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Environmental Stresses Constrain Soil Microbial Community Functions by Regulating Deterministic Assembly and Niche Width

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ABSTRACT

Increasing evidence indicates that the loss of soil microbial α-diversity triggered by environmental stress negatively impacts microbial functions; however, the effects of microbial α-diversity on community functions under environmental stress are poorly understood. Here, we investigated the changes in bacterial and fungal α- diversity along gradients of five natural stressors (temperature, precipitation, plant diversity, soil organic C and pH) across 45 grasslands in China and evaluated their connection with microbial functional traits. By quantifying the five environmental stresses into an integrated stress index, we found that the bacterial and fungal α-diversity declined under high environmental stress across three soil layers (0–20 cm, 20–40 cm and 40–60 cm). Metagenomic-based analyses showed that the diversity of functional genes decreased along the stress gradients. High stress enhanced the abundance of genes associated with broad functional categories (e.g., glycolysis/gluconeogenesis, TCA cycle, DNA replication/repair and cell growth/death) but reduced the abundance of genes linked to specialised functional categories (e.g., C, N, S and methane metabolism). Phylogenetic null models and niche analyses indicated that stochastic assembly processes predominated in high-diversity communities, in which bacterial and fungal taxa had a narrow ecological niche. However, in low-diversity communities, deterministic assembly processes were dominant, and taxa had wide niches, correlating with the reduction in gene abundance observed for broad and specialised functional categories. Given the essential role of the microbiome in regulating ecosystem functions, our findings suggest that low-diversity-induced deterministic community assembly processes and a wide niche under high environmental stress may regulate microbial functions. These findings emphasise the ecological mechanisms through which microbial biodiversity regulates terrestrial ecosystem functioning.

1 | Introduction

Owing to human activities and global changes, various environmental stresses (such as drought, warming, water scarcity and soil degradation) are expected to intensify in the coming decades, thus posing significant threats to ecosystem services (Zhang et al. 2021; Xiu et al. 2018; Boretti and Rosa 2019; Petrosillo et al. 2023; Isbell et al. 2017). A growing body of evidence suggests that soil microorganisms, which constitute a substantial proportion of global biodiversity, play a crucial role in maintaining ecosystem functional stability (Yan et al. 2021; Li et al. 2022; Ma et al. 2024). Most studies investigating the relationship between microbial diversity and community function have focused on local species diversity (i.e., α-diversity) because it more directly highlights the significance of soil microbial diversity loss for ecosystem functions (Cho et al. 2016; Liu et al. 2020; Wang et al. 2021). However, understanding the intrinsic mechanisms underlying the relationship between microbial diversity and community functions is crucial for comprehensively understanding the impact of species extinctions triggered by environmental stressors on ecosystem functions.

A widely accepted hypothesis is that habitats with high species α-diversity often exhibit more stable ecosystem services (Tilman et al. 1997; Duffy et al. 2017), but the intrinsic mechanisms controlling this pattern remain unclear. In general, the generation of diversity and function in spatially distributed soil microbial communities over time is referred to as the community assembly process (Knelman and Nemergut 2014). Microbial community assembly is a collection of spatial and temporal processes that reflect the diversity, functional potential and responsiveness of the community to environmental change, and is mainly categorised into deterministic and stochastic processes (Stegen et al. 2013; Xun et al. 2019). Regardless of which of these two processes is dominant, community assembly determines the formation of community structure (i.e., species presence and abundance). Thus, microbial community assembly processes inevitably impact downstream ecosystem functions by influencing soil microbial diversity and composition. In addition, the niche overlap among species in high α-diversity communities creates an 'insurance effect' that buffers ecosystems against environmental fluctuations (Loreau et al. 2021). Although we believe that high α-diversity leads to functional redundancy in certain microbial functions, it remains unclear how this 'insurance effect' influences microbial functions through niche dynamics as diversity changes. Previous studies have suggested that the width of microbial niches mainly depends on the spatial turnover rate and ecological tolerance of the microbes (Fournier et al. 2020; Kivlin and Hawkes 2020). When environmental filtering intensifies, the survival of a species in a community depends on the width of the niche it occupies. Unlike specialist species, generalist species might survive by reoccupying new niches because of their high turnover rates and persistence advantages (Sriswasdi et al. 2017). Conversely, specialist species may go extinct (Pandit et al. 2009). Although recent evidence provides partial support for the intrinsic connection between microbial diversity and community function, to our knowledge, these assessments have not yet been empirically validated, particularly under multiple environmental stresses. This knowledge gap hinders a comprehensive understanding of the loss of microbial diversity and changes in associated ecological functions.

In this study, 810 standard soil samples were collected along a natural stress gradient formed by 45 grasslands in the northern Chinese Loess Plateau. These grasslands form a series of natural environmental stress gradients from southeast to northwest that include changes in plant diversity, temperature, precipitation, nutrient availability and pH, thus providing an ideal experimental model for our research. By combining process measurements with amplicon and metagenomic sequencing, we investigated the intrinsic links between community assembly mechanisms and niche processes triggered by the loss of microbial α-diversity under multiple environmental stresses. Additionally, we explored the connections between these changes and ecosystem functionality. We hypothesised that (I) the loss of microbial α-diversity will lead to the gradual domination of deterministic assembly processes along the environmental stress gradient and significantly broaden the microbial niche width, and (II) changes in deterministic community assembly processes and microbial niches, due to their crucial roles in species composition, biotic interactions and resource utilisation, may be closely related to changes in community function along the environmental stress gradient. The results provide a foundation for elucidating the relationships between soil microbial interactions and ecosystem functions under environmental stress.

2 | Materials and Methods

2.1 | Study Area and Sample Collection

The research area is located on the Loess Plateau in northern China, which falls within the semi-arid and arid climatic region. The region exhibits a decreasing trend in mean annual precipitation (MAP) (750–160 mm), mean annual average temperature (14.3°C–4.3°C), plant diversity and soil nutrient content from southeast to northwest. Based on the climatic conditions, 45 county-level grasslands were selected. The sampling sites spanned the geographic coordinates 33°43′–41°16′N and 100°54′–114°33′ E in northern China (Figure S1a).

From August to September 2020, we collected samples and conducted vegetation surveys in the study area. To minimise interference from human activities, all selected grassland sites were located at least 5 km from human settlements and at least 1 km from major roads. In each grassland, six survey points were established along a 1 km wide transect. At each point, a 1 × 1 m plot was established. Each plot was divided into three soil depths: surface (0–20 cm), subsoil (20–40 cm) and bottom layer (40–60 cm), resulting in 810 soil samples (3 depths × 6 samples × 45 grasslands). When collecting samples from each plot, soil cores were collected from five points (four corners and the centre) and thoroughly mixed to create composite samples. The samples were tagged with sampling point information on-site and then divided into two parts, with one part stored in a refrigerator at 4°C until soil physical and chemical property analyses and the other part rapidly frozen in liquid nitrogen on-site, brought back to the laboratory and

immediately stored in a −80°C freezer for subsequent DNA sequencing analysis.

2.2 | Vegetation and Soil Properties Analysis

For the plant diversity surveys, the species richness of each plot was defined as the number of different plant species present. The 810 standard soil samples stored at 4°C were sieved through a 2-mm mesh to remove roots and rocks. Subsequently, their physicochemical properties were analysed using standard methods (Bao 2000), including soil pH, soil moisture, bulk density, particle size distribution (sand, silt and clay), organic carbon, total nitrogen, mineral nitrogen (nitrate and ammonium) and available phosphorus. Climate data for all sampling points, including the mean annual temperature (MAT) and MAP, were obtained from the WorldClim database (www.worldclim.org).

