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Abstract

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Full Text

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From structure to assembly processes: how salinity regulates soil bacterial communities in arid regions

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croorganisms, its comprehensive effects on soil microbial community structure and assembly processes remain poorly understood, particularly in arid regions prone to salinization. In this study, soil bacterial communities along a natural salinity gradient at the edge of Ebinur Lake in Northwest China were investigated. Using 16S ribosomal RNA (16S rRNA) sequencing, we examined variations in soil bacterial community structure, co-occurrence patterns, and assembly mechanisms across different soil salinity groups, including lightly salinized soils (LSS), moderately salinized soils (MSS), and heavily salinized soils (HSS). The results showed that soil bacterial diversity varied significantly among salinity groups, with the highest value observed in LSS. Community dissimilarity increased notably with greater variations in salinity. Notably, a systematic shift in soil bacterial composition occurred along the salinity gradient, with salt-sensitive bacterial phyla (e.g., Acidobacteria and Gemmatimonadetes) being progressively replaced by salt-tolerant ones (e.g., Firmicutes and Bacteroidetes). Network analysis underscored that increased salinity led to reduced soil bacterial network complexity and stability. More positive correlations among soil bacteria occurred in HSS, suggesting a potential shift toward cooperative microbial strategies under severe salt stress. Moreover, the assembly processes governing soil bacterial communities transitioned from stochastic process, predominantly in LSS (71.43%) and MSS (80.00%), to deterministic process in HSS (66.66%). In summary, the results emphasize the multifaceted role of soil salinity in shaping soil bacterial communities in arid ecosystems, thereby enhancing the understanding of the impacts of soil salinization on soil microbial dynamics.

Keywords: salinity; soil bacteria; bacterial community structure; co-occurrence network; community assembly; Ebinur Lake

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1 Introduction

Soil salinization represents a significant environmental challenge that was evident in ancient times and persists in the modern era (Rath et al., 2017). Globally, more than 8.0×10^6 km^2 of soil is affected by varying levels of salinity (Rath and Rousk, 2015), with the majority located in arid

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and semi-arid regions (D'Odorico et al., 2013). Excessive amounts of salt may inhibit plant and microorganism growth and strongly influence their distributions, thereby serving as a major environmental stressor (Rath et al., 2016, 2019). Although previous studies have focused on the effects of salinity on soil properties and plant distribution, considerably less is known regarding its impacts on soil microbial communities (Zhang et al., 2019; Zhang et al., 2024). As the most diverse biological component in saline soils, microorganisms possess multiple adaptive mechanisms that enable them to remain active and functional under high-salinity conditions (Van Horn et al., 2014). Further, studies in hypersaline ecosystems have identified novel organisms and enzymes with unique features, highlighting their potential for various applications (Hollister et al., 2010), including bioremediation of damaged ecosystems, control of desertification, and biomolecule production (Canfora et al., 2015). Therefore, elucidating how soil microbial communities vary with salinity is essential to understanding ecosystem function under stress and to formulating effective strategies to alleviate the impacts of soil salinization.

In recent decades, microbial diversity and community composition have been shown to vary predictably with aridity (Maestre et al., 2015; Delgado-Baquerizo et al., 2020), pH (Fierer and Jackson, 2006), and climate variables (Tedersoo et al., 2014). Notably, although salinity is widely recognized as a key environmental factor, most supporting evidence derives from aquatic or sedimentary environments (Wang et al., 2018), and its role in structuring soil microbial communities remains debatable (Rath and Rousk, 2015; He et al., 2024). For example, a study from a hypersaline lake showed that substrate and pH had a greater influence on microbial community variation than salinity (Hollister et al., 2010); however, another research in a desert zone identified salinity as a decisive factor shaping the diversity and structure of soil microbial communities (Zhang et al., 2019). Thus, additional research is necessary to clarify the degree to which salinity variations along natural salinity gradients drive the divergence of soil microbial communities, particularly in arid and semi-arid regions severely impacted by soil salinization.

In natural ecosystems, microbes engage in intricate networks of interactions (Freilich et al., 2010; Deng et al., 2012). The analysis of co-occurrence networks has emerged as a powerful method for exploring these interactions, providing an enhanced understanding of the structure of microbial associations that traditional diversity metrics might overlook (Zhou et al., 2011; Barberán et al., 2012; Ma et al., 2016). For instance, through co-occurrence network analysis, Feng et al. (2021) observed significant decreases in total nodes and links in soil bacterial networks along a precipitation gradient in desert zones, highlighting the potential differentiation of microbial interactions and niche sharing under various levels of precipitation. Additionally, the attributes of soil bacterial co-occurrence

patterns may reveal specific environmental preferences and habitat variability, indicating community stability (de Vries et al., 2018; Delgado-Baquerizo et al., 2020; Feng et al., 2021). Microbial communities assemble through deterministic and stochastic processes (Pan et al., 2022). Deterministic process encompasses environmental filtering and biotic interactions, whereas stochastic process refers to random demographic fluctuations (Zhang et al., 2019). The significance of these processes can be assessed by analyzing the fit of random models (e.g., the neutral community model (NCM)) or by examining deviations from the expected outcomes (e.g., the null model). Recent studies have utilized these approaches to explore the co-occurrence patterns of microorganisms and the processes involved in their community assembly across a variety of habitats, including aridity gradients (Delgado-Baquerizo et al., 2018; Pan et al., 2022), forest types (Ma et al., 2016; Huo et al., 2023), and aquatic ecosystems (Needham et al., 2017; Mo et al., 2021). However, uncertainty persists regarding how soil microorganism networks and the mechanisms underlying their community assembly differ along salinity gradients.

