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Bacterial and fungal communities exhibit contrasting patterns in response to marsh erosion: A fine-scale observation,

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Highlights

- Marsh erosion had contrasting effects on soil bacterial and fungal communities.
- Bacterial diversity decreased but fungal diversity increased with marsh erosion.
- Erosion had specific effects on soil microbial composition, especially bacteria.
- The complexity of fungal networks increased substantially with erosion.
- Erosion-induced changes in microbes may affect soil function and nutrient cycling.

Abstract:

Coastal salt marshes, especially their seaward boundaries, are experiencing severe erosion and area loss worldwide because of human disturbances and natural changes. However, how marsh erosion affects soil microbial communities and their potential functions remains poorly understood in subtropical coastal ecosystems. Herein, simultaneous measurements of the abundance, diversity, and composition of bacterial and fungal communities were conducted along a marsh erosion gradient, based on Illumina sequencing of 16S rRNA and ITS genes. Our results indicate that marsh erosion is often accompanied by a loss of plant biomass and a decrease in soil total carbon, total nitrogen, and organic matter concentrations, but an increase in soil water content. We found that the abundance of bacteria and fungi tended to decrease with erosion, especially for bacterial communities. Marsh erosion had opposite effects on the alpha-diversity of bacterial and fungal communities, with bacterial diversity decreasing but fungal diversity increasing with marsh erosion. The beta-diversity and composition of bacterial and fungal communities were altered by marsh erosion, and in particular bacterial communities were clustered into three groups: uneroded, eroding, and eroded. Network analysis demonstrated that the inter-relationships of the bacterial community did not significantly change with the erosion gradient, but the complexity of the fungal networks increased. The diversity and composition of the bacterial and fungal communities can be jointly explained by plant biomass, soil nutrient dynamics, and bulk density. We conclude that marsh erosion-induced changes in soil properties and plant loss altered the diversity and composition of bacterial and fungal communities,

which decrease bacterial abundance and diversity but increase fungal diversity and network complexity, suggesting that these microbial taxa contribute differently to soil function and nutrient cycling as marsh erosion continues.

Keywords: Bacteria; Fungi; Soil function; Plant loss; Edge erosion; Coastal marsh

Highlights:

- ◆ Marsh erosion had contrasting effects on soil bacterial and fungal communities.
- ◆ Bacterial diversity decreased but fungal diversity increased with marsh erosion.
- ◆ Erosion had specific effects on soil microbial composition, especially bacteria.
- ◆ The complexity and stability of fungal networks increased substantially with erosion.
- ◆ Erosion-induced changes in microbes may affect soil function and nutrient cycling.

1. Introduction

Acting as natural buffer zones between terrestrial and marine ecosystems, coastal salt marshes play vital ecological and economic roles (McLoughlin et al., 2014; Tommasini et al., 2019). Not only do they protect coastlines, provide habitats, and sequester carbon, but they also improve water quality and support food webs (Kirwan et al., 2016; Schepers et al., 2020). However, salt marshes, especially their edges, are experiencing severe erosion and area loss worldwide because of land use (Borrelli et al., 2017), sea-level rise (Schepers et al., 2020), wave erosion (Leonardi et al., 2015; Mariotti and Fagherazzi, 2013), and their combination. Globally, more than half of the marsh area has been lost since 1900 (Browne, 2017; Davidson, 2014; Hinshaw et al., 2017).

This global trend is also reflected along China's 18,000 km coastline, where the combined effects of climate change, coastal erosion, and reclamation pressure have resulted in an approximately 59% loss of coastal marsh area since the 1980s (Gu et al., 2018). Coastal marsh erosion can replace salt-tolerant vegetation communities and accelerate wetland degradation, which has substantial implications for primary productivity, microbial communities, and nutrient and carbon cycles, thereby regulating ecosystem services and functions (Hinshaw et al., 2017; Steinmuller et al., 2020). Nevertheless, previous studies have focused largely on identifying and quantifying the mechanisms causing marsh erosion (Mariotti and Fagherazzi, 2013; Schepers et al., 2020), and knowledge of soil bacterial and fungal shifts following marsh erosion is particularly limited, especially in subtropical coastal marshes (Hinshaw et al., 2017).

Soil contains the most diverse microbial community on earth, which is the pivotal driving force in nutrient cycling and soil function in many ways (Bahram et al., 2018; Wu et al., 2013). Soil microorganisms, particularly bacteria and fungi, drive nutrient transformation, organic matter decomposition, and soil function (Bahram et al., 2018). However, the diversity, structure, and function of the soil microbial community are very sensitive to environmental change and disturbance. Numerous microbial-biogeography studies have demonstrated that bacteria and fungi show niche differentiation that is often dramatically correlated with the change of environmental factors, such as soil pH, salinity, and geographic distance (Lozupone and Knight, 2007; Mohamed and Martiny, 2011; Wu et al., 2013).

Previous research deepened our understanding of how environmental variations affect the distribution patterns of bacterial and fungal communities at regional and global scales, but microbial adaptation strategies and functional shifts with coastal habitat change are still unclear. Edge erosion along the shoreline is a critical driver of marsh loss because concentrated waves can release large amounts of previously stored sediment, nutrients, and carbon, thus altering the marsh biogeochemical cycles (Haywood et al., 2019; Sapkota and White, 2021). Therefore, understanding the diversity and composition of soil bacterial and fungal communities and their responses to marsh erosion is of great importance for the effective management of coastal vulnerable zones, in order to mitigate and restore soil functional degradation caused by human activity and natural disturbances.