2.3 | Amplicon and Metagenomic Sequencing

Amplicon sequencing was performed to analyse the bacterial and fungal communities. Following the manufacturer's instructions, total genomic DNA was extracted from the 810 soil subsamples using the FastDNA SPIN Kit (MP Biochemicals, Solon, OH, USA). Specific amplification was performed using primers 338F/806R for the bacterial 16S rRNA gene and ITS1F/ITS2 for the fungal internal transcribed spacer 1 region. Paired-end sequencing was performed on an Illumina MiSeq platform (Illumina, 2×300 bp, USA) according to standard protocols. Raw sequencing data were processed using the DADA2 method for quality control, denoising, splicing and de-chimerisation (Callahan et al. 2016). Amplicon sequence variants (ASVs) were then merged using default parameters. The featured ASV sequences were subsequently compared to reference sequences from the Silva and UNITE databases to obtain taxonomic information for each ASV (Kõljalg et al. 2013).

We selected 25 grasslands (one soil sample was randomly selected from the six plots included in each grassland), and a total of 75 samples (25 grasslands ×3 soil depths) were obtained for shotgun metagenomic sequencing (Figure S2). The total genomic DNA extracted for amplicon sequencing (as described above) was also used for metagenomic DNA sequencing on the Illumina platform (150 bp paired-end reads). The extracted DNA fragments were focused to an average size of approximately 150 bp using a Covaris M220 (Gene Company Limited, China), and blunt-end fragments were ligated to adapters with fully complementary sequencing primer hybridisation sites and prepared as paired-end sequencing libraries using the NEXTflex Rapid DNA Seq Kit (Bioo Scientific, Austin, TX, USA). Subsequently, paired-end sequencing was performed on an Illumina NovaSeq (Illumina Inc., San Diego, CA, USA) according to the manufacturer's instructions using NovaSeq reagents at Majorbio BioPharm Technology Co., Shanghai, China. For raw sequencing data, quality control was performed using Fastp (v0.20.0) to remove adaptor sequences and low-quality reads (reads with N bases reached 10 bp, a minimum length threshold of 50 bp and a minimum quality threshold of 20) (Jiao et al. 2022). The high-quality sequences were then assembled into contigs using MEGAHIT (v1.1.2), and contigs with lengths ≥300 bp were selected as the final assembly results (Wu et al. 2025). Open reading frames (ORFs) in contigs were identified using MetaGene (v 2.0.0) (Noguchi et al. 2006). A non-redundant gene catalogue was constructed using CD-HIT (v 4.6.1), applying a sequence identity threshold of 90% and a coverage threshold of 90% (Fu et al. 2012). The quality control reads were aligned to the non-redundant gene reference using SOAPaligner (v 2.21) with a 95% identity threshold (Li et al. 2008). The NR (v 20,200,604), COG (v 4.5.1), KEGG (v 94.2) and CAZy (v 8) databases (He et al. 2022) were used for annotation and classification (data analysis software information can be found in Table S1). The sequencing depths of the prepared samples ranged from 8 to 12 Gb, with an average sequencing depth of 10 Gb.

2.4 | Quantification of Multiple-Environmental Stresses

We developed a unified metric to reflect microbial patterns in response to environmental stress. Prior to quantifying the environmental stress, we conducted an initial screening of the environmental factors. Single environmental factors included the MAT, MAP, soil organic carbon (SOC), soil pH and plant diversity (PD). Given the strong influence of SOC on microorganisms and its strong correlation with other soil nutrients (Figure S3), we chose SOC as an indicator of soil nutrients. In addition, soil pH and plant diversity were chosen as important factors driving microbial parameters. The ranges of environmental factors in the different soil layers are shown in Figures S4 and S5. Subsequently, all single environmental factors were categorised into two groups. One group included parameters for which lower values corresponded to greater environmental stress on microorganisms, such as MAT, MAP, SOC and PD. The other group included parameters for which higher values corresponded to greater environmental stress on microorganisms, such as soil pH. The specific method of quantifying environmental stress is as follows.

2.4.1 | Step 1: Co-Trending Transformation of Environmental Factors

To ensure a consistent directional effect of all environmental factors on microbial stress, we conducted a co-trending transformation of soil pH. The method is outlined as follows:

$$B_{Qj} = \frac{Q_{\min}}{Q_j} \times 100 \left(Q_j \geq Q_{\min}\right) \quad (1)$$

where B_{Qj} represents the pH value of sample j after the co-trending transformation; Q_j is the pH value of sample j; and $Q_{\min}$ denotes the minimum value within the measurements for the sample. Following the co-trending transformation of soil pH, we z-standardised all single environmental factor data.

2.4.2 | Step 2: Eigenvalue Calculation

We subjected the standardised data for all individual environmental factors to PCA. The variance explained by the first axis (PCA1) varied by approximately 60% across the different soil

depths (PCA1: 59.10% (0–20 cm); PCA1: 64.90% (20–40 cm); PCA1: 60.20% (40–60 cm)). Therefore, we used the data from the first axis of the PCA as the corresponding eigenvalues.

2.4.3 | Step 3: Calculation of Multiple Environmental Stress

A larger calculated eigenvalue for a particular point indicated that the point was subjected to less environmental stress. Therefore, the following formula was used to calculate the multiple environmental stress values for each sampling point:

$$S_j = 1 - E_j \quad (2)$$

where S_j is the multiple environmental stress value of sample j and E_j is the eigenvalue of sample j obtained after normalisation in the range of 0–1. According to this formula, the maximum and minimum environmental stress values for a specific point were 1 and 0, respectively. Finally, we plotted the quantified environmental stress values on a map using ordinary kriging interpolation (Figure S1b). A consistent trend of increasing environmental stress was observed from southeast to northwest across all soil depths, with environmental stress increasing with greater soil depth.

2.5 | Statistical Analysis

Microbial α-diversity and Bray–Curtis dissimilarity were calculated using the 'vegan' package (v 2.6.2) in *R*. The distance decay rate (DDR) was calculated as the slope of the ordinary least squares regression between geographical distance and community dissimilarity (Bray–Curtis dissimilarity). Data were visualised using the 'geom_polygon' function from the 'ggplot2' package in *R*. Microbial species niche width was determined using the 'niche.width' function in the ''spaa' package for *R*, with the method set to 'levins'. The differences in the quantified environmental pressure values of the different grasslands were plotted using the ordinary kriging interpolation method. The process is analysed using the 'automap' package (v1.1.9) for *R* (Hiemstra et al. 2013).

Community assembly processes were inferred following the framework described by Stegen et al. (2013). First, the mean nearest taxon distance (MNTD) was calculated using the 'picante' package (v1.8.2) for *R*. Subsequently, a null model, as previously described, was employed to compute the β-nearest taxon index (βNTI). Significant deviations ($|\beta NTI| > 2$) indicated that deterministic processes were dominant. $\beta NTI > 2$ indicated variable selection, suggesting that phylogenetic turnover was significantly higher than expected, while $\beta NTI < 2$ indicated homogenising selection, implying that phylogenetic turnover was significantly lower than expected. Moreover, $|\beta NTI| < 2$ indicated that stochastic processes were dominant. The percentage values represent the statistical averages of the ecological process outcomes.