To address these knowledge gaps, we collected soil samples along a natural salinity gradient at the edge of Ebinur Lake in Northwest China, a representative salt-affected area where soil salinity varied from light to severe. Based on 16S ribosomal RNA (16S rRNA) sequencing, we assessed multidimensional responses of soil bacterial communities to increasing salinity, including shifts in community structure, co-occurrence patterns, and assembly mechanisms. It was hypothesized that: (i) soil bacterial communities in soils with lower salinity level will display higher taxonomic

and phylogenetic diversity due to diminished osmotic stress and reduced ion toxicity; (ii) rising salinity levels will lead to a decline in the complexity and stability of bacterial co-occurrence networks, resulting in more simplified and fragmented modular structures under high salinity conditions; and (iii) the dominant assembly mechanism varies with soil salinity levels. The findings of this study will advance the understanding of how soil salinization affects soil microbial dynamics and the restoration of saline soils.

2 Materials and methods

2.1 Site description and soil sampling

This study was conducted in a transitional zone encompassing the northern bank of the Aqikesu River to the fringe of the Mutter Desert, adjacent to the Ebinur Lake (44°30′-45°29′N, 82°36′-83°16′E), Northwest China. This region exhibits an arid continental climate, with an annual mean temperature between 6.6°C and 7.8°C, an annual precipitation of less than 100.0 mm, and an annual potential evaporation exceeding 1600.0 mm. Along this transitional zone, dominant plants vary from typical salt-tolerant or riparian species (e.g., *Tamarix ramosissima* and *Populus euphratica*) to drought-tolerant species (e.g., *Haloxylon persicum* and *Haloxylon ammodendron*), with plant coverage ranging from

Fig. 1 Layout of the experimental design and representative landscape views of different soil salinity groups.

Figure 1: Fig. 1 Layout of the experimental design and representative landscape views of different soil salinity groups.

approximately 60.00% to less than 15.00%.

In June 2022, three parallel transects were established across the study zone (Fig. 1). Along each transect, nine sampling sites were selected at an average interval of 700 m. For each site, three 20 m(×)20 m quadrats were used for planting surveys, and one of the three quadrats was randomly selected for soil sampling. Within each selected quadrat, a detailed vegetation survey was conducted, including the recording of plant species composition, richness, and coverage. For soil sample collection, five soil cores (0–10 cm depth) were sampled at each site using a serpentine sampling method and pooled to form a composite sample. In total, 27 mixed soil

Fig. 1 Layout of the experimental design (a) and representative landscape views of different soil salinity groups (b–d). A1–A9, B1–B9, and C1–C9 represent the sampling sites along the three transects. LSS, lightly salinized soils; MSS, moderately salinized soils; HSS, heavily salinized soils.

samples were collected. The use of composite soil samples in this study was essential to capture the representative microbial community structure at the site level, minimizing the influence of localized microhabitats (e.g., the patchy distribution of desert plants). Each soil sample was separated into three parts: one was used to determine soil water content (SWC), the second was immediately frozen at −20.0°C for molecular analyses, and the third was retained for physical-chemical testing.

2.2 Measurement of soil physical-chemical properties and classification of soil salinity levels

Soil pH and electrical conductivity (EC) were determined in a soil–water suspension at a ratio of 1:5 (w/v) using a pH meter (PHS-3C; INESA, Shanghai, China) and a conductivity meter (DDSJ-318T; INESA, Shanghai, China). The SWC was measured using oven-drying method. The gravimetric method was utilized to evaluate soil salt content (SSC). Soil organic carbon (SOC) was determined using the $K_2Cr_2O_7$-oxidation method, and soil total nitrogen (TN) was measured using a total carbon/nitrogen analyzer (Multi C/N 3100; Analytik Jena, Jena, Germany). According to the classification standard of soil salinity in arid regions (Wang et al., 2008), we determined three groups of salinity in the soil samples based on SSC: lightly salinized soils (LSS) containing 3–6 g/kg, moderately salinized soils (MSS) containing 6–9 g/kg, and heavily salinized soils (HSS) containing >9 g/kg. Based on this classification, samples with equivalent salinity levels were considered biological replicates: 6 for LSS, 11 for MSS, and

10 for HSS (Table S1).

2.3 Soil bacterial community analysis

Soil bacterial molecular analysis was conducted using standard amplicon sequencing protocols. Briefly, 16S rRNA gene was extracted using a commercial kit (DM401-C3-P2; Nanjing Vazyme Biotech Co., Ltd., Nanjing, China). Bacterial 16S rRNA gene was amplified using universal primer sets 338F and 806R targeting the V3 and V4 regions. For each sample, triplicate Polymerase Chain Reaction (PCR) products were pooled, purified, and sequenced on an Illumina NovaSeq 6000 platform (Illumina Inc., San Diego, USA). The subsequent bioinformatic processing, including quality control, operational taxonomic unit (OTU) clustering, and taxonomic classification, was performed following the standard Quantitative Insights Into Microbial Ecology 2 (QIIME2) pipeline (Edgar, 2010; Bolyen et al., 2019). Raw sequences were deposited in the public National Center for Biotechnology Information (NCBI) database (www.ncbi.nlm.nih.gov) under accession number: PRJNA1477015.

