Hydro-saline synergy regulates ecosystem multifunctionality via microbial biomass in semi-arid grasslands, China (Postprint)

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Abstract

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Full Text

Preamble

J Arid Land (2026) 18(3): 524–546 Hydro-saline synergy regulates ecosystem multifunctionality microbial biomass semi-arid grasslands, China HU Jinpeng, HE Yuanyuan, LI Yuanhong, ZHANG Yuewei, ZHANG Jinlin State Key Laboratory of Herbage Improvement and Grassland Agro-ecosystems, Engineering Research Center of Grassland Industry, Ministry of Education; Center for Grassland Microbiome; College of Pastoral Agriculture Science and Technology, Lanzhou University, Lanzhou, 730000, China

Abstract

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Further analysis identified the soil water content and salinity as the key determinants of soil microbial diversity and community complexity. Soil enzyme activities exhibited contrasting relationships with microbial composition, correlating positively with the richness of bacterial amplicon sequence variants (ASVs) but negatively with the richness of fungal ASVs. Notably, microbial biomass, which varied significantly across different groups, emerged as a key predictor of changes in EMF, with its critical role confirmed through structural equation modeling. These findings collectively elucidate the responses of ecological communities to synergistic soil hydro-saline stress in semi-arid ecosystems, while highlighting the critical role of microbial biomass in maintaining EMF.

Keywords

hydro-saline; soil microbial; enzyme activity; ecosystem multifunctionality; semi-arid grassland Citation:

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1 Introduction

Climate change intensifies synergistic drought and salinity stress, which disrupt soil processes, reduce biodiversity, and threaten the ecosystem services in arid areas (Yang et al., 2021; Ji et al., 2023; Zhang et al., 2024a). This combined drought-salinity stress has an extremely wide-ranging

impact in arid areas. According to a report, approximately $4.24\$\times10 of surface soil and 8.33\times10 of deep soil world affected (FAO, 2021), and this issue is driven by both anthropogenic activities and natural processes (Li et al., 2014 (Mao et al., 2018). Critically, drought and salinization frequently co-occur, thereby giving rise to a pervasive and intricate combined stress (Ahluwalia et al., 2021; Muhammad et al., 2024). This combined stress is not merely an additive effect, moreover, it likely imposes unique, potentially amplified, and mechanistically distinct challenges to ecosystem resilience compared with the stresses alone (Wei et al., 2023), though systematic understanding of these interactions remains limited.

Soil underpins terrestrial life, serving as a habitat and a critical component of biogeochemical cycles and ecosystem balance (Banwart et al., 2019). Its heterogeneous environment shapes the assembly and evolutionary trajectories of plant and soil microbial communities (Banwart et al., 2019), which in turn regulate ecosystem processes (Hartmann and Six, 2023). Soil microorganisms, via processes like nutrient cycle, organic matter decomposition, and disease suppression, are fundamental to soil health and plant performance (Kang et al., 2022; Jansson et al., 2023). Plants, on the other hand, modify soil structure and soil nutrient status through root exudates and litter inputs (Bais et al., 2006; Chai and Schachtman, 2022), providing essential carbon that enhances microbial activity and improves soil carbon storage (Trivedi et al., 2020; Wang et al., 2022b). This tightly coupled plant-soil-microbe system is the bedrock of terrestrial ecosystem sustainability.

Salinity and drought stress in saline-alkali ecosystems disrupt the delicate plant-soil-microbe interplay, resulting in biodiversity loss, decreased primary productivity, and impaired ecosystem functioning (Ahluwalia et al., 2021; Li et al., 2024). Given these impacts, researchers have introduced the concept of ecosystem multifunctionality (EMF) to comprehensively assess the overall impact of such environmental stressors (Manning et al., 2018; Zheng et al., 2023). As a comprehensive indicator of ecosystem service capacity, EMF integrates multidimensional functions and processes such as biodiversity maintenance (e.g., microbial and plant diversity), biological productivity (e.g., plant biomass), soil nutrient cycle (e.g., C, N, and P cycles), and soil enzyme activity, highlighting the complex interactions among ecosystem components (Manning et al., 2018; Hu et al., 2021). Understanding how stressors affect EMF, rather than isolated

functions, is crucial for predicting ecosystem resilience.

While the individual impacts of drought or salinity on specific ecosystem components (e.g., plant growth, microbial activity, or soil properties) have been documented (Yan et al., 2015; Xi et al., 2016), substantial knowledge gaps persist regarding their combined effects, particularly in relation to integrated EMF. Most current studies primarily focus on individual ecosystem components under single stress condition or simplified experimental setup (Token et al., 2022; Li et al., 2024). For example, previous research has explored how plant and microbial diversity, soil nutrients, soil enzyme activities, and environmental factors influence EMF (Manning et al., 2018; Hu et al., 2021). Notably, synergistic or complementary interactions between plant and soil microbial diversity often enhance the predictive accuracy of biodiversity–EMF relationships (Hu et al., 2021). However, these approaches still struggle to comprehensively capture the overall functional shifts of ecosystems. Critically, few studies have linked multidimensional responses (soil physical-chemical properties, microbial community structure, and plant community traits) to the outcome of changes in integrated EMF. Thus, how these components interact and collectively drive EMF under combined hydro-saline stress remains largely unaddressed.