For metagenomic sequencing data, gene abundance within each functional category was calculated as the sum of the reads mapped to it, as described by Xun et al. (2019). To normalise the variations in sequencing depth across different samples, the dataset size was adjusted to mitigate the impact of varying sequencing depths. Subsequently, functional gene α-diversity (akin to microbial α-diversity) was computed based on the gene abundance within each functional category. An ecological network between functional categories was constructed using the 'WGCNA' package (v1.71) for *R*, following the parameters set by Fan et al. (2023). Indicator Value Analysis (IndVal), which combines the gene abundance and occurrence rate for a given gene, was performed to identify the characteristic functional genes that increased or decreased along environmental stress gradients. IndVal values were calculated using the 'indicspecies' package (v1.7.6) for *R*. All statistical analyses were conducted using *R* software (v4.3.2). All correlations were calculated using Spearman's correlation analyses. A conceptual figure (Figure 7) was created using Adobe Illustrator (v28.0).

3 | Results

3.1 | General Patterns of Soil Microbial α- Diversity Along Environmental Stress Gradients

In all habitats surveyed in this study, bacterial α-diversity (as measured by the species richness) was significantly higher than fungal α-diversity (Figure 1). We conducted a comparative analysis of the general patterns of microbial α-diversity under single and multiple environmental stressors. Environmental stress significantly affects microbial α-diversity. Although a weak correlation was observed between fungal α-diversity and MAT, significant positive correlations were observed between both bacterial and fungal α-diversity and factors such as MAP, SOC and PD (Table S2 and Figure 1a–c,e). Conversely, a significant negative correlation was observed between bacterial and fungal α-diversity and soil pH (Table S2 and Figure 1d). Under multiple environmental stressors, bacterial and fungal α-diversity significantly decreased along the environmental stress gradient at different soil depths (Table S2 and Figure 1f).

Subsequently, we estimated the distance-decay relationships of the microbial communities at different soil depths across all habitats. Although significant differences were observed in the slopes of the microbial distance decay curves between the different soil layers ($p < 0.001$, Figure S6), these slopes were relatively small (slope < 0.02), indicating a weaker decay of community similarity with geographical distance in grassland soil on the Loess Plateau.

3.2 | Responses of Community Assembly Processes and Niche Width Along Environmental Stress Gradients

To distinguish between deterministic processes ($|\beta NTI| > 2$) and stochastic processes ($|\beta NTI| < 2$) in microbial community assembly under environmental stress, we calculated the βNTI in different soil layers. The percentage values represent the statistical averages of the ecological process outcomes. The results of the null modelling analyses showed that both bacterial and fungal community assembly processes exhibited a tendency towards enhanced deterministic processes with

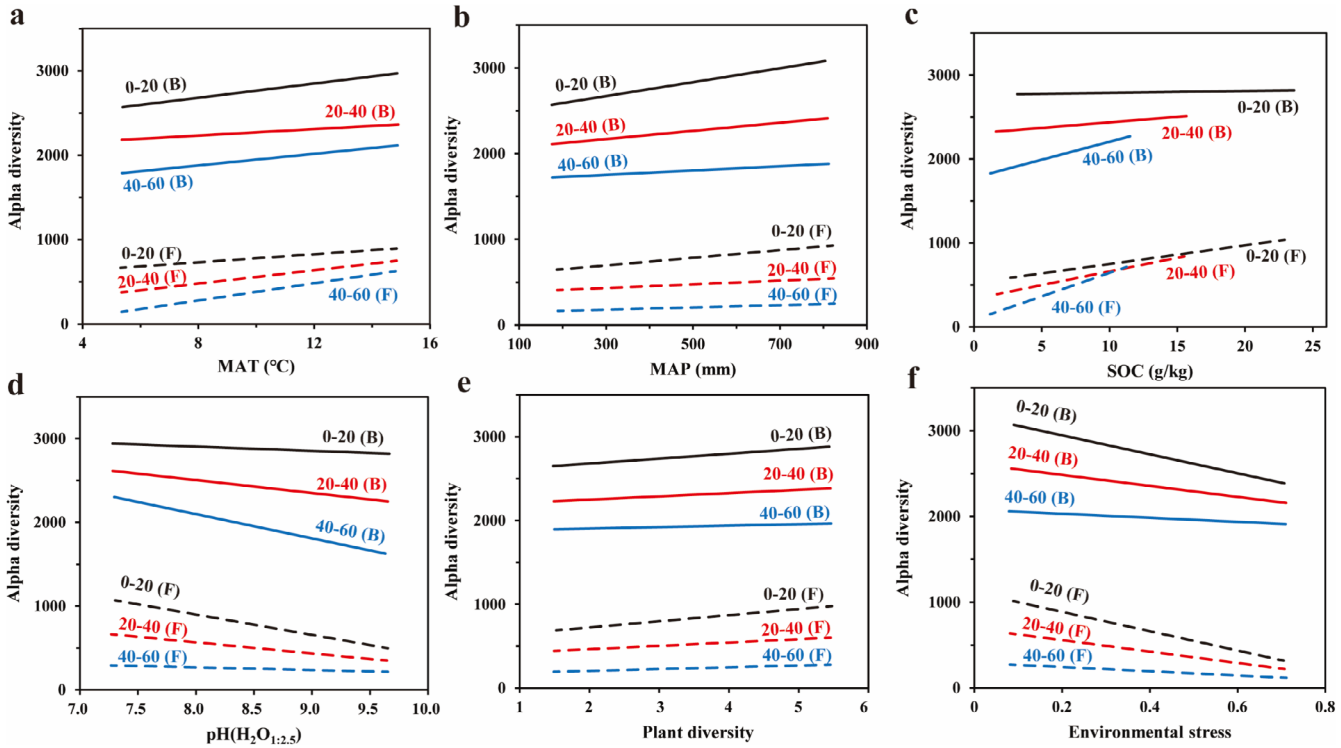

FIGURE 1 | General pattern of microbial α-diversity under a single environmental factor and stress gradient. (a–e): Single environmental factors: (a) mean annual temperature (MAT); (b) mean annual precipitation (MAP); (c) soil organic carbon (SOC); (d) pH; (e) plant diversity. (f) Stress gradients (*X*-axis represents the multiple environmental stress gradients formed by the combination of multiple environmental factors). Black, red and blue lines indicate 0–20 cm, 20–40 cm and 40–60 cm soil depths, respectively. The solid and dotted lines labelled "B" and "F" represent bacteria and fungi, respectively. The correlation coefficients with adjusted *p*-values are presented in Table S2. [Colour figure can be viewed at wileyonlinelibrary.com]

increasing environmental stress (bacteria: Figure 2a–c; fungi: Figure 2d–f, $p < 0.02$). Across soil depths, bacterial (percentage of $|\beta NTI| > 2$, 0–20 cm: 40.4%; 20–40 cm: 63.3%; 40–60 cm: 75.9%) and fungal (percentage of $|\beta NTI| > 2$, 0–20 cm: 41.1%; 20–40 cm: 59.2%; 40–60 cm: 80.7%) community assembly processes shifted from stochastic to deterministic processes (Figure 2g–i). The response of $|\beta NTI|$ values to individual environmental factors varied. Specifically, MAT, MAP, SOC and PD were significantly negatively correlated with $|\beta NTI|$ values (Table S3 and Figure S7a–c,e) while soil pH was significantly positively correlated with $|\beta NTI|$ values (Table S3 and Figure S7d).

In addition, environmental stress altered the niche widths of microorganisms. Across all habitats, the average niche width of the bacteria was significantly greater than that of the fungi (Figure 3). Specifically, environmental stress in different soil layers was significantly positively correlated with the microbial niche width (bacteria: Figure 3a–c; fungi: Figure 3d–f, $p < 0.01$). For individual environmental factors, bacterial niche width was primarily significantly correlated with pH, SOC and PD, while fungal niche width was primarily correlated with MAT and MAP (Table S4 and Figure S8).