Substantial research efforts have been focused on investigating the effects of soil erosion on organic carbon mineralization (Xiao et al., 2018), denitrification capacity (Hinshaw et al., 2017), and soil parameters (Steinmuller et al., 2020) in terrestrial ecosystems, and linked soil erosion to a decreased biogeochemical function. In contrast, only a few studies have examined the effects of erosion on microbial diversity and composition, and they have focused on agricultural and forest soils (Li et al., 2015; Mabuhay et al., 2004). For example, a recent study of agroecosystems demonstrated

that soil erosion negatively affects microorganisms by reducing microbial abundance and diversity, simplifying microbial network complexity and correlation, and altering microbial community composition (Qiu et al., 2021). Soil bacteria and fungi have important but differentiated functions in driving nutrient and carbon biogeochemical cycles, but it is less known how the diversity and composition of these microorganisms respond to marsh erosion. In addition, because marsh erosion is a dynamic process, clarifying the effects and driving mechanisms of erosion on the composition and activity of microbial communities is critical for assessing microbial function and maintaining ecosystem services in coastal marshes, especially in the context of increasing human activities and extreme climate events.

The Min River is the largest river in southeast China that flows into the East China Sea. The Min River estuary has a long macrotidal course because of the intersection of strong runoff and ocean tides, and the upstream seawater intrusion affects the dynamics and fates of the marshes, including strong edge erosion (Hu et al., 2017; Sun et al., 2015). In this study, simultaneous measurements of the abundance, diversity, and composition of bacterial and fungal communities were taken along an erosion gradient (uneroded, eroding, and eroded), based on the quantitative PCR (qPCR) and Illumina sequencing of 16S rRNA and ITS genes. The specific objectives were to (1) determine the abundance, diversity, and composition of the bacterial and fungal communities along the erosion gradient; (2) estimate the effects of such erosion on the network complexity and co-occurrence patterns of soil microorganisms; (3) reveal the key environmental drivers (e.g., substrate availability, plant biomass, and physicochemical factors) that are beyond the shifts in microbial community structure and functions along the erosion gradient.

We hypothesize that marsh erosion has a negative impact on microbial communities by reducing taxonomic abundance and diversity, and changing community composition. Furthermore, bacteria and fungi could exhibit contrasting patterns because they respond differently to the changes in substrate availability and soil physicochemistry.

2. Materials and methods

2.1. Site description

The study area (Figure 1) is located in the Min River estuary in south-eastern China ($26^{\circ} 01' 08''$ – $26^{\circ} 03' 39''$ N, $119^{\circ} 36' 28''$ – $119^{\circ} 41' 15''$ E), which has a subtropical monsoon climate with intense seasonal downpours and storm surges. At the time of the study, the dominant plant cover in this zone was *Cyperus malaccensis* and *Phragmites australis*.

Because of the interaction of runoff and tides, there are long intertidal zones along the sea-land gradient, forming numerous associated coastal tidal marshes. These marshes, especially their seaward boundaries, are under threat from rising sea levels, inadequate supply of river sediment, and human influences (wetland reclamation and vegetation destruction), which are causing edge erosion and localized subsidence. There are clear erosion gradients from uneroded and eroding to eroded from land to sea, providing a good and unique opportunity to investigate and predict the effects of erosion at the marsh edge. More detailed descriptions of the Min River estuarine marshes are available in previous studies (e.g., Hu et al., 2022b).



Figure 1. Location of study site in the Min River estuary, southeast China; 5UE and 1UE represent 5 m and 1 m off the marsh edge up into the uneroded salt marsh, respectively; EI represents eroding; 1ED and 5ED represent 1 m and 5 m off the marsh edge down into the eroded open bay, respectively.

2.2. Experimental design and soil collection

Field experiments were conducted in a degraded *C. malaccensis*-dominated marsh. The sampling sites were chosen along the erosion gradient from uneroded and eroding to eroded from land to sea. Specifically, five sites were selected, representing the 5 m (5UE) and 1 m (1UE) off the marsh edge up into the uneroded salt marsh (uneroded), the erosion edge (EI; eroding), and 1 m (1ED) and 5 m (5ED) off the marsh edge down into the open bay (eroded). At each site, three plots (2 m × 2 m; triplicate), 2 m apart were established, for a total of 15 plots.

Soil samples were collected during the summer (July) and winter (January) of 2021. At each plot, three topsoil samples (20 cm) were randomly collected using a cylindrical auger and then homogenized into a composite sample. The samples were stored in plastic bags and promptly transported to the laboratory in a portable refrigerator. In the laboratory, the samples were divided into two subsamples: one was air-dried, for the determination of soil physicochemical parameters, and the other was stored at -80°C, for DNA extraction and microbial analysis. In addition, plant biomass (above and below ground) was harvested simultaneously near the sampling site, in a 25 × 25 cm² quadrat, at a depth of 40 cm, which is the dominant root zone.

2.3. DNA extraction and qPCR assay

Total microbial DNA was extracted using the OMEGA Soil DNA Kit (M5635-02) (Omega Bio-Tek, Norcross, GA, USA), following the manufacturer's instructions, and stored at -20°C prior to further analysis. The quantity and quality of extracted DNAs were measured using a NanoDrop NC2000

spectrophotometer (Thermo Fisher Scientific, Waltham, MA, USA) and agarose gel electrophoresis, respectively. The abundance of the bacteria and fungi gene copies was quantified by quantitative PCR (qPCR) using an ABI 7900 Real-Time PCR System (Applied Biosystems, Foster, USA).

2.4. Illumina sequencing and sequence analysis

PCR amplification of the bacterial 16S rRNA and fungal ITS genes was performed using primer sets 338F/806R and ITS5F /ITS2R, respectively. Sample-specific 7-bp barcodes were incorporated into the primers for multiplex sequencing. The PCR components contained 5 µl of buffer (5×), 0.25 µl of fast-Pfu DNA polymerase (5U/µl), 2 µl (2.5 mM) of dNTPs, 1 µl (10 uM) of each forward and reverse primer, 1 µl of DNA template, and 14.75 µl of ddH₂O. Thermal cycling consisted of initial denaturation at 98°C for 5 min, followed by 25 cycles consisting of denaturation at 98°C for 30 s, annealing at 53°C for 30 s, and extension at 72°C for 45 s, with a final extension of 5 min at 72°C.