Addressing these critical gaps, this study specifically aims to answer the following key scientific questions: (1) how do drought (D), saline-alkaline (SA), and their combined (DSA) stress differentially affect key indicators of ecosystem structure and function, including soil enzyme activities, soil microbial biomass and diversity, plant biomass and height, plant community diversity, and soil nutrients? (2) what is the overall impact of these stressors,

particularly the effects of DSA on integrated EMF? and (3) which specific components of the plant-soil-microbe system are the primary drivers of EMF responses under these contrasting soil hydro-saline stress regimes? To address this, we conducted an experiment on a semi-arid grassland ecosystem, China. We used the natural gradient method to investigate the influence of different soil hydro-saline conditions (D, SA, and DSA) on soil properties (e.g., enzyme activities and nutrient levels), soil microbial communities (e.g., biomass and diversity via sequencing), plant communities (e.g., productivity, height, and diversity), and EMF. Through integrated analysis of this multidimensional dataset, our study provides a mechanistic understanding of how semi-arid grasslands respond to single and combined water-salt stresses, filling a critical gap in stress ecology and informing strategies for the restoration and sustainable management of vulnerable saline-alkaline ecosystems. 2 Materials and methods

2.1 Study area and experimental design

The study was performed in Shidong Town, Gaolan County, Gansu Province of China (36°21′N, 103°59′E). The study area belongs to a semi-arid temperate climate, characterized by an annual temperature of 7.4°C, precipitation of 246 mm (predominantly occurring June–September), and evaporation of 1675 mm. These

arid climatic conditions, coupled with anthropogenic factors such as unsustainable irrigation practices and excessive fertilization, have led to widespread soil degradation, manifesting as drought stress, salinity stress, or a combination of them (Hu et al., 2024).

The experimental site in this study is a natural area free from planting or management. The vegetation community is dominated by Reaumuria songarica (Pall.) Maxim, with associated species including Leymus angustus (Trin.) Pilg., Allium mongolicum Regel, Kalidium gracile Fenzl., Peganum harmala L., exhibiting >15.00% cover and plant heights <0.65 m (Table S1).

Together, these species form a typical natural vegetation community characteristic of arid and semi-arid areas. In this study, we divided experimental blocks (each with an area of >30 km a minimum distance >0.3 km between adjacent blocks) into three soil groups based on measurements of soil water content (SWC) and electrical conductivity (EC). Group D: low SWC (<7.00%) and low EC (<2.5 mS/cm); Group SA: high SWC (>10.00%) and high EC (>5.0 mS/cm); Group DSA: intermediate SWC (7.00%–10.00%) and EC (2.5–5.0 mS/cm) relative to Groups D and SA. The classification criteria were independently developed with reference to multiple literatures (Mo and Lettenmaier, 2014; Cong, 2018; FAO, 2021). Within each soil group, ten replicate sample plots (1 m$×$1 m) were established, with a minimum distance of $ 60*m between adjacent plots to avoid spatial autocorrelation. 2.2 Plant community survey and soil sampling A surv* m), total vegetation and species cover, species richness and abundance, and the height of randomly chosen plants of each species were recorded. Afterward, the above-ground components of the plants were cut off, and fresh weights of each species per plot were recorded. We calculated the importance value (IV) of each plant species based on the relative species cover, relative frequency, and relative density (Sheng et al., 2024). The community-weighted means (CWM) of plant height was calculated from the vegetation cover for each plot (Xiao et al., 2021): where is the species is the average height for species (cm); is the cover of species

is the species richness in the plot. Within each plot, we collected five soil cores at random points 15 cm away from the edge of the quadrat, utilizing a soil auger that drilled to 15 cm depth, then mixed samples into a bulk soil sample for each plot, after removing the floating loose soil and surface debris (stones, branches, leaves, etc.) (Ye et al., 2024). In total, 30 soil samples were taken. An ice box was used to transfer the soil samples to the lab. Then, all the soil samples were passed through a 2-mm sieve and were split into two parts. One of them was air-dried naturally for soil property and soil enzymatic activity analysis, and the other was stored at −80°C for subsequent high-throughput sequencing (Hu et al., 2024; Li et al., 2024). 2.3 Soil physical and chemical property determination We weighed samples before and after drying them at 105°C for 48 h to determine SWC (Li et al., 2024). Soil pH and EC were determined by using a pH meter (Yoke P711; Shanghai Yoke Instrument Co., Ltd., Shanghai, China) and a conductivity meter (Leici DDSJ-319L, INESA Scientific

Instrument Co., Ltd., Shanghai, China), respectively, after soil solution was extracted with soil and deionized water at a ratio of 1:5 (w/v). To determine soil organic carbon (SOC), we utilized the potassium dichromate external heating method. Soil total nitrogen (TN) was determined by the Kjeldahl method (Zhang et al., 2024b). Soil total phosphorus (TP) was measured by the alkali fusion-Mo-Sb Anti spectrophotometric method. Soil magnesium (Mg calcium (Ca), sodium (Na), and potassium (K) concentrations were determined by inductively coupled plasma-atomic emission spectrometry (iCAP 7400, Thermo Fisher Scientific, Irvine, USA). Sulfate radical (SO) content was determined by Ethylene Diamine Tetraacetic Acid (EDTA) indirect complexometric titration. Carbonate (CO) and bicarbonate (HCO) levels were measured using the dual indicator neutralization titration method. Chloride (Cl) content was determined by the silver nitrate titration method. Soil microbial biomass nitrogen (MBN), carbon (MBC), and phosphorus (MBP) were quantified by the chloroform fumigation extraction method (Zhou et al., 2024). Soil extracellular enzyme activities, including urease (UE), β-1,4- -acetyl- glucosaminidase (NAG), β-glucosidase (β-GC), α-glucosidase (α-GC), alkaline phosphatase (AKP), and neutral phosphatase (NP), were measured in accordance with the guidelines provided by Suzhou Michy Biomedical Technology Co., Ltd., Suzhou, China (Maestre et al., 2012). 2.4 Deoxyribonucleic acid (DNA) extraction, polymerase chain reaction (PCR) amplification, sequencing, and bioinformatics analysis Total DNA of soil samples was extracted using the TIANamp Soil DNA kit (TianGen Ltd., Beijing, China). The integrity and concentration of DNA were determined by a 2.00% agarose gel electrophoresis, with the results obtained by an Agilent Fragment Analyzer 5400 (Agilent Technologies Co., Ltd., Santa Clara, USA). The primer design and PCR amplification process were conducted in accordance with the previously established experimental method (Hu et al., 2023).