2.4 Statistical analysis

Soil bacterial alpha-diversity, including the Chao1 and Shannon indices, and phylogenetic diversity were calculated in R (version 4.5.0) using the 'vegan' and 'picante' packages. One-way analysis of variance (ANOVA) was conducted to assess the differences in soil physical-chemical properties and bacterial diversity metrics among salinity groups. The shared and unique OTUs across salinity groups were visualized using Venn diagrams generated by the 'VennDiagram' package. The analysis and visualization of community similarity patterns were performed using principal coordinate analysis (PCoA). Permutational multivariate tests were used to assess the significance of community similarity. Relationships between soil bacterial communities and environmental variables (e.g., soil physical-chemical properties) were examined using Mantel test and partial Mantel test. Furthermore, a constrained analysis of principal coordinates (CAP) was performed to assess the impact of environmental variables on soil bacterial community composition. To minimize collinearity, we filtered soil variables by retaining those with a variance inflation factor (VIF) of less than 10.

To explore how soil salinity influences bacterial co-occurrence patterns, we independently conducted network analyses for each of the three salinity groups. Correlations were calculated using the Sparse Correlations for Compositional data (SparCC) method (Friedman and Alm, 2012). To minimize potential spurious correlations related to rare taxa, we retained OTUs that had a detection frequency >50.00% across samples within a salinity group and a mean relative abundance >0.02%. The widely used cutoffs of $|r| > 0.60$ (where r is the correlation coefficient) and

$P < 0.01$ were applied for network construction (Jiao et al., 2019; Mo et al.,

2021). Network visualization was completed using the Gephi platform (version 0.9.1). A suite of topological indices (e.g., number of nodes and edges, network diameter, and modularity) was calculated using the methods reported by Deng et al. (2012). For comparison, 500 random networks were generated under the same node and edge size using the 'igraph' package. Topological roles of species (OTUs) were evaluated using their among-module connectivity (Pi) and within-module connectivity (Zi). Following the criteria used widely (Zhou et al., 2010; Deng et al., 2012), four types of OTUs were identified: connectors ($Zi < 2.5$ and $Pi > 0.62$), module hubs ($Zi \geq 2.5$ and $Pi \leq 0.62$), network hubs ($Zi \geq 2.5$ and $Pi > 0.62$), and peripherals ($Zi < 2.5$ and $Pi \leq 0.62$). Species categorized as connectors, module hubs, and network hubs were recognized as keystone taxa (Banerjee et al., 2016).

In this study, we calculated robustness and cohesion to further quantify how salinity influences the stability of soil bacterial networks. Robustness indicates the network' s resistance to perturbations and is measured as the rate at which natural connectivity declines after the random removal of a proportion of nodes (Deng et al., 2012). Conversely, cohesion quantifies the extent of connectivity within the community (Herren and McMahon, 2017). Specifically, positive cohesion arises from positive correlations and reflects cooperative interactions among species, whereas negative cohesion can indicate competitive interactions within the community (Yuan et al., 2021). Previous research has indicated that increases in negative correlations or reductions in positive associations are associated with more stable microbial communities (Fu et al., 2022). Thus, the ratio of absolute negative cohesion to positive cohesion serves as an indirect indicator of network stability. Further details regarding the meaning and methodologies of robustness and cohesion are available in Yuan et al. (2021).

Two complementary approaches were used to assess the contributions of stochastic and deterministic processes to community assembly across soil salinity groups. Initially, the NCM was applied to investigate the impacts of random dispersal. This model was implemented using the 'MicEco' package, with the goodness-of-fit (R^2) indicating the fraction of variance attributed to neutral processes, and Nm representing the dispersal rate within communities. Following this, a null model analysis was used to quantitatively disentangle the relative impacts of stochastic and deterministic processes (Stegen et al., 2013). Using the 'picante' package, the β nearest taxon index (βNTI) and Bray–Curtis-based Raup–Crick (RCbray) values were calculated. Community assembly processes were inferred as follows: homogeneous selection or heterogeneous selection was assigned when $|\beta\text{NTI}|$ exceeded 2; when $|\beta\text{NTI}|$ was below 2, the process was classified as homogeneous dispersal if RCbray was less than -0.95, dispersal limitation if RCbray was greater than 0.95, and undominated process if RCbray fell between -0.95 and 0.95.

3 Results

3.1 Variations in soil physical-chemical properties along the salinity gradient

The key soil and plant community characteristics along the sampling transect are summarized in Table S1. SSC ranged from 3.56 ((±)1.18) to 26.46 ((±)2.96) g/kg, with LSS situated in the desert fringe, HSS near the riverside, and MSS located in the intermediate zone. All soils were alkaline with pH values exceeding 8.20, which did not differ significantly among the three salinity groups ($P > 0.05$). In contrast, SWC showed considerable fluctuations, but no marked differences were observed between LSS and MSS ($P > 0.05$). Regarding soil nutrients, SOC ranged from 2.14 ((±)0.31) to 10.44 ((±)2.65) g/kg, with significantly higher levels in HSS than in LSS and MSS. TN exhibited a similar trend to that of SOC.

3.2 Soil bacterial community diversity and structure

From all soil samples, a total of 1,607,226 high-quality nucleotide sequences were obtained, and 2462 unique OTUs were identified (Fig. 2). More unique OTUs were identified in LSS and HSS (Fig. 2b). Soil bacterial communities were dominated by six phyla, which collectively accounted for nearly 90.00% of the total relative abundance. These included Proteobacteria (25.38%),

Firmicutes (17.92%), Actinobacteria (17.90%), Bacteroidetes (12.87%), Acidobacteria (9.31%), and Chloroflexi (6.22%). Additionally, a clear salinity-driven distribution was observed: Firmicutes were significantly enriched in sites with HSS, whereas Actinobacteria were significantly enriched in sites with LSS. Statistically, the abundances of Firmicutes and Cyanobacteria tracked positively with SSC ($P<0.05$), whereas Actinobacteria, Acidobacteria, and Chloroflexi declined linearly as SSC increased ($P<0.05$; Table S2). The remaining two dominant phyla, Bacteroidetes and Proteobacteria, displayed no significant associations with the measured environmental factors ($P>0.05$).