PCR amplicons were purified with Vazyme VAHTSTM DNA Clean Beads (Vazyme, Nanjing, China) and quantified using the Quant-iT PicoGreen dsDNA Assay Kit (Invitrogen, Carlsbad, CA, USA). After the individual quantification step, amplicons were pooled in equal amounts, and pair-end 2 × 250 bp sequencing was performed on the Illumina NovaSeq platform with NovaSeq 6000 SP Reagent Kit (500 cycles). Raw sequences were deposited in the NCBI Sequence Read Archive under accession number SRP375586. A summary of sequencing data based on 16S rRNA and ITS genes is given in Supplementary Information Table S1.

Microbiome bioinformatics analysis was performed with QIIME2 2019.4 (Bolyen et al., 2018) with slight modification according to the official tutorials (<https://docs.qiime2.org/2019.4/tutorials/>). Briefly, raw sequence data were demultiplexed using the *demux* plugin following primers' cutting with the *cutadapt* plugin (Martin, 2011). Sequences were then quality filtered, denoised, and merged, and chimera removed using the *DADA2* plugin (Callahan et al., 2016). Non-singleton amplicon sequence variants (ASVs) were aligned with *mafft* (Katoh et al., 2002) and used to construct a phylogeny with *fasttree2* (Price et al., 2009). Alpha-diversity metrics (Chao1, Observed species, Shannon, Simpson, Faith's PD, Pielou's evenness, and Good's coverage) and beta diversity metrics (weighted UniFrac, unweighted UniFrac, Jaccard distance, and Bray–Curtis dissimilarity) were estimated using the *diversity* plugin. Taxonomy was assigned to ASVs using the *classify-sklearn* naïve Bayes taxonomy classifier in the *feature-classifier* plugin (Bokulich et al., 2018) against the SILVA Release 132 (bacteria)/UNITE Release 8.0 (fungi) Database (Kõljalg et al., 2013).

Table S1. Summary of sequencing data based on 16S rRNA and ITS genes with marsh erosion

Season	Sample	Bacteria				Fungi			
		Raw sequence s	Clean sequence s	OTUs	Coverage	Raw sequences	Clean sequences	OTUs	Coverage
Summer	5UE1	143220	119443	4534	0.960	91376	81466	223	0.9999
	5UE2	133082	112352	4881	0.956	85751	77636	198	0.9998
	5UE3	132658	110008	4489	0.960	85483	77610	286	0.9998
	1UE1	141587	116734	4598	0.957	88133	80048	93	0.9997
	1UE2	143591	120935	4777	0.956	85407	75969	358	0.9997
	1UE3	135850	113331	4748	0.958	82379	71075	336	0.9998
	EI1	143235	122765	4200	0.966	97000	87964	84	0.9998
	EI2	144782	121769	4658	0.960	91327	81131	128	0.9999
	EI3	134914	114443	4753	0.961	89852	77145	197	0.9999
	1ED1	143170	123246	4801	0.961	79851	70293	775	0.9993
	1ED2	132471	115096	4326	0.967	74209	65171	597	0.9995

Winter	1ED3	144194	122688	4566	0.966	77068	67890	689	0.9994
	5ED1	140672	119643	4370	0.962	72060	64003	1143	0.9989
	5ED2	145320	124153	4448	0.960	79450	70610	200	0.9999
	5ED3	132883	114698	3977	0.965	82125	72821	1039	0.9990
	5UE1	56795	48127	3453	0.987	70879	59058	473	0.9997
	5UE2	54889	46723	3129	0.990	93577	82645	282	0.9994
	5UE3	57939	49835	3491	0.984	71082	56923	510	0.9998
	1UE1	61297	51246	3791	0.982	72549	46064	634	0.9999
	1UE2	58706	51008	3559	0.984	115250	100647	518	0.9991
	1UE3	60972	53133	3250	0.985	108081	92840	318	0.9992
	EI1	56361	48764	3473	0.988	109211	79701	386	0.9995
	EI2	58445	49832	3638	0.984	93181	68353	682	0.9994
	EI3	58131	50509	3393	0.985	105667	93457	222	0.9995
	1ED1	61188	53133	3333	0.984	97713	73983	722	0.9992
	1ED2	62851	54765	3339	0.982	96656	86582	820	0.9991
	1ED3	59722	51023	3176	0.984	78668	69668	648	0.9994
	5ED1	59149	51765	3291	0.983	75554	66692	603	0.9997
	5ED2	56287	48584	3429	0.983	64047	56130	675	0.9997
	5ED3	56044	48820	3425	0.984	104496	82056	552	0.9993

Notes: OUT stands for operational taxonomic unit; 5UE and 1UE represent 5 m and 1 m off the marsh edge up into the uneroded salt marsh, respectively; EI stands for eroding; 1ED and 5ED represent 1 m and 5 m off the marsh edge down into the eroded open bay, respectively.

2.5. Physicochemical soil variables

Soil samples were assayed for pH, salinity, soil temperature (ST), soil water content (SWC), bulk density (BD), soil total C (TC), soil total nitrogen (TN), soil organic matter (SOM), and particle size according to the standard methods as described in Hu et al. (2022a) and Hu et al. (2022b). Briefly, soil pH and salinity were determined in 1:2.5 soil-water suspensions using a pH meter (IQ Scientific Instruments, Carlsbad, USA) and a salinity meter (Oakton Instruments, Springfield, USA), respectively. SWC was analysed by drying samples to constant weight at 105°C, and BD was determined as the ratio of dry weight to volume. SOM was measured by loss on ignition. Soil TC and TN concentrations were determined using an elemental analyser (Elementar, Frankfurt, Germany). ST was measured in situ using a 2265FS EC meter (Spectrum Technologies Inc., Aurora, USA). Particle size was determined using a particle-size analyser (Mastersizer 2000, Malvern, UK). Moreover, whole plant biomass was measured by drying samples to constant weights at 70°C.