In brief, the V3-V4 region for bacteria was amplified by using primers 341F (5′-CCTAYGG- GRBGCASCAG-3′) and 806R (5′-GGACTACNNGGGGTATCTAAT-3′), and the ITS1-5F region for fungi was amplified by using primers ITS5-1737F (5′-GGAAGTAAAAGTCGTAA- CAAGG-3′) and ITS2-2043R (5′-GCTGCGTTCTTCATCGATGC-3′). Each PCR reaction was performed in a 20.0-μL volume with 15.0 µL of Phusion® High-Fidelity PCR Master Mix (New England Biolabs, Ipswich, USA), 0.5 µL of forward and reverse primers, and about 10 ng template DNA, and finally, ddH O was added up to 20.0 μL. The PCR amplification was carried out using the following protocol: an initial denaturation step at 95°C for 3 min, followed by 30 cycles of denaturation at 95°C for 30 s, annealing at 53°C for 30 s, and extension at 72°C for 45 s, with a final extension step at 72°C for 10 min, ending at 10°C. PCR products were purified using QIAquick gel extraction kits (Qiagen, Hilden, Germany) and were detected using electrophoresis on a 2.00% agarose gel.

Sequencing libraries were made using TruSeq DNA PCR-Free sample preparation kits (Illumina, San Diego, USA). The libraries were quantified by Qubit 2.0 Fluorometer (Thermo

Fisher Scientific, Eugene, USA) and Agilent Bioanalyzer 2100 System (Agilent Technologies, Santa Clara, USA). To generate 250 bp paired-end reads, we utilized an Illumina NovaSeq platform from Novogene Co., Ltd., located in Beijing, China. We distinguished data from the paired-end reads of each sample from others according to the barcode sequence. Paired-end reads were merged to obtain Raw Tags by FLASH v.1.2.1 software (Chen et al., 2023). To obtain clean tags, we used the FASTP v.0.23.1 software to filter the raw tags obtained by splicing. Clean tags were compared with reference databases to detect and remove chimeric sequences using VSEARCH v.2.16.0 software. Effective tags were then obtained. The effective tags were subjected to denoising using the quantitative insights into microbial ecology 2 (QIIME2) v.2022 software to obtain initial amplicon sequence variants (ASVs) and associated feature tables. The species were annotated using QIIME2. Finally, the data from each sample was subsampled, and the least sequence was used as the standard for subsampling. We conducted all subsequent analyses based on this procedure. Finally, 13,854 and 5799 ASVs were obtained for bacterial and fungal samples. The raw data for the 16S and Internal Transcribed Spacer (ITS) analyses were submitted to the National Center for Biotechnology Information (NCBI) database (BioProject ID:

PRJNA1054217).

2.5 Data analytics

The data analysis was performed using the R v.4.1.0 software. One-way analysis of variance at a significance level of <0.050 and Duncan' s multiple range tests were used to determine differences among groups (de Vries et al., 2018). The ° vegan'' package was employed to calculate the alpha diversity of the plant and microbial communities. We conducted non-metric multidi- mensional scaling (NMDS) analysis of plant and soil microbial communities based on Bray-Curtis distances after standardization, and Anosim and Adonis' s tests were performed (de Vries et al., 2018). The composition of bacteria and fungi was visualized using the ° circlize'' and ° ggalluvial'' packages (Hu et al., 2023). The Mantel test was used to assess the correlation between Bray-Curtis dissimilarities at the ASV level for microbial community composition and Euclidean distances for SWC and EC. ASVs detected in over 40.00% of all samples were used to create co-occurrence networks. Spearman' s correlation coefficients among ASVs were determined.

After correcting the -value with false discovery rate, we retained links with <0.050 and absolute >0.9 using the ° vegan'' package, and the networks were visualized with the °igraph" package (de Vries et al., 2018). Keystone taxa were identified by analyzing both within-module connectivity (Zi) and among-module connectivity (Pi) within the microbial networks. Based on Zi and Pi thresholds, we categorized nodes as: network hubs (Zi>2.5 and Pi>0.62), module hubs (Zi>2.5 and Pi<0.62), connectors (Zi<2.5 and Pi>0.62), or peripherals (Zi<2.5 and Pi<0.62).

Among them, network hubs, module hubs, and connectors are defined as keystone taxa (Hu et al., 2023).

In total, 12 indices that might be used to quantify EMF were collected, including plant community characteristics (vegetation cover, species richness, total biomass, CWM of height, Shannon-Winner, and Simpson indices), soil properties (SOC, TP, and TN), and microbial biomass (MBC, MBP, and MBN). We calculated Z-scores for EMF corresponding to the 12 indices, based on the average of Z-scores for all indices within each plot (Maestre et al., 2012; Hu et al., 2024). In addition, we calculated the biogeochemical cycles of carbon (C), nitrogen (N), and phosphorus (P) via a Z-score averaging approach based on relevant enzyme activities and soil properties. Specifically, C cycle includes SOC, α-GC, and β-GC; N cycle includes TN, NAG, and UE; and P cycle includes TP, AKP, and NP. Additionally, structural equation modeling (SEM) was constructed using the ° lavvan'' package to assess the effects of soil heterogeneity on the plant, microbial communities, and EMF, with the model considered a good fit when <0.050 and the root mean square error of approximation (RMSEA)<0.08 (Wu et al., 2022). We calculated Spearman' s correlation and performed regression analyses with the ° linkET'' package. The ° FactoMineR'' and ° Factoextra'' packages were employed to execute a principal component analysis (PCA) (Niu et al., 2021).