Fig. 2 Soil bacterial community composition across three salinity groups. (a), average relative abundance of major bacterial phyla in total soil samples and soils across three salinity groups (LSS, MSS, and HSS); (b), Venn diagram showing shared and unique bacterial operational taxonomic units (OTUs) among the three salinity groups. The number and percentage of shared and unique OTUs are indicated in the Venn diagram.

The bacterial phylogenetic diversity, as well as the Shannon and Chao1 indices, showed a significant linear decrease with increasing salinity levels (Fig. 3). Although LSS and MSS showed no significant difference, HSS indicated a marked reduction in diversity indices. For example, the mean Chao1 index values in LSS and MSS were 1884.65 and 1779.56, respectively, but it dropped sharply to 1515.11 in HSS. The PCoA results (Fig. S1) revealed clear separation among the bacterial communities across the three soil salinity groups with each forming

a distinct cluster, indicating structural divergence. This divergence was further supported by dissimilarity tests (Table S3), including multi-response permutation procedure (MRPP: A=0.49 (A is the chance corrected within-group agreement statistic), P<0.01), analysis of similarities (ANOSIM: R=0.78 (R is the between-group separation effect size), P<0.01), and permutational multivariate analysis of variance (PERMANOVA: R^2=0.54 (R^2 is the coefficient of determination), P<0.01).

3.3 Effects of environmental factors on soil bacterial structure

According to the Mantel test, notable correlations were observed between variations in soil bacterial community composition, and all six environmental variables retained after VIF selection, except for soil pH (Table S4). When controlling for other variables through partial Mantel test, significant associations with soil bacterial community dissimilarity were maintained for SSC (Mantel' s r=0.58, P<0.01) and SWC (Mantel' s r=0.16, P=0.04) (Table S4). SSC exhibited the highest correlation coefficient among all environmental variables, suggesting that it may be the most influential factor. This finding was further corroborated by CAP analysis (Fig. 4; Table S5), showing that SSC alone explained 32.74% of the community variation and was the only statistically significant factor in the model (P<0.01, 999 permutations).

Fig. 3 Correlations between soil salt content (SSC) and soil bacterial community diversity indices. (a), Shannon index; (b), Chao1 index; (c), phylogenetic diversity index. R^2 indicates the coefficient of determination. The shaded area denote the 95.00% confidence intervals. The subplot within each panel shows the difference in each diversity index across three salinity groups. In each boxplot, the central line indicates the median, and the box bounds the interquartile range (IQR). Whiskers extend to the most extreme data points within 1.5×IQR. Different lowercase letters above boxplots indicate significant differences at the $P < 0.05$ level using Tukey' s post hoc test.

Fig. 4 Constrained analysis of principal coordinates (CAP) for assessing the relationship between soil bacterial communities across three salinity groups and main environmental variables. SWC, soil water content; C/N, ratio of soil carbon to nitrogen. CAP1, the first axis of CAP; CAP2, the second axis of CAP.

3.4 Characteristics of soil bacterial co-occurrence networks under various soil salinity levels

To explore potential interactions among microbes, we constructed bacterial co-occurrence networks for each distinct soil salinity group and compared with random networks. The structural attributes of the three empirical networks, including average path length (APL), clustering coefficient, and modularity, were all significantly higher than those of the random networks (Table 1). This indicated that soil bacterial co-occurrence networks are non-random and exhibit small-world structure, scale-free distribution, and modularity.

The topological features of soil bacterial co-occurrence networks exhibited significant differences across salinity groups (Table 1; Fig. 5). With increasing soil salinity levels, key

metrics, including node, edge, and average degree counts, showed a declining trend in the order LSS>MSS>HSS (Table 1). In contrast, the APL (4.57) reached its maximum in the HSS network. Within the conceptual framework of microbial co-occurrence networks, features such as a larger number of nodes and edges, a higher clustering coefficient, and a shorter APL indicated greater network complexity and stability. Accordingly, the LSS network exhibited the highest network complexity, followed by the MSS network, whereas the HSS network was identified as the simplest. Furthermore, the network stability (calculated as the absolute value of negative cohesion divided by positive cohesion) was notably lower in the HSS network (0.65 ± 0.03) compared with the LSS (0.83 ± 0.01) and MSS (0.81 ± 0.01) networks (Fig. 5d). Additionally, when subjected to a simulated loss of species at random, the LSS (slope: -0.50) and MSS (slope: -0.54) networks maintained a greater proportion of nodes compared with the HSS network (slope: -0.31) (Fig. 5e). These findings collectively suggested that the stability of the soil bacterial community networks diminishes with rising salinity levels. Regarding the topological roles of individual nodes, 8, 38, and 5 keystone species (OUTs) were identified in the LSS, MSS, and HSS networks, respectively (Fig. 5f). However, no keystone nodes were shared across salinity groups, suggesting that soil salinity also affect the soil bacterial community networks at the level of keystone nodes.