Finally, a least-squares linear regression model was used to assess the relationship between microbial α-diversity under environmental stress in different soil layers and the $|\beta NTI|$ and niche width values. A significant negative correlation was observed between $|\beta NTI|$ values and microbial α-diversity for bacteria and fungi (bacteria, 0–20 cm: $R^2 = 0.386$, $p < 0.001$; 20–40 cm: $R^2 = 0.027$, $p < 0.05$; and 40–60 cm: $R^2 = 0.024$, $p < 0.05$, two-tailed test, Figure 4a; fungi, 0–20 cm: $R^2 = 0.080$, $p < 0.001$; 20–40 cm: $R^2 = 0.102$, $p < 0.001$; 40–60 cm: $R^2 = 0.055$, $p < 0.01$, two-tailed test, Figure 4b). Similarly, a significant negative correlation was observed between niche width and α-diversity of microorganisms (bacteria, 0–20 cm: $R^2 = 0.102$, $p < 0.001$; 20–40 cm: $R^2 = 0.101$, $p < 0.001$; 40–60 cm: $R^2 = 0.061$, $p < 0.001$, two-tailed test, Figure 4c; fungi, 0–20 cm: $R^2 = 0.159$, $p < 0.001$; 20–40 cm: $R^2 = 0.407$, $p < 0.001$; 40–60 cm: $R^2 = 0.323$, $p < 0.001$, two-tailed test, Figure 4d).

3.3 | Functional Changes in Microbial Communities Along Environmental Stress Gradients

To better estimate how the potential functions of microbial communities change under environmental stress, we conducted shotgun metagenomic sequencing analyses of the soil samples and generated microbial functional profiles across the different environmental stress gradients. We selected 16 functional categories closely associated with ecosystem services (Figure 5b) such as nutrient cycling and energy metabolism in grassland microbial systems, including carbon (C), nitrogen (N), phosphorus (P) and sulphur (S) metabolism and turnover; amino acid, lipid and nucleotide metabolism; glycolysis; the TCA cycle; and DNA replication and repair. These functional categories are crucial for maintaining the stability and health of grassland

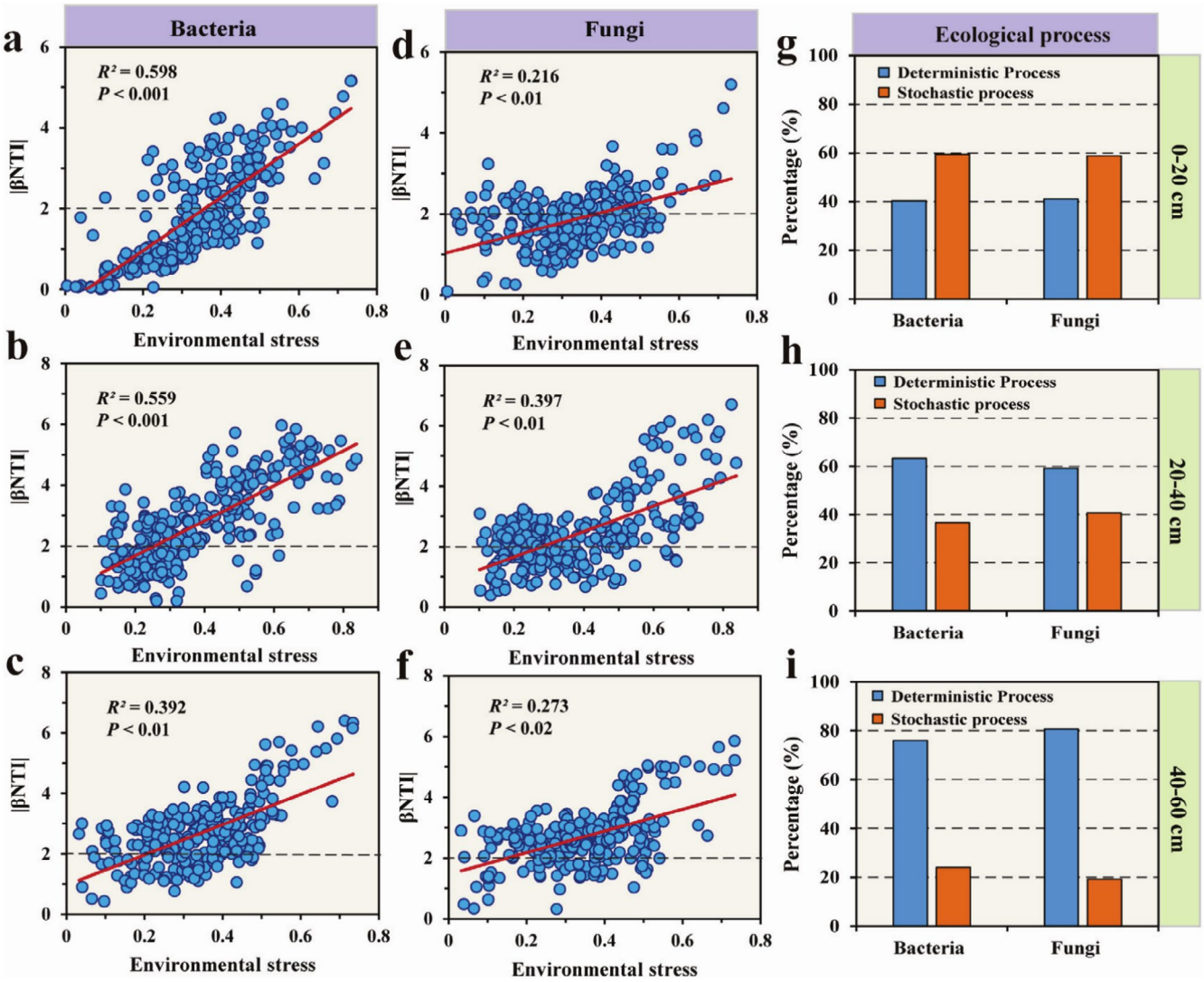

FIGURE 2 | Microbial community assembly process under environmental stress. (a–f) Relationship between |βNTI| values and environmental stress. Bacteria: (a) 0–20 cm; (b) 20–40 cm; (c) 40–60 cm. Fungi: (d) 0–20 cm; (e) 20–40 cm; (f) 40–60 cm. (g–i) Percentage values of stochastic and deterministic processes of microbial community assemblies at different soil depths (g: 0–20 cm; h: 20–40 cm; i: 40–60 cm). Linear regression model with a two-sided test was used for the statistical analysis, and adjusted *R*-squared values were used. Relationships are denoted with solid lines and fit statistics (R^2 and *p* values) for each soil depth. The red solid line indicates significant linear relations ($p < 0.05$). [Colour figure can be viewed at wileyonlinelibrary.com]

ecosystems. The abundance and diversity of all functional categories varied significantly along the environmental stress gradient; however, their responses to environmental stress differed. We employed an ecological network-based approach to identify highly correlated clusters of functional categories within the functional network to further distinguish their response patterns. Our analysis revealed two independent dimensions for microbial function (dimensions 1 and 2; Figure 5c). Dimension 1 encompassed glycolysis and gluconeogenesis, starch and sucrose metabolism, glycan biosynthesis and metabolism, DNA replication and repair, cell growth and death, nucleotide metabolism, the TCA cycle, lipid metabolism and amino acid metabolism. Dimension 2 encompassed oxidative phosphorylation, terpenoid and polyketide metabolism, xenobiotic biodegradation and metabolism, carbon fixation pathways in prokaryotes and nitrogen, sulphur and methane metabolism. Dimensions 1 and 2 are intimately linked through a '1 × 2' hub that includes lipid metabolism and amino acid metabolism.