3 Results

3.1 Soil properties, soil microbial biomass, and soil enzyme activities Ecological properties, including soil characteristics, microbial biomass, and enzymatic activities, were investigated across the D, SA, and DSA groups. The values of pH, SWC, and EC in the SA group are higher than those in the DSA group, and the corresponding values in the DSA group were higher than those in the D group (<0.050; Fig. 1 [Figure 1: see original paper]). SOC, TN, and TP were significantly higher in the DSA group than in the D and SA groups. MBC and MBN mirrored this pattern, being highest in the DSA group (Fig. 1). In contrast, the SA group had significantly higher concentrations of major cations (K , Ca^2 , and Mg^2) than the D and DSA groups (<0.050; and SO were significantly lower in the D group than in the DSA and SA groups, whereas the content of HCO was markedly higher in the D group than in the SA group (<0.050; Table 1). The β-GC and α-GC activities were significantly reduced in the Soil properties and soil microbial biomass in different groups. (a), pH; (b), SWC (soil water content); (c), EC (electrical conductivity); (d), SOC (soil organic carbon); (e), TN (total nitrogen); (f), TP (total phosphorus); (g), MBC (microbial biomass carbon); (h), MBN (microbial biomass nitrogen); (i), MBP (microbial biomass phosphorus). D, drought; SA, saline-alkaline; DSA, combined stress of D and SA. Boxes indicate the IQR (interquartile range, 75 to 25 of the data). The median value is shown as a line within the box. Outlier is shown as black point. Whiskers extend to the most extreme value within 1.5×IQR. Different lowercase letters indicate significant differences at <0.050 level among different groups.

Soil ions content and soil enzyme activities in different groups Index Soil ion α-glucosidase (α-GC; μmol/(g 1.486$±0.1400.737±0.1441.697±$0.195 β-glucosidase (β-GC; μmol/(g 5.331$±0.5752.695±0.1543.220±$0.348 Urease (UE; μg/(g 204.517$±3.166182.473±2.669143.673±$4.576 β-1,4- -acetyl-glucosaminidase (NAG; μmol/(g 2.180$±0.2261.576±0.2882.342±$0.200 enzyme activity Neutral phosphatase (NP; μmol/(g 0.227$±0.0100.157±0.0060.107±$0.013 Alkaline phosphatase (AKP; μmol/(g 5.402$±0.2292.383±0.0981.160±0.066$Note$: $D, drought; SA, saline-alkaline; DSA, combined stress of D and SA. Different lowercase letters within the same$ $0.050 level among different groups. Mean$±$SE.

DSA group compared with the D group (<0.050; Table 1), suggesting a potential limitation in C cycle. Furthermore, the activities of UE, AKP, and NP were the highest in the D group, intermediate in the DSA group, and the lowest in the SA group, indicating that soil salinization progressively inhibits the mineralization processes of N and P (<0.050; Table 1). 3.2 Vegetation community composition and plant traits Figures 2 and 3 show the vegetation community composition and plant traits. Across the three soil category groups, a vegetation survey recorded a total of 10 species belonging to 6 families and 10 genera.

R. songarica L. angustus were the dominant plant species (Fig. 2a [Figure 2: see original paper]; Table S1).

Vegetation cover, CWM of height, and total biomass were significantly different among the D, DSA, and SA groups (<0.050; Figs. 2b–d and 3a). The Shannon-Winner and Simpson indices of the plant community did not differ significantly among the three groups (Fig. 3b [Figure 3: see original paper] and c). However, the NMDS results indicated significant differences in plant communities across different groups <0.001), with the SA group showing a distinct separation from the D and DSA groups (Fig. 3d).

The regression analyses indicated no significant correlation of species richness with SWC and >0.050; Fig. 2e1 and f1), indicating that the number of plant species in the community was not significantly affected by SWC or soil salinization in the study area. Meanwhile, the regression of vegetation cover, CWM of height, and total biomass on SWC and EC was significant (<0.001; changes in SWC and soil salinization. Consequently, there was no significant change in species richness, while environmental conditions still limit their growth performance and productivity.

Additionally, concerning plant density, biomass, and IV, L. angustus displayed the highest density in the D group, R. songarica had the highest density in the DSA group, and C. album the SA group (Fig. 3e1–e3). However, R. songarica had the highest IV of all three soil groups, in which it had the highest predominance (Fig. 3f1–f3).

R. songarica provided the highest contribution to the total plant biomass in all three soil groups (Fig. 3g1–g3). Subsequently, we performed a further analysis of the dominant plant species, R. songarica , which showed a significant increase in leaf length, and chlorophyll , and total chlorophyll contents from the D group

to the DSA group, and from the DSA group to the SA group (<0.050; Fig. S1a–d).

Aboveground Na content of R. songarica was markedly higher in the DSA group than in the D and SA groups, and K content was the highest in the SA group, followed by the DSA and D

Plant community features and their relationship with SWC and EC. (a), Venn diagram showing the number of unique and shared plant species; (b), vegetation cover; (c), CWM (community-weighted mean value) of height; (d), total biomass; (e1–e4), relationships between plant community features and SWC; (f1–f4), relationships between plant community features and EC. Different lowercase letters in Figure 2b–d indicate significant differences at <0.050 level among different groups. Shaded area in Figure 2e1–e4 and f1–f4 indicates the 95.00% confidence interval. groups (<0.050; Fig. S1e and f), which may indicate that R. songarica has developed an ion regulatory adaptation strategy to cope with different soil water and salinity conditions. 3.3 Soil microbial community diversity and structure To evaluate the shift in microbial community characteristics among the D, DSA, and SA soil groups, we analyzed differences in abundance and diversity for distinct microbial taxonomic groups (Fig. 4 [Figure 4: see original paper]). There was a significant variation in the Shannon index for bacteria between the D group and the SA group (<0.050; Fig. 4a2). Furthermore, a difference was observed in the fungi community between the D and the SA groups in ASVs and Shannon indices (<0.050; Fig. 4b1 and b2). The NMDS analysis of bacteria and fungi at the ASV level showed significant differences in bacterial (<0.001) and fungal (<0.001) community composition among the three soil groups (Fig. 4c and d). We observed significant linear correlations between the dissimilarity distance of bacterial (=0.4161 for SWC and =0.4888 for EC; <0.001; Fig. 4e1 and e2) and fungal (=0.2652 for SWC and =0.2260 for EC; <0.010; Fig. 4f1 and f2) communities and soil properties. Specifically, the dissimilarity of microbial communities increased with an increase in SWC and EC, with bacteria displaying a more pronounced positive response to SWC and salinity. The abundance of Actinobacteriota was significantly greater in the D and DSA groups than in the SA group (<0.050). Conversely, the abundance values for Proteobacteria and Bacteroidota were found to be higher in the SA group, compared with the D and DSA groups (Fig.