Table 1 Topological properties of the random and empirical networks of soil microbial communities across three salinity groups

Salinity group	Node	Link	AD	ACCr	APLr	NDr	Mr
LSS	751	7310	19.47	0.05 ± 0.01	2.57 ± 0.02	5.02 ± 0.15	0.18 ± 0.01
MSS	750	5651	15.07	0.04 ± 0.01	2.74 ± 0.01	5.41 ± 0.51	0.21 ± 0.01
HSS	303	748	4.94	0.02 ± 0.03	3.69 ± 0.02	7.97 ± 0.73	0.43 ± 0.01

Salinity group	Me	PER (%)	NER (%)	ACCe	APLe	NDe	ADS
LSS	0.70	57.67	42.32	0.52	4.54	10.34	0.03
MSS	0.60	58.29	41.71	0.44	3.44	8.05	0.02
HSS	0.71	68.04	31.95	0.36	4.57	2.00	0.02

Note: AD, average degree; ACCr, average clustering coefficient of random networks; APLr, average path length of random networks; NDr, network diameter

Fig. 5

Figure 2: Fig. 5

of random networks; Mr, modularity of random networks; Me, modularity of empirical networks; PER, positive edge ratio; NER, negative edge ratio; ACCe, average clustering coefficient of empirical networks; APLe, average path length of empirical networks; NDe, network diameter of empirical networks; ADS, average density. # means that 100 random networks were generated by randomly rewiring all the links of a corresponding empirical network with identical numbers of nodes and links. Values for the random network indices are the mean values and standard deviations from 500 random networks.

3.5 Soil bacterial community assembly under different salinity levels

Stochastic process accounted for 27.40%, 36.30%, and 2.10% of the variance in soil bacterial communities in LSS, MSS, and HSS, respectively (Fig. 6). This suggested that stochastic process plays a considerable role under low salinity conditions, and its contribution diminishes as soil salinity increases. The results of the null-model further showed that the proportion of $|\beta$NIT$|$ values>2 was 28.57% in LSS and 20.00% in MSS, respectively, indicating that stochastic process, especially dispersal limitation, plays a major role in soil bacterial community assembly under low and mediate salinity conditions. In contrast, this proportion increased sharply to 66.66% in HSS, suggesting the predominance of deterministic process. Additionally, heterogeneous selection was identified as the driving factor behind the deterministic framework. Notably, irrespective of whether random or deterministic factors mainly influenced soil microbial community construction, the random process was predominantly linked to dispersal limitation, showing a decreasing trend as soil salinity increased. On the other hand, the deterministic process, which was largely driven by heterogeneous selection, exhibited a slight initial decrease but a significant overall increase with rising soil salinity levels.

Fig. 5 Co-occurrence networks and stability characteristics of soil bacterial communities across three salinity groups. (a–c), network structure in different salinity groups; (d and e), difference in stability and robustness of soil bacterial co-occurrence networks among salinity groups; (f), topological roles of soil bacteria. In Figure 5a–c, node size is proportional to degree; colors represent soil bacteria at the phylum level. Pink and blue edges indicate positive and negative correlations, respectively. In Figure 5d and e, the network stability was calculated as the absolute value of negative cohesion divided by positive cohesion. Robustness of each network was assessed by the slope of the fitted line between the proportion of removed nodes and the proportion of remaining nodes. In each boxplot, the central line indicates the median, and the box bounds the IQR. Whiskers extend to the most extreme data points within 1.5×IQR. Circles within and outside the box represent individual data points; circles beyond

Fig. 6

Figure 3: Fig. 6

the whiskers are outliers. Different lowercase letters above boxplots indicate significant differences at the $P<0.05$ level using Tukey' s post hoc test.

4 Discussion

4.1 Variations in soil bacterial structure under various salinity levels

The findings of this study indicated that changes in soil salinity significantly affect the structure of soil bacterial communities along this small-scale salinity gradient. In particular, a reduction in the alpha-diversity of soil bacterial communities is associated with increased soil salinity levels. Similar patterns have been reported in both arid and semi-arid soils (Zhang et al., 2019; Wei et al., 2024) and wetland environments (Zhang et al., 2021; Fang et al., 2025). The trend of decreasing soil bacterial community diversity with increasing salinity levels is attributable to higher extracellular osmotic pressure in high-salinity environments, potentially leading to cellular dehydration or the inactivation of microorganisms that cannot endure elevated salinity conditions (Rath et al., 2019; Fang et al., 2025). Additionally, elevated levels of specific ions, such as sodium and chloride, may exert a direct toxic impact on particular microbial species (Rath et al., 2016; Fang et al., 2025), providing an additional mechanism underlying the observed decline in soil bacterial community diversity.

Fig. 6 Relative importance of deterministic and stochastic processes in soil bacterial community assembly. (a), variations of the β nearest taxon index (βNTI) in bacterial communities in different soil salinity groups; (b and c), contributions of different ecological processes to soil bacterial community assembly in different soil salinity groups; (d–f), fit of the bacterial neutral community model (NCM) in LSS, MSS, and HSS, respectively. In Figure 6a, the central line in each subplot indicates the median, and the box bounds the IQR. Whiskers extend to the most extreme data points within 1.5×IQR. Circles within and outside the box represent individual data points; circles beyond the whiskers are outliers. In Figure 6d–f, the green dotted lines indicate the reference lines where $|\beta\text{NTI}|=2$; points falling between them represent the dominance of stochastic process. The best fit of NCM is shown by the blue solid line, and the blue dotted lines indicate the 95% confidence intervals of the model predictions. Green and orange points represent OTUs that occurred more frequently and less frequently than predicted, respectively. R^2 indicates the goodness-of-fit of NCM and Nm represents the dispersal rate within communities.