These parameters helped us assess the effects of marsh erosion on soil basic physicochemical properties, nutrient availability, and primary productivity.

2.6. Bioinformatics and statistical analysis

Sequence data analyses were mainly performed using QIIME2 and R packages (v3.2.0). ASV-level alpha diversity indices, such as Observed species, Shannon diversity, Simpson index, and Chao1 richness were calculated using the ASV table in QIIME2, and visualized as box plots. Beta diversity analysis was performed to investigate the structural variation of microbial communities across samples using Bray–Curtis metrics and visualized via nonmetric multidimensional scaling (NMDS) and the unweighted pair-group method with arithmetic means (UPGMA) hierarchical clustering (Ramette, 2007). The significance of the differentiation of the microbiota structure among groups was assessed by analysis of similarities (ANOSIM) (Warton et al., 2012) using QIIME2. Based on the

correlation coefficients and significance, we constructed a co-occurrence network with nodes representing genera and edges representing correlations between these taxa.

Moreover, differences in soil parameters and plant biomasses along the marsh erosion gradient were evaluated using one-way analysis of variance (ANOVA), and Tukey's HSD test was used for significance analysis. A multivariate analysis of variance (MANOVA) was performed to assess the impacts of erosion levels, season, and their interaction on environmental variables and microbial communities. Linear regression analysis was conducted to establish the relationship between microbial diversity and selected soil or plant properties (TC, TN, and plant biomass). Redundancy analysis (RDA) was used to identify the main factors driving the changes in bacterial and fungal communities due to marsh erosion. The Mantel test was used to assess the associations between the microbial community composition and diversity and environmental variables using the *vegan* R package. Additionally, the fungi to bacteria (F:B) abundance ratios were evaluated based on gene copy number of the fungal ITS and bacterial 16S rRNA genes after log transformation.

3. Results

3.1. Soil properties and plant biomass

The soil physicochemical parameters and plant biomass along the marsh erosion gradient are reported in Table 1. The eroded sites had lower soil TC, TN, and SOM concentrations than the uneroded sites in both seasons. Higher plant biomass values were observed at the uneroded sites than at the eroded sites. Soil pH values tended to decrease first and then increase with the erosion gradient, and were lowest at the eroding sites in summer. SWC decreased first and then increased with the erosion gradient during summer, whereas BD showed an opposite trend. Moreover, ST tended to fluctuate between sites and seasons and had no obvious pattern. In summary, these results indicate that the erosion levels, seasons, and their interactions significantly alter soil properties and plant productivity ($p < 0.05, 0.01, 0.001$).

Table 1. Soil physicochemical properties and plant biomass, and their significance (p values) with marsh erosion

Parameter	Season	Marsh erosion gradient					p		
		5UE	1UE	EI	1ED	5ED	Site	Season	Interaction
pH	S	6.1 (0.2) ^b	6.2 (0.1) ^b	5.7 (0.1) ^c	6.2 (0.1) ^b	6.7 (0.1) ^a	<0.01	<0.001	<0.01
	W	7.9 (0.1)	7.7 (0.3)	7.9 (0.3)	7.8 (0.3)	7.8 (0.3)			
Salinity (ppt)	S	4.65 (0.04)	4.64 (0.04)	4.61 (0.08)	4.52 (0.22)	4.51 (0.21)	0.283	<0.001	0.886
	W	6.53 (0.05)	6.54 (0.12)	6.46 (0.16)	6.31 (0.24)	6.48 (0.19)			
SWC (%)	S	74.7 (1.5) ^b	65.7 (6.0) ^b	68.8 (3.8) ^b	75.0 (1.7) ^b	89.2 (4.8) ^a	<0.05	0.521	0.989
	W	78.6 (15.4)	63.9 (28.5)	72.8 (12.2)	78.3 (4.7)	93.4 (2.5)			
BD (g cm ⁻³)	S	0.85 (0.03) ^{ab}	0.93 (0.04) ^a	0.92 (0.04) ^a	0.88 (0.02) ^a	0.78 (0.03) ^b	<0.001	<0.05	0.945
	W	0.84 (0.08)	0.87 (0.03)	0.88 (0.07)	0.83 (0.05)	0.74 (0.00)			
ST (°C)	S	29.6 (0.1) ^b	29.6 (0.1) ^b	29.9 (0.1) ^a	29.7 (0.1) ^b	30.0 (0.1) ^a	<0.01	<0.001	<0.01
	W	12.8 (0.1) ^b	12.9 (0.2) ^{ab}	13.0 (0.2) ^{ab}	13.2 (0.1) ^a	12.9 (0.1) ^{ab}			
TC (g kg ⁻¹)	S	14.5 (0.3) ^a	13.0 (0.2) ^a	13.3 (0.4) ^a	12.8 (0.4) ^b	11.8 (1.1) ^b	<0.001	0.107	0.356
	W	13.4 (0.4) ^a	12.7 (0.2) ^{ab}	12.9 (0.6) ^{ab}	12.7 (0.6) ^{ab}	12.0 (0.5) ^b			
TN(g kg ⁻¹)	S	1.24 (0.01) ^a	1.21 (0.04) ^a	1.16 (0.00) ^{ab}	1.10 (0.01) ^b	1.05 (0.06) ^b	<0.001	<0.001	0.100
	W	1.10 (0.05) ^a	1.10 (0.01) ^a	0.99 (0.01) ^b	1.02 (0.04) ^b	0.97 (0.02) ^b			
C:N	S	11.7 (0.2) ^a	10.8 (0.3) ^b	11.4 (0.3) ^{ab}	11.6 (0.3) ^{ab}	11.2 (0.5) ^{ab}	<0.01	<0.001	0.103
	W	12.2 (0.1) ^{ab}	11.5 (0.1) ^b	13.0 (0.5) ^a	12.4 (0.3) ^{ab}	12.4 (0.5) ^{ab}			
SOM (g kg ⁻¹)	S	8.6 (0.2) ^a	8.0 (0.2) ^{ab}	8.3 (0.3) ^{ab}	7.6 (0.3) ^b	7.4 (0.3) ^b	<0.001	<0.001	0.214
	W	10.5 (1.1) ^a	9.9 (0.1) ^a	9.8 (0.2) ^{ab}	8.7 (1.1) ^{ab}	7.9 (0.1) ^b			
PB (kg m ⁻²)	S	4.19 (0.38) ^a	3.62 (0.47) ^{ab}	3.33 (0.28) ^b	0.00 (0.00) ^c	0.00 (0.00) ^c	<0.001	0.326	0.921
	W	3.96 (0.29) ^a	3.50 (0.26) ^{ab}	3.23 (0.17) ^b	0.00 (0.00) ^c	0.00 (0.00) ^c			