S2a). The Basidiomycota abundance in the D group was found to be higher than in the DSA and SA groups (Fig. S2b). The dominant genera were Marinobacter Halomonas for bacteria (Fig.

S2c), and they were Geminibasidium Fusarium , and Preussia for fungi (Fig. S2d).

Composition of plant communities and species attributes. (a), species cover; (b), Shannon-Wiener index; (c), Simpson index; (d), non-metric multidimensional scaling (NMDS) analysis; (e1–e3), plant density; (f1–f3), importance value (IV); (g1–g3) biomass.

A. mongolicum Allium mongolicum Regel; A. capillaris Artemisia capillaris Thunb.; A. gobicus Asparagus gobicus Ivanova ex Grubov; C. album Chenopodium album gracile Kalidium gracile Fenzl.; L. angustus Leymus angustus (Trin.) Pilg.; N. tangutorum Nitraria tangutorum Bobrov; P. harmala Peganum harmala R. songarica Reaumuria songarica (Pall.) Maxim; Z. mucronatum Zygophyllum mucronatum Maxim Different lowercase letters indicate significant differences at <0.050 level among different groups or plant species. Bars in Figure 3e1-e3, f1-f3, and g1-g3 are standard errors. 3.4 Networks of bacterial and fungal communities Microbial coexistence was estimated in diverse taxonomic groups by establishing co-occurrence networks (Fig. 5 [Figure 5: see original paper]). When only significant correlations were examined, it became apparent that bacterial ASVs displayed stronger links than fungal ASVs, and fungal networks exhibited lesser negative correlations than bacterial networks (Fig. 5a1-a3 and b1-b3). The number of nodes and links decreased from the D group to the DSA group, and subsequently to the SA group in bacterial and fungal communities. However, the ratio of links to nodes and the average degree in the DSA group exceeded those of the D and SA groups (Fig. 5c1 and c2; Table 2). Results for the density and average degree, which represent network complexity, indicated that the DSA group had a higher network complexity than the D and SA groups (Fig. 5c2 and c3; Table 2). These results suggest that under drought and salinity conditions, microorganisms require more complex networks to optimize resource use and distribute environmental pressures, thus preserving the stability and functional integrity of the community. Additionally, to identify the keystone taxa in networks, we split the nodes into connectors, peripherals, network hubs, and module hubs. The identification of network hubs was not possible in any of the networks. There was a total of six module hubs, with the D group having two and the DSA group having four (Fig. 5d1 and d2).

Amplicon sequence variants (ASVs), alpha diversity, NMDS, and relationships of dissimilarity distance with SWC and EC. (a1-a3), bacterial ASVs and alpha diversity; (b1-b3), fungal ASVs and alpha diversity; (c), NMDS analysis for bacteria; (d), NMDS analysis for fungi; (e1 and e2), relationships of dissimilarity distance with SWC and EC for bacteria, respectively; (f1 and f2), relationships of dissimilarity distance with SWC and EC for fungi, respectively. Different lowercase letters in Figure 4a1-a3 and b1-b3 indicate significant differences at <0.050 level among different groups. ACE, abundance-based coverage estimation.

Moreover, there were six connectors, with each of the D group and DSA group having three. The module hubs all belonged to the bacterial communities from the D and DSA groups, while the connectors consisted of bacteria (ASV123, ASV676, and ASV1302) and fungi (ASV38, ASV42, and ASV57) (Fig. 5d1 and d2; Tables S2 and S3). Among these, only ASV123 belongs to the genus Rubrobacter , while no specific taxonomic information was obtained for the other keystone taxa (Table S3). 3.5 Effects of soil heterogeneity on vegetation, soil microbiota, and EMF The environmental conditions of the soil play vital

roles in the growth of microbes and plants and the development of EMF. C cycle in the DSA group was lower than in the D group, N cycle in the D and DSA groups was higher than in the SA group, P cycle showed a significant decrease from the D group to DSA group and then to SA group, and EMF was significantly higher in the DSA and the SA groups than in the D group (<0.050; Fig. S3).

Here, SEM was used to assess the indirect and direct impacts of soil properties on plants, soil microbes, and EMF (Figs. S4 and 6). We observed a significant positive effect of SWC on CWM of height (<0.001), as well as a positive trend in the richness of bacterial ASVs through CWM of height (<0.001; Fig. S4a). This result may be attributed to SWC directly promoting the increase in plant community, which in turn indirectly and significantly enhances the richness of bacterial ASVs through the "mediating effect" of vegetation. Additionally, the richness of bacteria ASVs

Co-occurrence networks and topological properties of networks. (a1–a3), bacterial networks in different groups; (b1–b3), fungal networks in different groups; (c1–c3), ratio of links to nodes, average degree, and density in different groups; (d1–d3), within-module connectivity (Zi) and among-module connectivity (Pi) plots showing the distribution of ASVs based on their topological roles and ability to predict keystone ASVs in networks, with red dashed lines on the -axis and -axis representing Pi=0.62 and Zi=2.5, respectively. In Figure a1–a3 and b1–b3, nodes represent ASVs. The node color represents the top 6 phyla, and node size indicates the degree.