The progressive decline in soil bacterial community diversity similarity with increasing salinity levels indicated that salinity serves as a key environmental filter in shaping soil bacterial community composition (Fig. S2). This community-level response was further evidenced by the variation in taxa-specific abundances,

in which the abundances of Firmicutes and Bacteroidetes increased significantly with salinity, whereas those of Actinobacteria and Gemmatimonadetes were reduced (Fig. 2). Such divergent responses among major bacterial phyla are consistent with previous observations in diverse saline environments (Hollister et al., 2010; He et al., 2024), and likely result from differences in physiological traits and salt tolerance across taxa (Zhang et al., 2024). For instance, the success of Firmicutes under elevated salinity conditions, as observed in this study, is related to their distinct traits, such as Gram-positive status, thick cell walls, and the ability to produce stress-resistant spores, enabling them to endure harsh conditions (Van Horn et al., 2014). Several well-recognized halotolerant bacteria exhibit a strong preference for high-salt niches because of their ability to produce compatible solutes for osmotic balance (Chen et al., 2022) or halophilic enzymes to maintain stable resistance (Liszka et al., 2012). In contrast, Acidobacteria, which often exhibit opportunistic response to resource availability (Maestre et al., 2015), are presumably replaced by Firmicutes and Bacteroidetes as salinity increases.

Disentangling how individual environmental factors influence soil microbial community

composition is challenging because these factors often co-vary (Rath et al., 2019). In arid regions, for example, high soil salinity frequently co-occurs with low moisture content and elevated pH (Zhang et al., 2019). Considering that microbial cells largely comprise water, a deficit in soil water restricts the mobilization of microbial resources within the soils (Banerjee et al., 2016) and imposes direct physiological stress on microorganisms (Zhang et al., 2021). A controlled experiment integrating salinity and moisture factors revealed that the negative impact of reduced water availability on bacterial growth intensifies with increasing salt stress, suggesting that aridity amplifies the effect of salinity on soil microbial communities (Rath et al., 2017). However, in this study, the relationship between soil moisture variation and bacterial community structure divergence was weak, underscoring the more dominant role of soil salinity in bacterial community divergence. Similarly, although soil pH is widely identified as a key driver of soil microbial communities (Fierer and Jackson, 2006; Zhou et al., 2017; Bahram et al., 2018), it has a limited impact in our study. This result aligns with previous findings in alkaline desert ecosystems (Fierer et al., 2012; Zhang et al., 2019). The limited response of soil bacterial community structure to pH can be explained by two main reasons: first, the range of soil pH in this study was relatively narrow (8.22–8.91), likely limiting its ecological influence; and second, long-term exposure to highly alkaline environments may have led to microbial adaptation or diminished sensitivity to pH variation (Maestre et al., 2015). Collectively, these results suggest that soil salinity represents a critical factor influencing soil microbial community structure across desert saline–alkaline soils. Moreover, these findings provide deeper insights into areas affected by extreme environments, such as deserts. Although soil microorganisms in such habitats have already undergone selection for drought or high temperature tolerance, they can still be clustered by salinity, highlighting the potential role

of localized environmental heterogeneity in shaping soil bacterial community composition.

4.2 Variations in soil bacterial co-occurrence patterns under various salinity levels

Previous research has shown that high levels of stress can weaken soil microorganism associations and thereby compromise the stability of bacterial community networks (Neilson et al., 2017; Feng et al., 2021; Hernandez et al., 2021; Wei et al., 2024). The results of this study support this well-documented pattern of reduced bacterial network complexity under salinity stress, as evidenced by declines in key topological parameters (e.g., total links, average degree, and clustering coefficients) and total cohesion as soil salinity increases (Table 1). Additionally, the diminished robustness of soil microbial co-occurrence networks under high salinity level further supports destabilization (Fig. 6), reflecting a diminished capacity of soil bacterial communities to resist disturbances such as species loss. Notably, compared with soil microbial networks in low-salinity environments, the connections declined remarkably in MSS, but the number of nodes remained unchanged. This observation suggests that, in addition to microbial diversity, shifts in community composition and environmental conditions play pivotal roles in shaping the complexity of soil microbial networks. Interestingly, the highest modularity was observed in HSS, in which soil microbial network stability was lowest. This observation is consistent with the results of Zhang et al. (2021) and Li et al. (2023), but contrasts with reports that associate higher modularity with greater network stability (Hernandez et al., 2021; Wei et al., 2024). Based on the ecological meaning of modularity, an increased modularity combined with fewer nodes, as observed in HSS, suggests a soil microbial structure characterized by more tightly connected internal connections within limited modules and increased isolation, namely a more simplified and fragmented network structure, thus supporting the second hypothesis. Diminished connectivity between modules may threaten the network's overall stability (Wu et al., 2016; Li et al., 2021). More importantly, because modules are typically regarded as potential functional groups within soil microbial communities (Li et al., 2023), increased modularity may reflect greater niche partitioning and functional specialization.

Species interactions, as demonstrated by positive and negative correlations within co-occurrence networks, are critical in shaping soil microbial communities and influencing their

stability (Hernandez et al., 2021). Positive associations typically signify cooperative relationships, such as cross-feeding or mutualism. In contrast, negative correlations generally reflect competition for scarce resources or contrasting niche preferences (Shi et al., 2016; Wei et al., 2024). The findings of this study showed that positive correlations among soil microbial taxa increase with increasing salinity levels (Table 1), implying that soil microbial communities may adapt to environmental stress by fostering inter-species collaboration, a pattern

that aligns with the "stress gradient hypothesis" (Gao et al., 2022; Yang et al., 2022). Such cooperative interactions may allow soil microorganisms to assist one another in mitigating salinity stress by improving nutrient utilization and facilitating energy and information exchange within the community (Dong et al., 2024). From a systemic equilibrium perspective, however, intensified microbial cooperation could destabilize microbial networks due to cascading effects of positive interactions (Yuan et al., 2021). Nonetheless, although soil microbial networks are frequently used to infer interactions among microorganisms, the observed patterns do not necessarily represent real biological associations (Ma et al., 2016; Fu et al., 2022). In future research, integrated approaches that combine network inference with experimental validation are required to clarify the precise mechanisms by which salinity influences microbial interactions (Fang et al., 2025).