Notes: Data represent means (standard deviations) ($n = 3$). Different superscripts *a*, *b*, *c* indicate significant differences between sites ($p < 0.05$, ANOVA). The use of bold type indicates significance at $p < 0.05$. In addition, 5UE and 1UE represent 5 m and 1 m off the

marsh edge up into the uneroded salt marsh, respectively; EI means eroding; 1ED and 5ED represent 1 m and 5 m off the marsh edge down into the eroded open bay, respectively. SWC is soil water content; BD is bulk density; TC is total carbon; TN is total nitrogen; C:N ratio is carbon to nitrogen ratio; SOM is soil organic matter; ST is soil temperature; PB is plant biomass; S stands for summer; W stands for winter.

3.2. Bacterial and fungal abundance and diversity

A total of 2528571 (46723 to 124153 per sample) qualified 16SrRNA sequences and 2235631 (46064 to 100647 per sample) ITS sequences were identified from all samples. These sequences were clustered into 119296 bacterial OTUs and 14391 fungal OTUs at 97% identity, respectively (Table S1).

The abundance (gene copies) of soil bacteria and fungi displayed decreasing trends along with the erosion gradient. The bacterial abundance at the uneroded sites was significantly higher than at the eroded sites ($p < 0.05$), but no significant shifts were detected in the fungal abundance (Figure 2b). Moreover, the F:B ratios (based on log copy number) also showed a decreasing trend along the erosion gradient, with the uneroded sites having higher F:B ratios (0.73) than the eroded sites (0.71).

[Figure 2 should be moved here]

The alpha-diversity indices of bacteria tended to decrease with the erosion gradient, especially Shannon and Simpson indexes, which were significantly lower at the eroded sites than at the uneroded sites ($p < 0.05$; Figure 3a-b). Conversely, fungal diversity increased remarkably with the erosion gradient, and higher fungal diversity was observed at the eroded sites ($p < 0.05$; Figure 3d-f). Furthermore, both bacterial and fungal diversity were strongly responsive to soil C, N, and plant biomass, although in opposite directions (Figure S1). Specifically, bacterial diversity was significantly and positively correlated with soil TC and TN concentrations and plant biomass, while fungi were negatively correlated with these variables.

These results show that the abundance of bacteria and fungi decreased with marsh erosion, but their diversity responded differently, with bacterial diversity decreasing but fungal diversity increasing with marsh erosion.

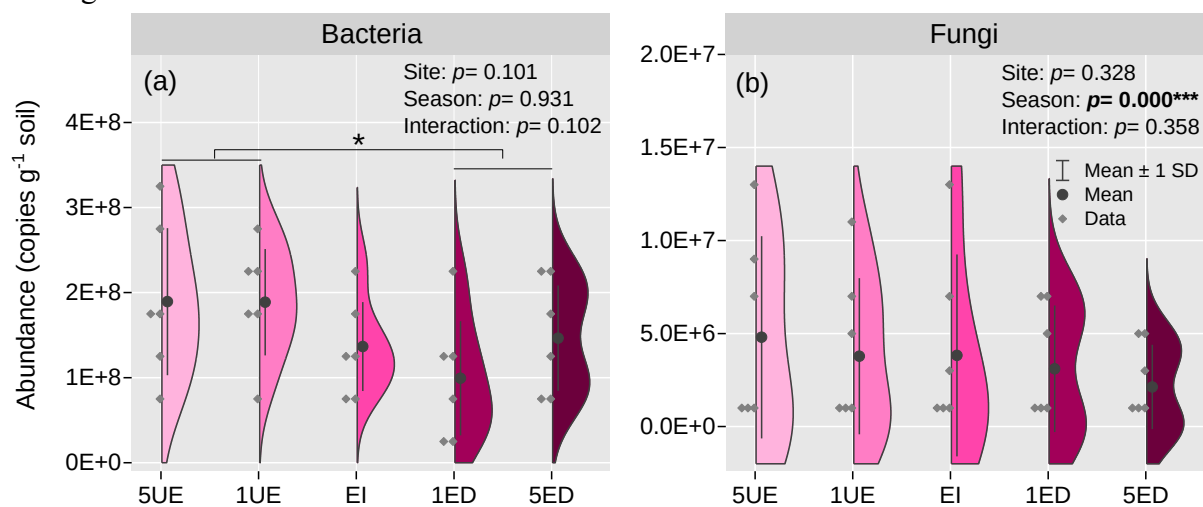


Figure 2. The abundances of bacterial 16S rRNA (a) and fungal ITS (b) genes along the marsh erosion gradient ($n = 6$) in our study. * represents $p < 0.05$; *** represents $p < 0.001$. 5UE and 1UE represent 5 m and 1 m off the marsh edge up into the uneroded salt marsh, respectively; EI means eroding; 1ED and 5ED represent 1 m and 5 m off the marsh edge down into the eroded open bay, respectively.