Topological properties of correlation networks for bacteria and fungi in different groups Bacteria Fungi Positive links and percentage (97.55%) (96.49%) (98.61%) (100.00%) (100.00%) (100.00%) Negative links and percentage (2.45%) (3.51%) (1.39%) (0.00%) (0.00%) (0.00%) Ratio of links to nodes

was significantly and positively affected by soil enzyme activities (<0.001) and microbial biomass (<0.010). Thus, CWM of height, microbial biomass, and soil enzyme activities played a direct and positive role in the construction of bacterial communities (Fig. S4a). Soil enzyme activities negatively and directly impacted the richness of fungal ASVs (<0.001), while CWM of height and soil microbial biomass played indirect roles through their effects on soil enzyme activities (<0.001; Fig. S4b). Regarding EMF, soil microbial biomass was negatively affected by <0.050), but it was positively affected by SOC (<0.001). The results revealed soil enzyme activities had a significantly negative effect on soil microbial biomass (<0.001), and microbial biomass was found to directly affect EMF positively (<0.050; Fig. 6a [Figure 6: see original paper]), suggesting its role as a key driver of EMF. Overall, the SEM explained, respectively, 38.50%, 35.00%, and 64.50% of the variation in the richness of bacteria and fungi ASVs and EMF (Figs. S4 and 6a). Additionally, Spearman' s correlation and regression analyses demonstrated that there were significant correlations between soil enzyme activities and the richness of bacteria and fungi ASVs.

Drivers of ecosystem multifunctionality (EMF). (a), SEM (structural equation modeling) showing the direct and indirect effects of factors; (b), contributions of biotic and abiotic factors to soil microbial ASVs and EMF based on Spearman' s correlation and regression model; (c), PCA (principal component analysis) result. GFI, comparative fit index; RMSEA, root mean square error of approximation; PC, principal component; UE, urease; NP, neutral phosphatase; AKP, alkaline phosphatase; β-GC, β-glucosidase; NAG, N-acetyl-glucosaminidase; α-GC, α-glucosidase. <0.050 level; <0.001 level.

Also, CWM of height was a significant factor in explaining the changes in the richness of bacterial ASVs. Soil microbial biomass and SOC were positively correlated with EMF (Fig. 6b).

The PCA showed that the effects of SWC and salinity on plants and soil microbial structure can be distinguished using the first (PC1) and the second (PC2) principal component. We found that EMF was positively correlated with MBC, MBN, TP, and SOC. The richness of fungal ASVs was positively correlated with CWM of height and vegetation cover, SWC, pH, and EC, but negatively correlated with soil enzyme activities. However, the richness of bacteria ASVs was positively correlated with soil enzyme activities, such as NP, AKP, UE, and β-GC (Fig. 6c).

4 Discussion

4.1 Effects of soil hydro-saline stress on plant community biomass Extensive research demonstrates that biodiversity is critical for sustaining ecosystem dynamics, functions, and stability (Tilman et al., 2014; Wagg et al., 2022), while environmental degradation frequently undermines stability by reducing biodiversity (Hooper et al., 2012; Li et al., 2021).

Contrary to this general pattern, our findings reveal a different pattern under combined water and salinity stress. Although plant species richness did not differ significantly among the experimental groups, aboveground biomass varied significantly. This pattern can be explained by the differential responses of plant functional traits to single stress and combined stresses. Studies have shown that halophytes can enhance growth through the active accumulation of ions such as and Cl (Cheeseman, 2015). In this study, the dominant species R. songarica possesses specialized salt-secreting leaves, which confer exceptional salt tolerance and thus grant it a significant competitive advantage in saline-alkali soils (Wang et al., 2022a), enabling it to dominate community biomass (Figs. 3 and S1). These adaptations highlight a mechanistic pathway whereby synergistic stress acts as an environmental filter, selecting species based on functional traits and disproportionately impacting ecosystem biomass.

Soil heterogeneity (e.g., SWC and salinity) typically shapes plant community structure (Pereira et al., 2022; Yao et al., 2025) and species distributions (Tilman et al., 2014; Yang et al., 2021). In the present study, however, species richness showed no significant response across treatments (Fig. 3b

and c), despite measurable variations in soil conditions. This result contrasts with studies reporting stronger richness responses to such stress gradients (Zhang et al., 2023). The limited spatial heterogeneity in this area may have attenuated diversity responses, yet the significant biomass differences highlight that synergistic stress acts as a strong environmental filter, selecting for key functional traits such as plant height, which in turn confers dominance and directly determines ecosystem-level productivity. This observation further supports that community biomass is primarily regulated not only by species richness, but also by the expression of these traits in dominant species that mitigate multiple stressors simultaneously (Cheng et al., 2018). In this context, R. songarica , with its high CWM of height and cover, emerged as the main contributor to community biomass and a determinant of its own dominance (Fig. S1). Collectively, the above results indicate that synergistic soil water-salt stress exerts a stronger influence on plant community biomass than on species richness, primarily through trait-based environmental filtering that promotes the dominance of stress-adapted species and shapes functional composition.