According to ecological network partitioning, functional categories within Dimension 1 (e.g., glycolysis/gluconeogenesis, DNA replication/repair and the TCA cycle) typically encompass a broad range of functions, and their abundance becomes enriched as environmental stress intensifies (Figure 5a,b). Compared with Dimension 1, the functional categories within Dimension 2 are often carried out by narrow-range microbial populations, meaning that related genes are distributed within specific microbial taxa. Their abundance decreases in habitats with higher levels of environmental stress and nutrient constraints. For instance, functional categories related to C, N, S and methane metabolism exhibited decreasing trends along the environmental stress gradient (Figure 5a,b). It suggests that the microbes employ distinct strategies. Additionally, among the functional categories within Dimension 1, a majority of the associated genes (24.03%–53.34%) showed increased abundance as the environmental stress increased, with only a small fraction (17.58%–2.12%) showing significantly decreased abundance

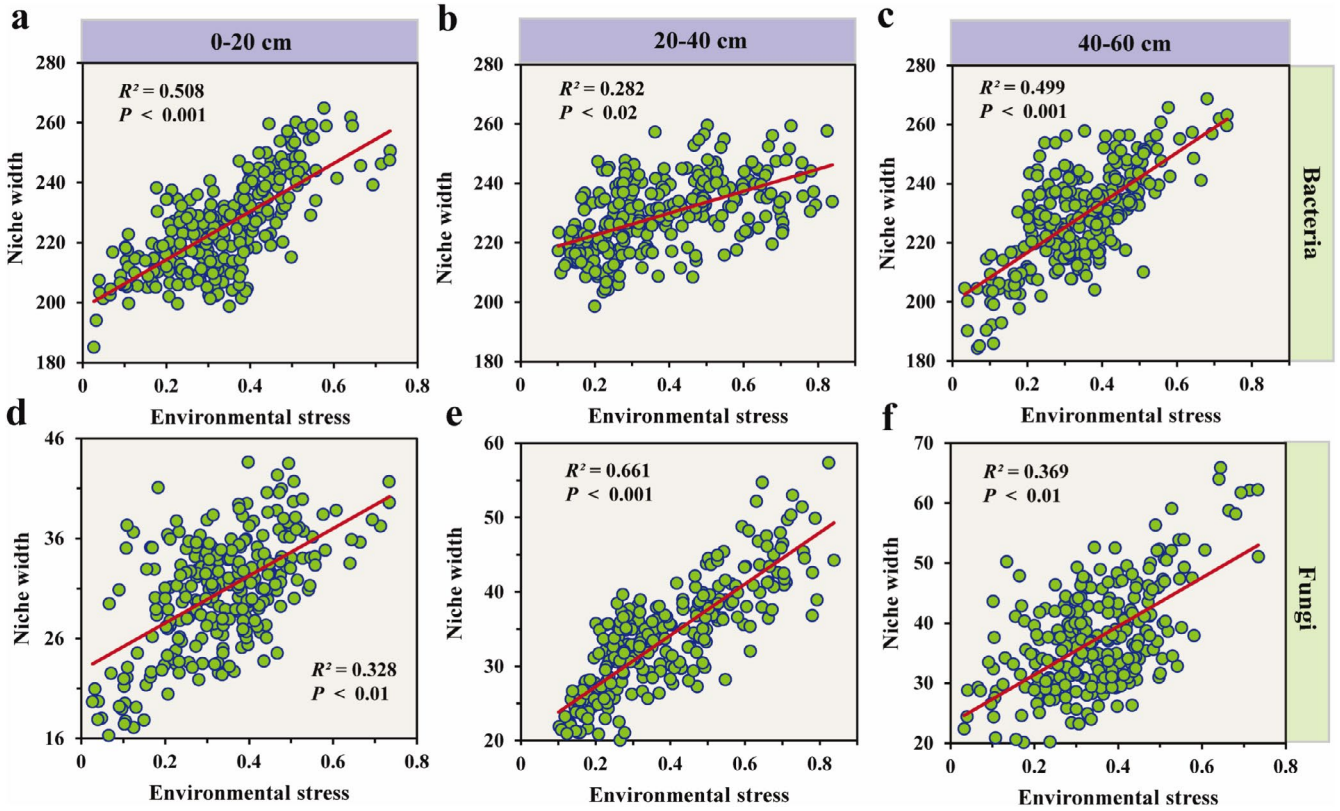

FIGURE 3 | Microbial niche width under environmental stresses. (a–f) Relationship between microbial niche width and multi-environmental stress. Bacteria: (a) 0–20 cm; (b) 20–40 cm; (c) 40–60 cm. Fungi: (d) 0–20 cm; (e) 20–40 cm; (f) 40–60 cm. A linear regression model with a two-sided test was used for the statistical analysis, and adjusted *R*-square values are presented. Relationships are denoted with solid lines and fit statistics (R^2 and *p* values) for each soil depth. The red solid lines indicate significant linear relations ($p < 0.05$). [Colour figure can be viewed at wileyonlinelibrary.com]

(Table S5). Among the functional categories within Dimension 2, 16.12%–56.88% of functional genes showed decreased abundance as the environmental stress increased, with only a small fraction (1.77%–8.02%) showing increased abundance. For these genes, the IndVal results indicated that the alcohol dehydrogenase 4 gene (*ADH4*) associated with glycolysis/gluconeogenesis (IndVal = 0.742, using the multipatt function of IndVal, $p = 0.002$) was enriched along the environmental stress gradient and represented an indicator gene in Dimension 1. In samples with higher stress levels, other genes such as the nitrite reductase gene (*NIT-6*) associated with nitrogen metabolism (IndVal = 0.897, using the multipatt function of IndVal, $p = 0.001$) were depleted along the environmental stress gradient and represented indicator genes in Dimension 2 (Table S6).

Although opposite response patterns in gene abundance were observed for the functional categories in both dimensions, gene diversity across all functional categories decreased with increasing environmental stress (Figure 5a). To further assess how environmental stress affects the relationship between community assembly and microbial functions, we examined the correlations among |βNTI| values, niche width and microbial functions. The diversity and abundance of genes within the functional categories of Dimension 2 and the diversity of genes within the functional categories of Dimension 1 exhibited a significant negative correlation with the |βNTI| values of the bacterial and fungal community assemblies and niche widths. Conversely, the gene abundance within the functional categories of Dimension 1 displayed a significant positive correlation with the |βNTI| values of the bacterial and fungal community assemblies and niche widths (Figure 6).

4 | Discussion and Conclusion

Continuing increases in environmental stress worldwide have had profound impacts on subterranean biodiversity, and these impacts are expected to intensify over the coming years (Yang et al. 2021). Although the loss of soil microbial diversity threatens the functional stability of ecosystems, the intrinsic connections between these factors remain unclear (Mori et al. 2018). In the present study, we investigated the effects of quantified environmental stressors on microbial diversity and community functions. Our findings provide critical insights into the intrinsic relationship between biodiversity and ecosystem functions. Increased environmental stress significantly reduced microbial species diversity (α-diversity) and constrained community functions by affecting subsequent community assembly processes and niche width. These results also confirm our hypothesis.