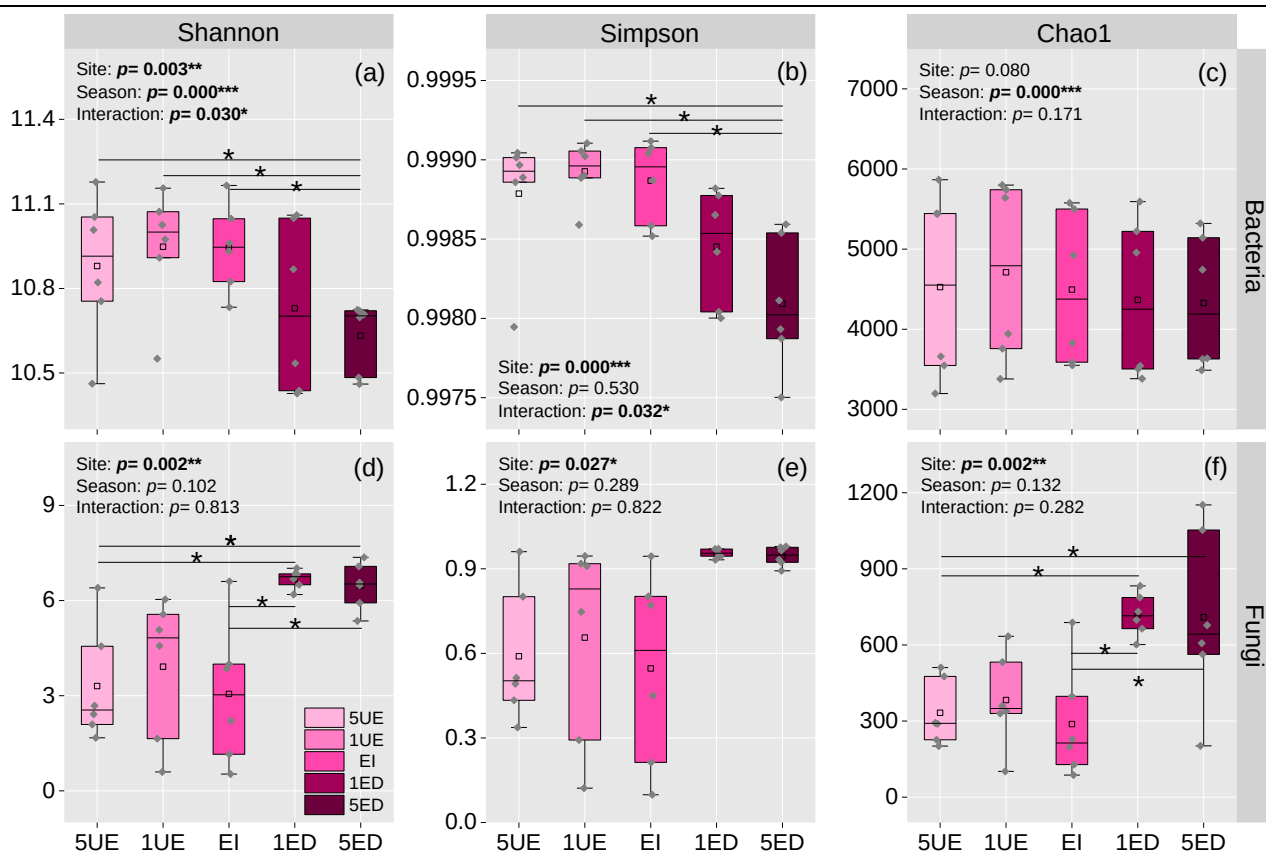


Figure 3. Changes in the alpha-diversity indices of bacterial (a–c) and fungal (d–f) communities along the marsh erosion gradient ($n = 6$). * represents $p < 0.05$; ** represents $p < 0.01$; *** represents $p < 0.001$. 5UE and 1UE represent 5 m and 1 m off the marsh edge up into the uneroded salt marsh, respectively; EI means eroding; 1ED and 5ED represent 1 m and 5 m off the marsh edge down into the eroded open bay, respectively.

