bao. MiSeq sequencing process and data analysis were carried by Junqiang Zheng and Feirong Ren. The manuscript was written by Mingming Cui with help from Yipu Wu, Nan Hui and Maihe Li. All authors discussed the methods and results and contributed to the final manuscript.

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Availability of data and materials

Data sets of AMF biomarker sequences are archived at the China National Microbiology Data Center (<https://nmcdc.cn>) under BioProject NMDC10018265.

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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