This result suggests that in semi-arid saline-alkali ecosystems, the trait-mediated dominance of key species—more than species number—plays a decisive role in maintaining ecosystem functions under complex environmental constraints. Future studies should explicitly address trait-based mechanisms and physiological thresholds that define species dominance under combined stresses. 4.2 Variations in soil microbial community structure and network complexity Soil microorganisms are fundamental to maintaining key ecosystem functions and ensuring ecological stability (Chen et al., 2020). These communities are highly sensitive to environmental changes, including changes in land use, drought, high or low temperatures, grazing practices,

desertification, and salinization (Guan et al., 2021; Coban et al., 2022; Shu and Huang, 2022; Hu et al., 2023). In line with previous research, our results confirm that elevated soil salinity suppresses bacterial diversity, as the Shannon index was significantly lower in the SA group than in the D group (Fig. 4a) (Guan et al., 2021; Wei et al., 2024). This decline can be attributed to the osmotic stress induced by salt accumulation, which damages cell membranes, proteins, and nucleic acids, ultimately leading to microbial cell lysis (Guan et al., 2021). Additionally, soil heterogeneity has been identified as a major driver of microbial spatial distribution (Zhou and Ning, 2017; Shu and Huang, 2022). Our analysis further reveals that a significantly positive correlation exists between microbial (both bacterial and fungal) community dissimilarity distance and Euclidean distance in SWC and EC. This result suggests that divergence in these edaphic factors corresponds to increasing differentiation in microbial composition. In addition, from the D group to the DSA group and then to the SA group, the richness of ASVs and Shannon index of bacteria and fungi showed a decreasing trend and an increasing trend, respectively (Fig. 4).

Specifically, in the SA group, the fungal ASVs richness and Shannon index were both higher than in the D group (Fig. 4). The potential factors contributing

to variations in the performance of soil bacteria and fungi may be attributed to differences in competition dynamics between these organisms for available soil resources and their distinct nutritional preferences (Hu et al., 2024; Philippot et al., 2024). Furthermore, the observed shifts are consistent with studies linking microbial community assembly to environmental filtering. For instance, previous research has shown a correlation between the pH preference of bacterial communities and the distribution of those communities (Delgado-Baquerizo et al., 2018), suggesting that salinity and moisture together act as hierarchical filters, reshaping community structure in a kingdom-specific manner.

Soil microorganisms form intricate co-occurrence networks, where taxa are nodes and their statistical associations are links (Chen et al., 2023). These networks are sensitive to environmental change but exhibit inherent resistance (Guan et al., 2021; Pan et al., 2021; Gao et al., 2022).

While these microbial networks are mathematical constructs, they provide profound insight into the organization of microbial communities and their responses to environmental changes (Wang et al., 2023). Both drought and saline-alkali stresses significantly impact microbial networks, often through cascading effects. Drought is thought to have enduring impacts on the microbial community structure and function and the networks by influencing the structure of vegetation communities (de Vries et al., 2018). Saline-alkali stress, primarily through ion imbalance and nutrient deficiency, reduces plant productivity, indirectly affecting soil microbes (Chen et al., 2022). Our findings reveal that the complexity of these networks is not uniformly diminished by environmental stress; instead, it depends on the type and intensity of the stressors. Specifically, the microbial networks in the DSA group exhibited greater complexity than that in the D or DSA group alone. Additionally, the SA group exerted a stronger detrimental effect on microbial network complexity than the D group (Fig. 5a–c). The combined D and salinity stress yields higher complexity than single stress, which can be explained by stress intensity gradients.

Previous studies show that under low-level D stress, microbial taxa exhibit closer and more frequent co-occurrences (Jiao et al., 2022), potentially aided by higher moisture availability (Wang et al., 2018). Similar results were observed in SA environments, where microbial network complexity in low-salinity conditions was higher than that in high-salinity conditions (Pan et al., 2021). In our study, the individual stress levels in the D and SA groups were more severe than those in the DSA group, where combined stress likely resulted in a moderated intensity for each stressor. This gradient explains the higher network complexity in the DSA group, suggesting that moderate, multi-faceted stress can foster a more interconnected microbial community.

It is also a finding of previous research that particular keystone taxa are essential for preserving the structural and functional integrity of microbial ecosystems (Guan et al., 2021; Hu et al., 2023).

In our study, six keystone taxa were identified from the D and DSA groups

(Fig. 5d). Among these taxa, ASV123, which was identified in the D group, was classified within the genus Rubrobacter . Microorganisms of this genus exhibit diverse stress-resistant traits, which confer a high level of insensitivity to environmental stressors (Kouřilová et al., 2021). This stress tolerance

enables their survival under adverse environmental conditions and plays a significant role in sustaining the stability of microbial communities. These findings provide further evidence that keystone species play a crucial role in sustaining microbial network complexity (Guan et al., 2021) and that their removal can result in a substantial alteration in the composition and functionality of the microbiome (Banerjee et al., 2018). In summary, synergistic soil hydrosaline stress is a critical factor affecting soil microbial diversity and structure in semi-arid and saline-alkali areas. 4.3 Drivers of soil microbial construction and EMF Soil properties, including pH, SWC, EC, and TC, have been demonstrated to influence the construc- tion of microbial communities (Bahram et al., 2018; Philippot et al., 2024). A global- scale study confirmed that soil pH is the primary factor correlated with the global distribution of both fungal and bacterial communities (Bahram et al., 2018). This finding aligns closely with our study, and we observed a notable correlation of SWC and salinity with the composition of microbial community (Fig. 4e and f). These factors exert direct physiological pressure on microbes, for instance, by altering cell surface charge and membrane integrity (Yan et al., 2015).

Beyond community structure, this study found that soil extracellular enzyme activities decreased after being affected by SA stress, such as UE, AKP, and NP (Table 1). This may be because soil extracellular enzyme activities were negatively affected by increased salinity, as high salt conditions directly denature proteins and reduce enzyme activities (Yan et al., 2015; Sritongon et al., 2022).