4.3 Variations in soil bacterial community assembly under various salinity levels

The ecological assembly of soil microbial communities has been a central topic in ecology, with a longstanding debate concerning the relative importance of deterministic versus stochastic processes (Stegen et al., 2013; Zhou and Ning, 2017). The findings of this study revealed a distinct transition in the interplay between these two processes along the salinity gradient. Stochastic process played a predominant role in LSS and MSS; however, its contribution significantly diminished in HSS (Fig. 6). This indicated that increasing salinity strengthens deterministic selection, a pattern also observed in aquatic environments (Zhang et al., 2021; He et al., 2024).

Under low salinity conditions, stochastic assembly process is reinforced by multiple factors. First, reduced salt stress enables soil microbes to reallocate metabolic resources from stress adaptation to growth and reproduction (Mo et al., 2021), thereby diminishing the significance of deterministic process. Additionally, considering the high functional redundancy and prevalence of rare species typical of soil microbial communities (Louca et al., 2018), stochastic process may be more important in environments with higher bacterial alpha diversity (Zhang et al., 2021; Wei et al., 2024), as observed in sites with low and mediate salinity levels (Fig. 3). Furthermore, water scarcity in these regions fragments resources into isolated patches and creates harsh barriers to dispersal, further reinforcing the role of random drift (Manzoni et al., 2012). In contrast, under the extreme salt stress present in sites with high salinity level, selection pressure intensifies, eliminating many bacteria unable to adapt to high-salt environments. Only microorganisms possessing specific traits (e.g., the "salt in" and "salt out" strategies) can survive, rendering deterministic filtering the overriding assembly process (Stegen et al., 2013; Mo et al., 2021; Fang et al., 2025). Consequently, the contribution of deterministic process increases with salinity levels. Furthermore, heterogeneous selection is dominant, implying higher phylogenetic turnover than expected (Mo et al.,

2021). Although this study identifies soil salinity as the primary driver of soil bacterial community assembly, the specific pathways remain to be elucidated. Future studies incorporating detailed measurements of ion composition and nutrient availability are required to disentangle these mechanisms.

5 Conclusions

In this study, the impacts of soil salinity on the structure, co-occurrence networks, and assembly processes of soil bacterial communities along a small-scale salinity gradient in an arid environment (the Ebinur Lake) were examined and quantified. The increase in soil salinity levels led to a decrease in taxonomic diversity and phylogenetic diversity, and an increase in the relative

abundance of salt-tolerant phyla (e.g., Firmicutes and Bacteroidetes). In addition, soil salinity simplified and destabilized the co-occurrence networks of soil bacterial communities. The transition toward deterministic assembly under high salinity condition suggests that strong environmental filtering overrides stochastic process, whereas an increase in positive correlations indicates a potential trend toward microbial cooperation under salt stress conditions. These findings collectively provide a mechanistic framework for soil microbial responses to salinization, spanning from taxonomic shifts to assembly principles, thereby providing key insights into potential outcomes for dryland ecosystems facing increased salt stress. Future work should integrate multi-omics and manipulative experiments to unravel the underlying molecular mechanisms and uncover the actual ecological interactions in arid regions.

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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Author contributions

Conceptualization: MOU Na, ZHANG Yu, MA Jie; Methodology: MOU Na, ZHANG Yu; Formal analysis: MOU Na, ZHANG Yu, MA Jie; Writing - original

draft and preparation: MOU Na, ZHANG Yu; Writing - review and editing: LIU Ran, XU Guiqing; Funding acquisition: MA Jie, LIU Ran, XU Guiqing; Supervision: MA Jie, XU Guiqing. All authors approved the manuscript.

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Appendix

Table S1 Soil physical-chemical properties and dominant plant species at 27 sampling sites across three salinity groups

Salinity group	Replicates	Sampling site	pH	EC (dS/m)	SWC (%)	SSC (g/kg)
LSS	6	A8–A9, B8–B9, and C8–C9	8.67 ± 0.12	0.35 ± 0.14	1.75 ± 0.10	3.56 ± 1.18
MSS	11	A5–A7, B4–B7, and C4–C7	8.53 ± 0.06	0.52 ± 0.06	1.74 ± 0.01	7.59 ± 0.60

Salinity group	Replicates	Sampling site	pH	EC (dS/m)	SWC (%)	SSC (g/kg)
HSS	10	A1–A4, B1–B3, and C1–C3	8.58 ± 0.04	6.00 ± 0.97	3.50 ± 0.51	26.46 ± 2.96
All	27		8.58 ± 0.04	2.51 ± 0.63	2.34 ± 0.21	13.65 ± 2.37

Salinity group	SOC (g/kg)	TN (g/kg)	C/N	Coverage (%)	Dominate species
LSS	2.14 ± 0.31	0.32 ± 0.03	6.57 ± 0.32	20.50±3.10	*Haloxylon persicum* and *Haloxylon ammodendron*
MSS	2.87 ± 0.11	0.40 ± 0.02	7.23 ± 0.39	31.52±2.63	*Reaumuria songarica*, *Haloxylon ammodendron*, *Seriphidium santolinum*, *Alhagi sparsifolia*, and *Reaumuria songarica*

Salinity group	SOC (g/kg)	TN (g/kg)	C/N	Coverage (%)	Dominate species
HSS	10.44±2.65	1.07 ± 0.19	8.86 ± 0.82	44.60±3.53	*Tamarix ramosissima*, *Populus euphratica*, *Apocynum venetum*, *Phragmites australis*, and *Nitraria tangutorum*
All	5.52 ± 1.12	0.63 ± 0.09	6.57 ± 0.32	33.94 ± 2.52	

Note: LSS, lightly salinized soils; MSS, moderately salinized soils; HSS, heavily salinized soils; EC, electrical conductivity; SWC, soil water content; SSC, soil salt content; SOC, soil organic carbon; TN, total nitrogen; C/N, ratio of soil carbon to nitrogen. Data are presented as mean±standard error. Different lowercase letters within the same column indicate significant differences among salinity groups (P<0.05).