We observed that the relative abundance of functional genes within Dimensions 1 and 2 responded differently to increased environmental stress. Specifically, the relative abundance of genes in Dimension 2 associated with nitrogen, sulphur and methane metabolism, oxidative phosphorylation, terpenoid and polyketide metabolism and xenobiotics biodegradation

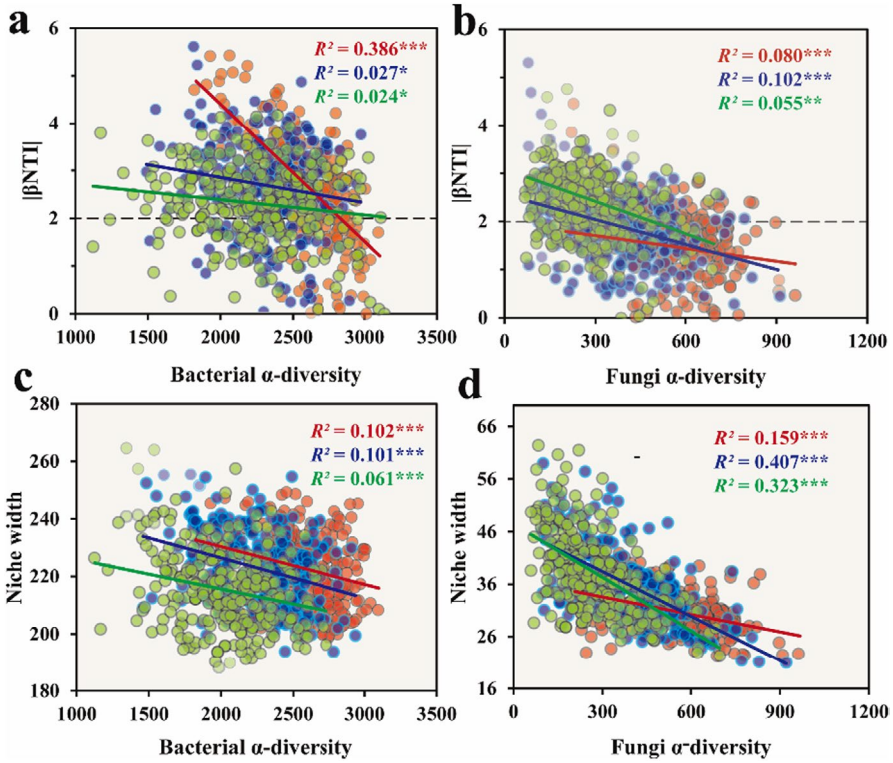

FIGURE 4 | Relationship between microbial α-diversity and community assembly (|βNTI| values) and niche width. (a, c) Bacteria; (b, d) fungi. The red, blue and green solid lines represent different soil depths (red: 0–20 cm; blue: 20–40 cm; green: 40–60 cm). A linear regression model and a two-sided test was used for the statistical analysis, and adjusted *R*-square values are presented. Relationships are denoted with solid lines ($p < 0.05$) and fit statistics (R^2 and *p* values) for each soil depth. [Colour figure can be viewed at wileyonlinelibrary.com]

decreased along the environmental stress gradient. The decline in microbial α-diversity with increasing environmental stress likely affected these specialised functions due to their typically low functional redundancy (Delgado-Baquerizo et al. 2016). Powell et al. (2015) suggested that such functional genes usually rely on narrow physiological pathways and their associated genes are distributed among specific microbial taxa (Rivett and Bell 2018). For instance, genes that encode specialised functions such as xenobiotics biodegradation/metabolism, ammonia oxidation and nitrogen fixation are carried by a small subset of microbial groups (e.g., Actinobacteria, Acidobacteria and certain taxa within Nitrospira) or occur only within some rare taxa (Singh et al. 2014; Gianfreda and Rao 2017; Deng et al. 2012; Banerjee et al. 2018). Consequently, increased environmental stress may significantly affect the abundance of these genes.

Additionally, the functional categories within Dimension 1, including DNA replication and repair, glycolysis and gluconeogenesis, the TCA cycle, lipid metabolism and amino acid metabolism, are crucial for microbial carbon and energy metabolism, for growth and reproduction (Delgado-Baquerizo et al. 2016). These categories, often referred to as broad or ubiquitous functions, are widely distributed among microorganisms and become enriched with increasing environmental stress (Delgado-Baquerizo et al. 2016). Among these broad functional categories, DNA replication and repair are the most pervasive. For instance, nearly all bacteria and fungi have evolved various DNA repair mechanisms to maintain genomic stability (Clancy 2008). Similarly, functional genes for lipid and amino acid metabolism are also widely distributed among organisms. For example, the biosynthetic processes of iso- and anteiso-fatty acids and non-essential amino acids are widespread among bacteria (Kaneda 1991; Min et al. 2002). However, the proportion of genes that increased (24.03%–25.89%) along the environmental stress gradient was only slightly higher than that of genes that significantly decreased (12.26%–17.58%). Therefore, a category of genes between specialised and broad functions should be considered. This finding aligns with previous research showing that most essential amino acid metabolic pathways are present in only a few microbial members (Xun et al. 2019; Wendisch 2007). For example, the metabolism of cycloheptane fatty acids is observed in only a limited number of bacteria (Kaneda 1991).

Although the responses of these two sets of functional categories to species diversity loss are generally consistent with most conclusions derived from laboratory culture experiments (Xun et al. 2019; Yan et al. 2017), we believe that our understanding of the underlying functional changes is affected by bias. For example, Gianfreda and Rao (2017) performed microcosm culture experiments and found that a sharp loss of α-diversity caused by dilution inoculation seemed to have no impact on soil respiration (considered a broad function). Therefore, we hypothesised that the decline in the relative abundance of specialised functional genes (e.g., methanogenesis (Kang et al. 2022), denitrification (Philippot et al. 2013) and soil mineralisation potential (Singh et al. 2014)) caused by low α-diversity led to an increased relative proportion of broad functional category genes. This, in turn, resulted in the enrichment of broad functions in communities with low species diversity. Similar to gene abundance, the gene diversity of both functional categories decreased with the loss of