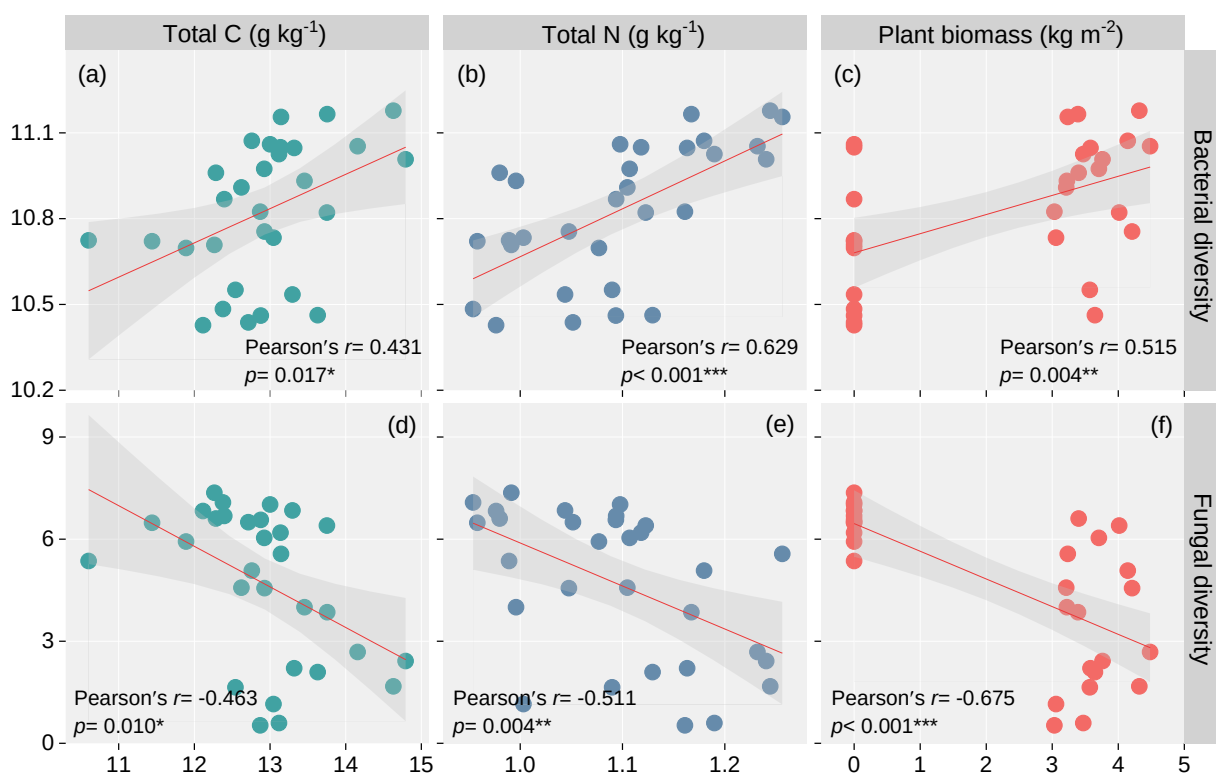


Figure S1. Relationships between bacterial (a–c) and fungal (d–f) diversity and selected soil or plant properties along the marsh erosion gradient. The shaded areas represent the 95% confidence intervals. C is carbon; N is

3.3. Bacterial and fungal community composition

The composition of bacterial and fungal communities were substantially altered by the different erosion gradient, although their responses to erosion were different. More precisely, based on the NMDS plot we used to identify the beta-diversity of bacterial and fungal communities, we can group the bacterial community into three clusters: uneroded, eroding, and eroded (Figure 4a). By contrast, fungal communities overlap and are not as clearly clustered as bacterial communities (Figure 4b). The ANOSIM tests (Bray–Curtis distance) further demonstrated that the composition of bacterial ($R = 0.635$, $p < 0.01$) and fungal ($R = 0.408$, $p < 0.01$) communities differed markedly among the various erosion sites, particularly the bacterial community.

[Figure 4 should be moved here]

Marsh erosion showed no significant effect on the relative abundance of the dominant bacterial phyla (Figure S2a). Proteobacteria were the predominant bacterial phylum across all samples (29228 OTUs), accounting for 44% of all bacterial sequences on average, followed by Chloroflexi (16%), Actinobacteria (8%), and Nitrospirae (6%). By contrast, the relative abundances of the dominant fungal phyla changed dramatically with marsh erosion (Figure S2b). The most abundant fungal phylum at the uneroded sites was Ascomycota, but its dominant status was replaced by the Basidiomycota at the eroded sites.

Hierarchical clustering of the abundant bacterial and fungal genera allowed classifying the samples into two groups: eroded and uneroded sites (Figure 5). More precisely, the relative abundances of the dominant genera varied along the erosion gradient (Figure S3). Regarding bacteria, the relative abundances of *SBR1031*, *KD4-96*, *MBNT15*, and *MND1* were higher, but the relative abundances of *Woeseia* were lower, at the uneroded sites. Regarding fungi, *Papiliotrema*, *Leptoxylum*, and *Hannaella* were the dominant genera at the uneroded sites, and *Dictyophora* and *Verticillium*, at the eroded sites.

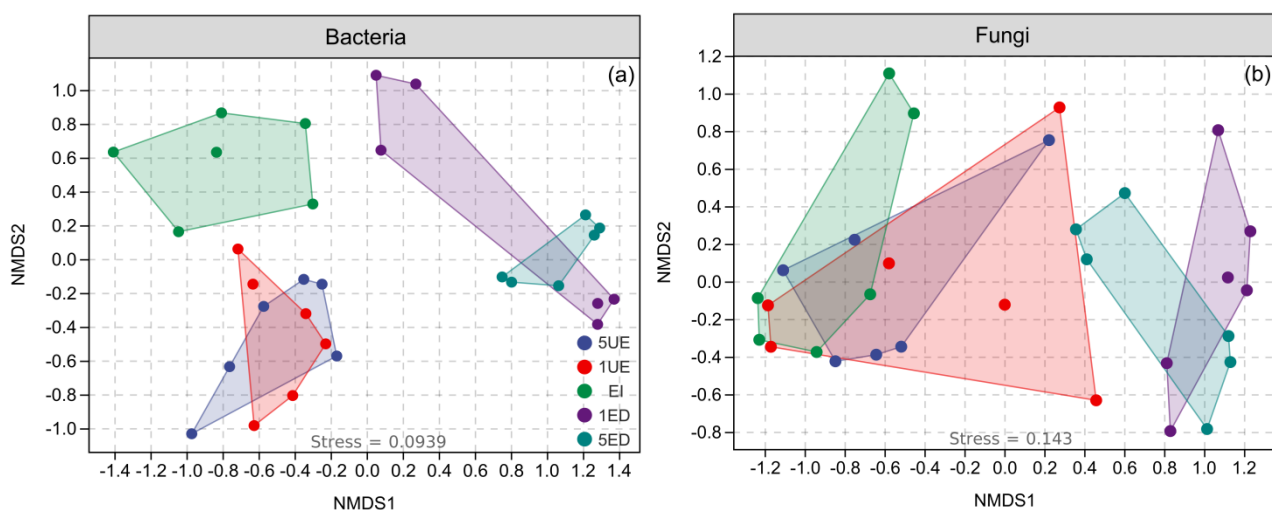


Figure 4. Non-metric multidimensional scaling (NMDS) ordination of the beta-diversity of bacterial (a) and fungal (b) communities following marsh erosion based on Bray–Curtis distance. The shaded areas represent 95% confidence intervals. 5UE and 1UE represent 5 m and 1 m off the marsh edge up into the uneroded salt marsh, respectively; EI means eroding; 1ED and 5ED represent 1 m and 5 m off the marsh edge down into the eroded open

bay, respectively.