Table S2 Correlations between the main soil bacterial phyla and environmental variables

Phylum	pH	EC	SOC	TN	SWC	C/N	SSC	Plant coverage
Acidobacteria	−0.22	−0.57**	−0.35	−0.39*	−0.43*	−0.21	−0.57**	−0.48*
Actinobacteria	0.05	−0.75**	−0.72**	−0.73	−0.52**	−0.33	−0.80**	−0.66**
Bacteroidetes	0.13	−0.02	0.10	0.11	0.06	0.07	0.05	0.21
Chloroflexi	0.21	0.63*	0.43*	0.54	−0.51**	−0.12	−0.51**	−0.33
Cyanobacteria	0.12	0.58**	0.38	0.45*	0.51**	0.10	0.55**	0.33
Firmicutes	0.10	0.63**	0.51*	0.44*	0.56**	0.36	0.63**	0.38
Gemmatimonadetes	−0.22	0.51**	0.50*	0.43*	−0.73**	−0.31	−0.68**	−0.54*
Proteobacteria	0.06	−0.08	−0.04	0.03	0.01	−0.24	−0.08	−0.06
Verrucomicrobia	−0.20	0.08	0.31	0.30	0.12	0.01	0.23	0.13

Note: , P*<0.05 level; **, P<0.01 level.

Fig. S1 Principal coordinate analysis (PCoA) of soil bacterial communities across three salinity groups based on Bray–Curtis dissimilarity. LSS, lightly salinized soils; MSS, moderately salinized soils; HSS, heavily salinized soils; PCoA 1, the first axis of PCoA; PCoA 2, the second axis of PCoA.

Table S3 Dissimilarity tests of soil bacterial community between different salinity groups

Test method	Statistic	All groups	LSS versus MSS	LSS versus HSS	MSS versus HSS
MRPP	Delta	0.28	0.44	0.57	0.50
MRPP	A	0.49	0.09	0.18	0.31
MRPP	P	<0.01	<0.01	<0.01	<0.01
ANOSIM	R	0.78	0.66	0.94	1.00
ANOSIM	P	<0.01	<0.01	<0.01	<0.01
PERMANOVA	R^2	0.54	0.24	0.38	0.56
PERMANOVA	P	<0.01	<0.01	<0.01	<0.01

Note: MRPP, multi-response permutation procedure; ANOSIM, analysis of similarities; PERMANOVA, permutational multivariate analysis of variance. A is the chance-corrected within-group agreement statistic, R is the between-group separation effect size, and R^2 is the coefficient of determination.

Table S4 Mantel' s correlations between soil bacterial communities and environmental variables

Environmental variable	Mantel test	Mantel test	Partial Mantel test	Partial Mantel test
Environmental variable	Mantel' s r	P value	Mantel' s r	P value
SSC	0.73	<0.01	0.58	<0.01
TN	0.59	<0.01	0.16	0.07
SWC	0.58	<0.01	0.16	0.04
SOC	0.53	<0.01	0.03	0.37
C/N	0.36	<0.01	−0.01	0.48
pH	−0.15	0.99	−0.07	0.85

Note: Partial Mantel test was used to examine the relationship between a certain factor and community composition (based on Bray–Curtis distance) while controlling for other variables.

Table S5 One-way analysis of variance (ANOVA) of the main environmental variables correlated with soil bacterial beta-diversity in constrained analysis of principal coordinates (CAP) with 999 permutations

Fig. S2 scatter plot showing the relationship between differences of soil salt content (ΔSSC) and Bray–Curtis dissimilarity of soil bacterial communities. The x-axis is ΔSSC (g/kg), the y-axis is Bray_Curtis dissimilarity, and a linear regression line with 95% confidence interval is shown. The plot annotation reads: Linear regression line; $R^2 = 0.48$, $P < 0.01$.

Figure 4: Fig. S2 scatter plot showing the relationship between differences of soil salt content (ΔSSC) and Bray–Curtis dissimilarity of soil bacterial communities. The x-axis is ΔSSC (g/kg), the y-axis is Bray_Curtis dissimilarity, and a linear regression line with 95% confidence interval is shown. The plot annotation reads: Linear regression line; $R^2 = 0.48$, $P < 0.01$.

Environmental variable	*df*	Explained variance	*F* value	*P* value
SSC	1	0.84	6.69	<0.01
SWC	1	0.19	1.53	0.05
C/N	1	0.18	1.46	0.17
pH	1	0.13	1.02	0.34
Residual	23	2.78		

Axis	*df*	Explained variance	*F* value	*P* value
CAP1	1	2.06	16.29	<0.01
CAP2	1	0.26	2.58	0.05
CAP3	1	0.17	1.38	0.32
CAP4	1	0.08	0.61	0.87
Residual	22	2.78		

Note: *df*, degrees of freedom. The model explained 38.63% of the variation (adjusted $R^2 = 0.39$) and was statistically significant ($F = 5.09$, $P < 0.01$). CAP1, the first axis of CAP; CAP2, the second axis of CAP; CAP3, the third axis of CAP; CAP4, the fourth axis of CAP.

Fig. S2 Relationship between differences of soil salt content (ΔSSC) and Bray-Curtis dissimilarity of soil bacterial communities. R^2 represents the coefficient of determination. The shaded area denotes the 95.00% confidence intervals.

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