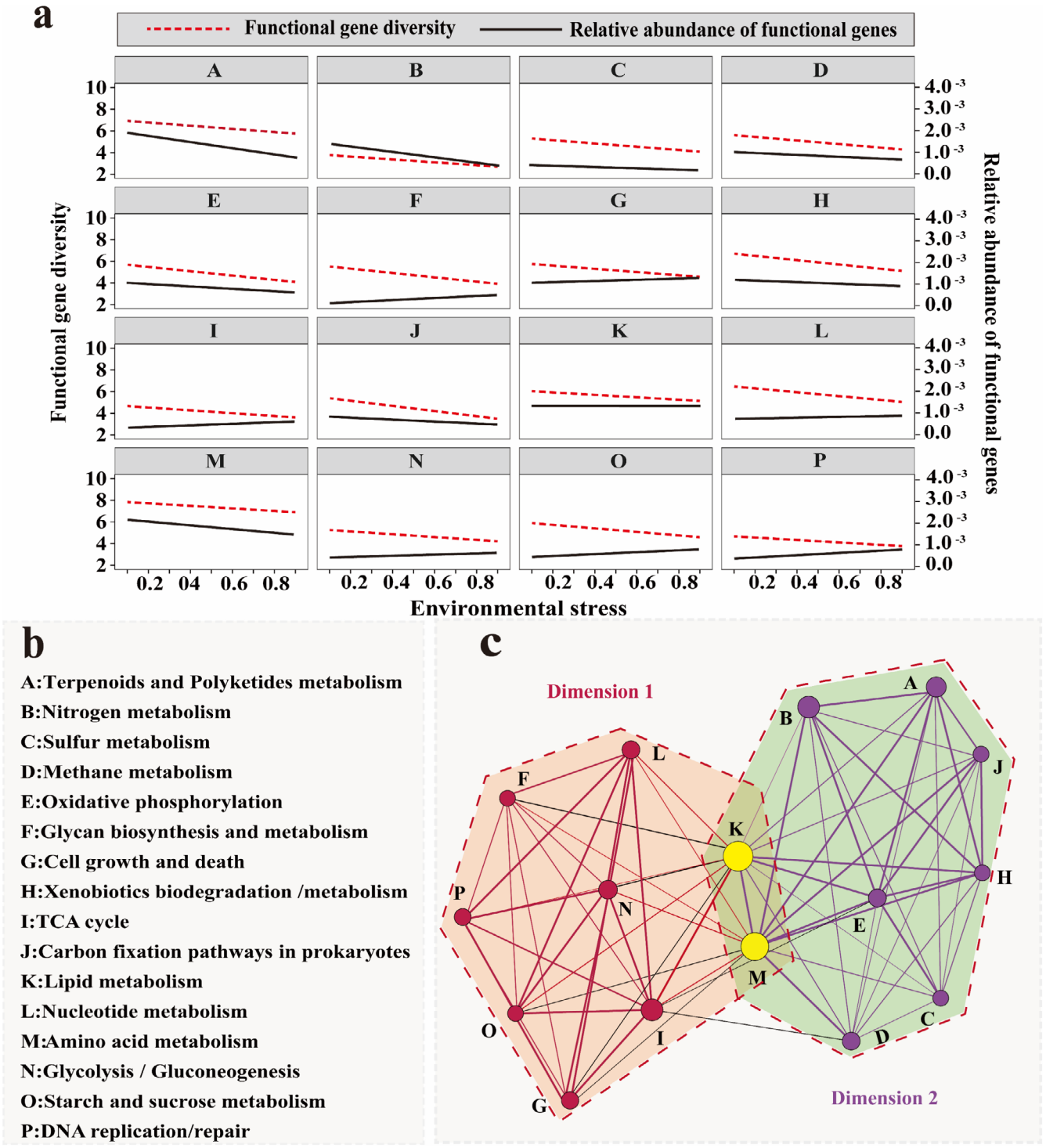

FIGURE 5 | Comparison of response patterns of gene abundance and diversity under environmental stresses. (a) Black and red lines indicate the effect of environmental stress on the relative abundance and diversity of functional genes. (b) Names of the 16 selected functional categories corresponding to the letters in the upper panel of (a). (c) Sixteen functional categories were categorised into two independent dimensions based on the ecological network of functional gene abundance. [Colour figure can be viewed at wileyonlinelibrary.com]

species diversity. This result also confirms that broad functions have greater functional redundancy than specialised functions (Eisenhauer et al. 2023).

In this study, we also found a close relationship between |βNTI| values (associated with community assembly processes) and the relative abundance of functional genes. This clearly indicates that low α-diversity often induces the dominance of deterministic community assembly processes. However, Evans et al. (2017) and Vellend et al. (2014) suggested that microbial communities with lower biomass or population sizes were more susceptible to drift (stochastic processes) or founder effects. Indeed, this dynamic was observed during the initial construction of communities with smaller population sizes and scales (Chase and

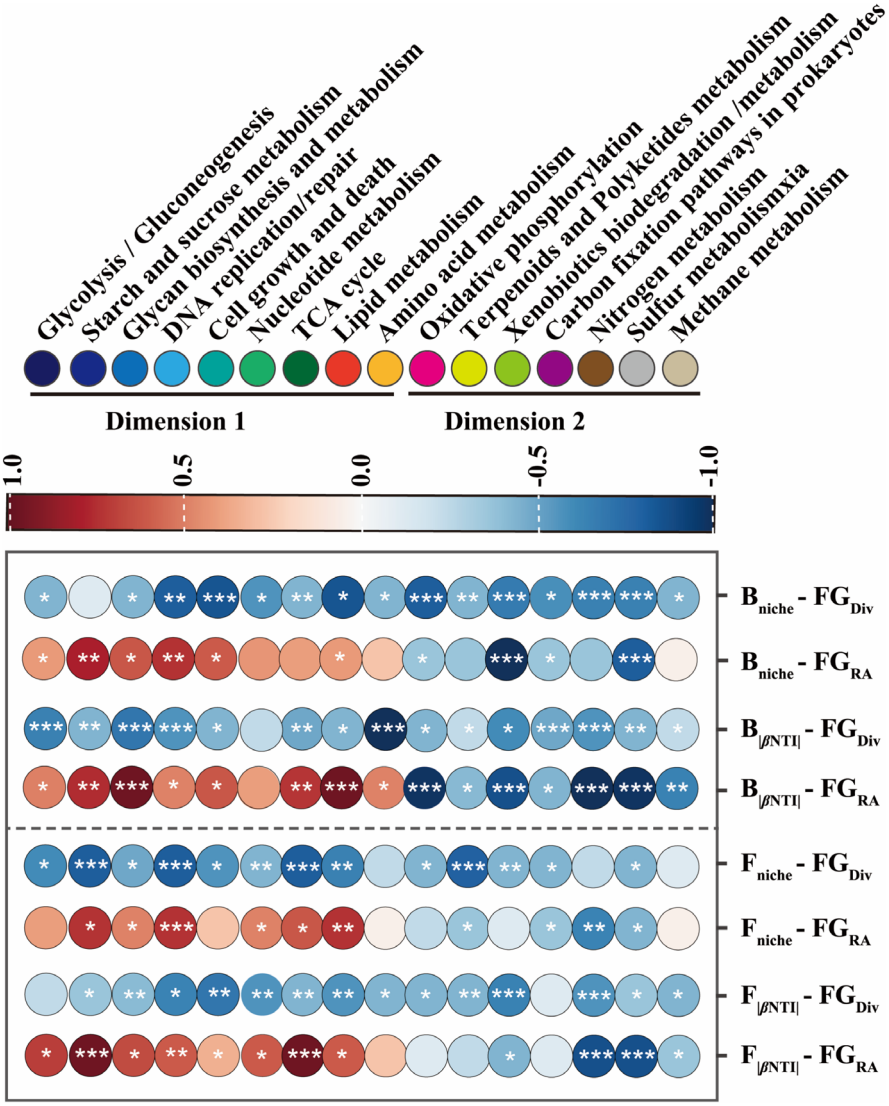

FIGURE 6 | Relationship among microbial niche width, |βNTI| values, functional gene abundance and functional gene diversity. $B_{|\beta NTI|}$: Bacterial community assembly; $F_{|\beta NTI|}$: Fungal community assembly; B_{Niche}: Bacterial niche width; F_{Niche}: Fungal niche width; FG_{Div}: Functional category diversity; FG_{RA}: Functional category relative abundance. The colours in the heatmap indicate the correlation coefficients (deeper red colour indicates a stronger positive correlation, and a deeper blue colour indicates a stronger negative correlation). *, ** and *** indicate $p < 0.05$, $p < 0.01$ and $p < 0.001$, respectively. [Colour figure can be viewed at wileyonlinelibrary.com]

Myers 2011). Nevertheless, in established communities with determined population sizes and scales, the dominant role of stochastic or deterministic processes at a local scale may depend on the local environment (Vellend et al. 2007). Therefore, in our study, deterministic community assembly processes dominated in low α-diversity communities and increased in proportion with soil depth (|βNTI| > 2, bacteria: 40.4%–75.9%; fungi: 41.1%–80.7%). This is clearly related to the greater environmental stress in the subsoils. This phenomenon was further confirmed by calculating the relationship between species richness and |βNTI| values.