EMF is governed by complex interactions between biotic and abiotic factors (Jing et al., 2015; Zheng et al., 2023). Our study elucidates the mechanistic pathways through which plant functional traits, microbial community dynamics, and soil properties collectively regulate ecosystem functioning in semi-arid and saline-alkali environments. For example, dryland EMF was significantly affected by plant biodiversity (Maestre et al., 2012). Plant functional traits serve as a critical bridge transmitting environmental stressors to microbial communities and ecosystem processes. In this work, we found that CWM of height was significantly influenced by SWC, and the soil microbial biomass was also affected by SOC. Significantly positive effects were observed on the richness of bacterial ASVs due to CWM of height, microbial biomass, and soil enzymatic activity. Additionally, while soil enzymatic activity exhibited a markedly adverse effect on the richness of fungal ASVs that were indirectly and negatively affected by CWM of height (Fig. S4), it was also essential for the composition of bacterial and fungal communities (Fig. 6b). Serving as a critical dynamic C, N, and P pools in soil ecosystems, soil microbial biomass can rapidly respond to environmental changes and plays a vital role in nutrient cycle and the regulation of ecological functions (Singh and Gupta, 2018; Hartmann and Six, 2023). In this study,

the trends of microbial biomass, as well as soil C, N, and P, were consistent (Fig. 1). This finding suggests that soil microbial biomass exerts a crucial influence on maintaining the stability of soil C, N, and P levels (Singh and Gupta, 2018). Similarly, SEM and PCA analyses indicated that microbial biomass has a significant impact on the stabilization of EMF (Fig. 6). And also other previous studies have shown that soil and plant indices were the principal factors that determine the composition of soil microbial communities and influence EMF (Maestre et al., 2012; Wan et al., 2020; Zheng et al., 2023). The above results confirm that EMF is influenced by the combined effects of soil physical-chemical properties and the plant and microbial communities in the surrounding environment.

5 Conclusions

This study investigated D, SA, and DSA on plant-soil-microbe systems and EMF in a semi-arid grassland. Soil hydro-saline conditions were a critical regulator. Increasing soil hydro-salinity (from D group to DSA group and then to SA group) significantly reduced soil enzyme activities.

SOC, TN, TP, MBC, and MBN were lower in the D and SA groups than in the DSA group. Plant biomass increased with soil hydro-salinity, driven by dominant species, while plant diversity remained unaffected. Microbial communities proved more sensitive than plants to direct

hydro-saline stress, with SWC and salinity primarily driving their diversity and complexity. Soil enzyme activities were key drivers of bacterial community structure, and microbial biomass significantly stabilized EMF. These findings clarify the distinct and synergistic impacts of hydro-saline stresses on semi-arid grassland ecosystems, providing a basis for predicting responses and guiding management in vulnerable semi-arid areas.

Conflict of interest The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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Appendix

Table S1 Distribution of plants in each group Plant species Family Genus Group Reaumuria songarica (Pall.) Maxim Tamaricaceae Reaumuria D, DSA, SA Leymus angustus (Trin.) Pilg.

Poaceae Leymus D, DSA, SA Allium mongolicum Regel Liliaceae Allium D, DSA Peganum harmala Zygophyllaceae Peganum DSA, SA Asparagus gobicus Ivanova ex Grubov Liliaceae Asparagus Zygophyllum mucronatum Maxim.

Zygophyllaceae Zygophyllum Artemisia capillaris Thunb.

Compositae Artemisia Chenopodium album Chenopodiaceae Chenopodium Nitraria tangutorum Bobrov Zygophyllaceae Nitraria Kalidium gracile Fenzl.

Chenopodiaceae Kalidium Note: D, drought; SA, saline-alkaline; DSA, combined stress of D and SA.

Fig. S1 Traits of the dominant plant species (songarica). (a), leaf length; (b), chlorophyll ; (c), chlorophyll (d), total chlorophyll; (e), Na content; (f), K content. D, drought; SA, saline-alkaline; DSA, combined stress of D and SA; DW, dry weight. Boxes indicate the IQR (interquartile range, 75 to 25 of the data). The median value is shown as a line within the box. Whiskers extend to the most extreme value within 1.5×IQR. Different lowercase letters indicate significant differences at <0.050 level among different groups.

Fig. S2 Relative abundance of microbial communities in different soil groups. (a and b), bacterial and fungal relative abundance at phylum level, respectively; (c and d), bacterial and fungal relative abundance at genus level, respectively.

Table S2 Classification of nodes to identify keystone taxa in bacterial and fungal networks Classification of nodes Bacteria Fungi Connectors Module hubs Network hubs

Table S3 Distribution of keystone taxa in bacterial and fungal networks Name of ASVs Group Classification Kingdom Phylum Genus ASV123 Connectors Bacteria Actinobacteriota Rubrobacter ASV676 Connectors Bacteria Planctomycetota ASV1368 Module hubs Bacteria Proteobacteria Steroidobacter ASV1932 Module hubs Bacteria ASV57 Connectors Fungi Basidiomycota ASV123 Module hubs Bacteria Actinobacteriota Rubrobacter ASV296 Module hubs Bacteria Actinobacteriota ASV414 Module hubs Bacteria Proteobacteria Woeseia ASV715 Module hubs Bacteria ASV1302 Connectors Bacteria Chloroflexi ASV38 Connectors Fungi ASV42 Connectors Fungi Note: ASVs, amplicon sequence variants. "-" indicates that the ASV has no annotations at this taxonomic level.

Fig. S3 Soil carbon (C; a), nitrogen (N; b), and phosphorus (P; c) cycles and ecosystem multifunctionality (EMF; d). Different lowercase letters indicate significant differences at <0.050 level among different groups.

Fig. S4 Structural equation modeling (SEM) showing the direct and indirect effects of drivers of soil microbial amplicon sequence variants (ASVs). (a), bacteria; (b), fungi. EC, electrical conductivity; SWC, soil water content; SOC, soil organic carbon; CWM, community-weighted means; GFI, goodness-of-fit index; RMSEA, root mean square error of approximation; <0.010 level; <0.001 level.

Note: Figure translations are in progress. See original paper for figures.