In communities with high α-diversity, stochastic community assembly processes may involve more complex metabolic networks (Coyte et al. 2015; Brophy 2017) influenced by species birth, death, migration and extinction (Chave 2010); moreover, studies have indicated that resource availability is a key driving factor (Coates and Astrup 2013). For example, under low environmental stress, sufficient nutrients can support a large number of microorganisms. As nutrients gradually decrease in the environment, specialised functions such as nitrogen, sulphur and methane metabolism and oxidative phosphorylation maintain the stability of the metabolic network, thus providing available energy and nutrients to microorganisms (Xun et al. 2019). This significantly reduces the competition between species, highlighting the important role of specialised functions in maintaining community functional stability. However, with increasing environmental stress, competition among species intensifies and strong environmental selection coupled with diversity loss leads to a reduction in specialised functions (Singh et al. 2014). During this process, the microbial community assembly transitions from stochastic to deterministic. For example, recent studies have suggested that dispersal effects in communities with low species diversity help strengthen environmental selection in deterministic processes (Ron et al. 2018). Homogeneous selection in habitats affected by the same environmental factors

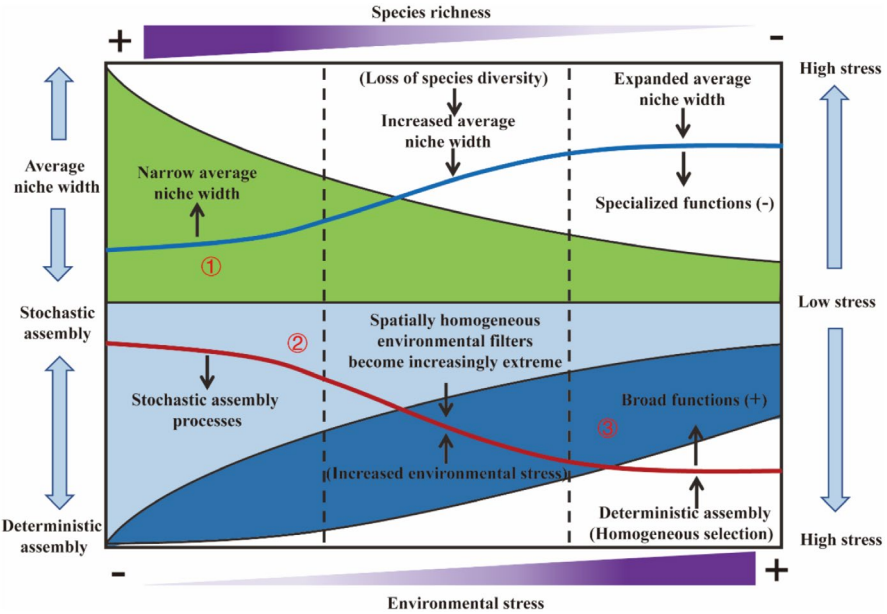

FIGURE 7 | Conceptual framework illustrating the intrinsic mechanisms linking environmental stress-induced microbial diversity loss to community functional shifts. Solid red lines indicate changes in community assembly processes, whereas solid blue lines indicate changes in the average niche width. The shaded area consists of three parts: (①) specialised functions; (②) + (③) broad functions. The dark blue shaded area (③) represents the redundancy of broad functions along the environmental stress gradient, while the green (①) and light blue (②) shaded areas represent perfectly symmetrical functions. Phase 1: Community assembly and niche processes under low environmental stress/high species diversity conditions. At this stage, sufficient nutrient resources may lead to reduced environmental selection and species competition. Community assembly is likely to be associated with stochastic processes related to birth, death, speciation and extinction. Microorganisms with narrow niches can survive, which results in relatively small average niche widths. Phase 2: With increasing environmental stress, a sharp loss in species diversity occurs. Increased environmental filtering leads to a shift from stochastic to deterministic processes. A reduction in the abundance of genes for specialised functions and the loss of microorganisms with narrow niches may weaken functional metabolic networks and increase the average niche width. Phase 3: Community assembly and niche processes under high environmental stress/low species diversity. At this stage, uniform environmental stress filtering leads to strong homogenising selection (deterministic processes). Under homogenising selection, a reduction in the abundance of genes in different functional categories may follow different decrement patterns. Compared with specialised functions, species presenting broad functions decrease less because of their broader niches. Therefore, the relative abundance of genes for broad functions is significantly enriched under high environmental stress. [Colour figure can be viewed at wileyonlinelibrary.com]

causes reassembled microbial communities to become taxonomically and functionally homogenised (Van Der Plas 2016). This explains why microbial communities become increasingly similar under high environmental stress.

Under high environmental stress caused by limited resource availability, it is impossible to maintain species combinations that support all functions simultaneously (Mitri et al. 2016). Deterministic community assembly processes result in biotic homogenisation, leading to the enrichment of broad functions in low-biodiversity communities (Mori et al. 2018; Xun et al. 2019). For example, broad functions related to DNA replication and repair and stress tolerance are retained through environmental filtering due to their broader ecological niches (Muller 2019; Xu et al. 2023). This hypothesis is supported by the niche outcomes. Compared to fungi, bacteria occupy broader niches because of their high spatial turnover rates and ecological tolerance (Malard et al. 2022). For instance, bacteria typically range in size from 0.5 to 5 μm and can survive in high-salinity, high-temperature and extreme conditions (Caron 2009; Taylor and Sinsabaugh 2015; Luan et al. 2022). This explains the close link between the variations in niche width and |βNTI| values for bacteria with genes associated with broad functions. In contrast, fungi are more closely associated with genes with specialised functions.

In conclusion, within the microbial ecosystems investigated in this study, our findings illustrated how differences in microbial community assembly and changes in niche width under environmental stress constrain the functional potential induced by microbial diversity loss. We proposed a conceptual model (Figure 7) to depict the general pattern of microbial diversity loss and functional shifts in grassland ecosystems under environmental stress gradients. First, environmental stresses led to a significant reduction in both the species and functional diversity of soil microorganisms. Second, deterministic assembly processes predominated in microbial communities in habitats with low environmental stress and high species diversity. In habitats with high environmental stress and low species diversity, microbial species occupied broader niches than in those with low environmental stress and high species diversity. This was correlated with a decline in specialised functional categories and an increase in broad functional categories. That is, deterministic assembly processes and broader niches triggered by the loss of microbial diversity due to environmental stress may constrain community functionality. Given the significance of microorganisms in the overall functioning of ecosystems, gaining a deeper understanding of the microbial diversity and functional shifts triggered by environmental stress is crucial for addressing the mechanisms underlying current and future environmental changes.

Author Contributions

X.W.: writing and bioinformatics analyses. J.W.: investigation, conceptualization and formal analysis. T.M.B.: conceptualization, methodology, review and editing. W.W.: methodology, review and editing. Z.S.: methodology, review and editing. J.C.: methodology, review and editing. G.L.: advice for this manuscript. C.Z.: experimental design and manuscript revision. All authors read and approved the final manuscript.

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The authors have nothing to report.

Conflicts of Interest

The authors declare no conflicts of interest.

Data Availability Statement

Raw sequence reads and metadata are deposited in the GSA and SRA (CRA014763 and PRJNA1265876).

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Supporting Information

Additional supporting information can be found online in the Supporting Information section. **Data S1:** mec70096-sup-0001-Supinfo.pdf.