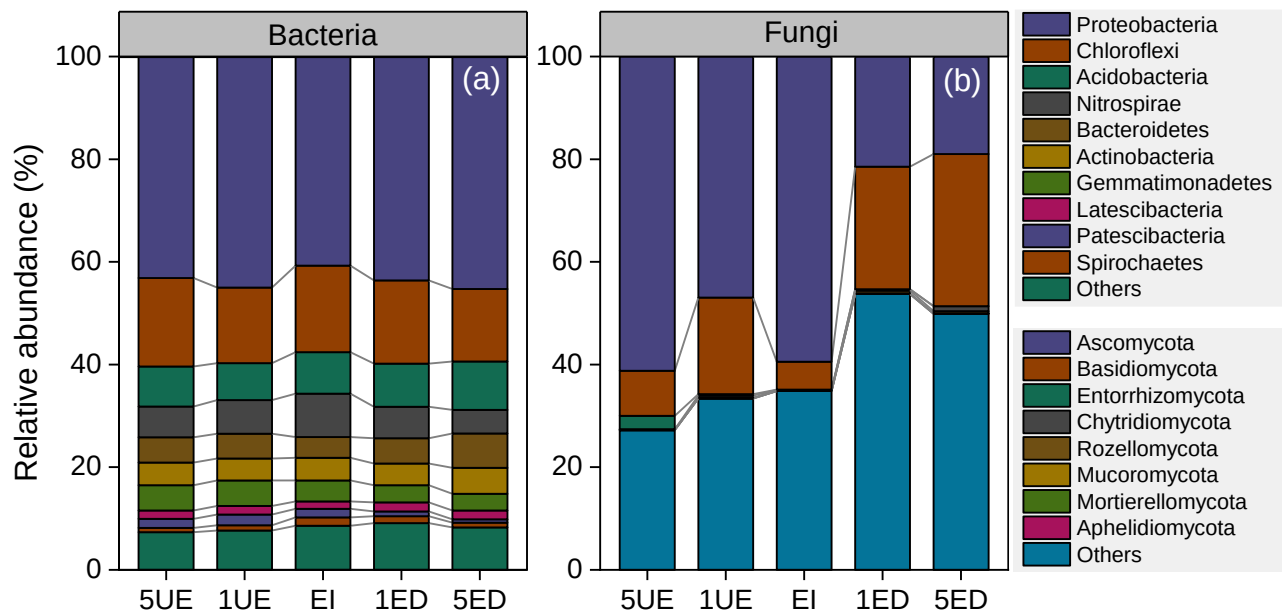


Figure S2. Relative abundances of the dominant bacterial (a) and fungal (b) phyla across all samples following marsh erosion. 5UE and 1UE represent 5 m and 1 m off the marsh edge up into the uneroded salt marsh, respectively; EI means eroding; 1ED and 5ED represent 1 m and 5 m off the marsh edge down into the eroded open bay, respectively.

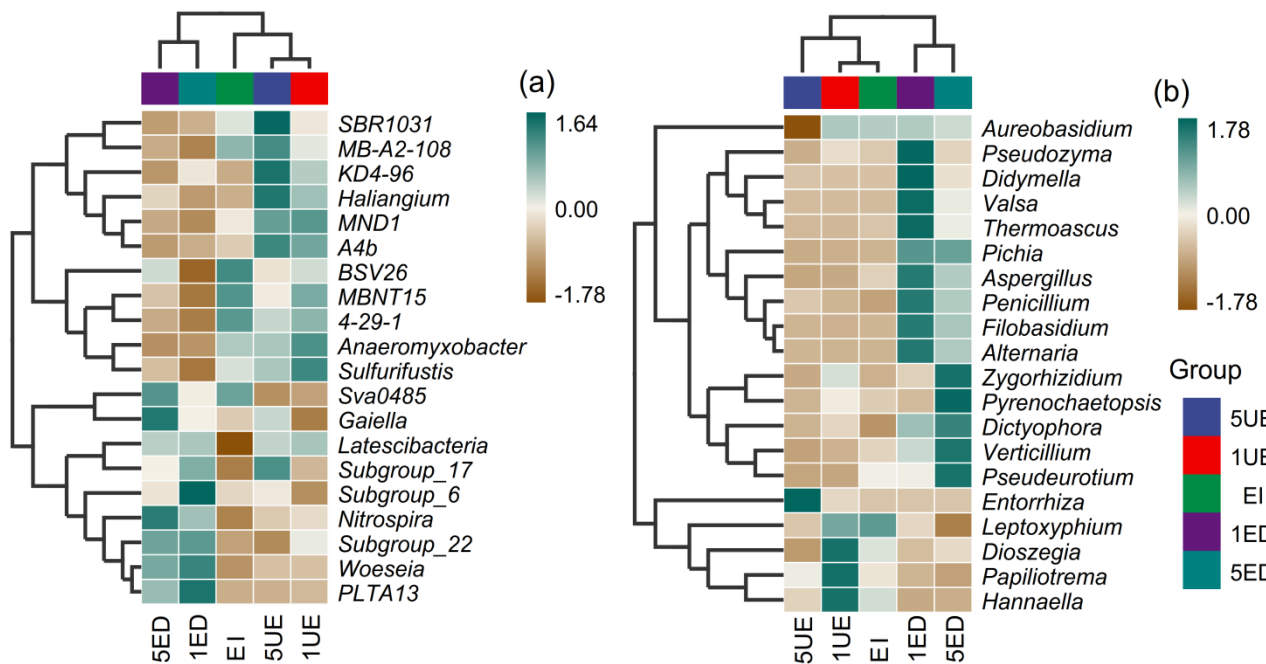


Figure 5. Hierarchical heatmap showing the relative abundances of the dominant bacterial (a) and fungal (b) genera following marsh erosion. Sites were clustered using the UPGMA dendrogram based on Bray–Curtis similarities. 5UE and 1UE represent 5 m and 1 m off the marsh edge up into the uneroded salt marsh, respectively; EI means eroding; 1ED and 5ED represent 1 m and 5 m off the marsh edge down into the eroded open bay, respectively.

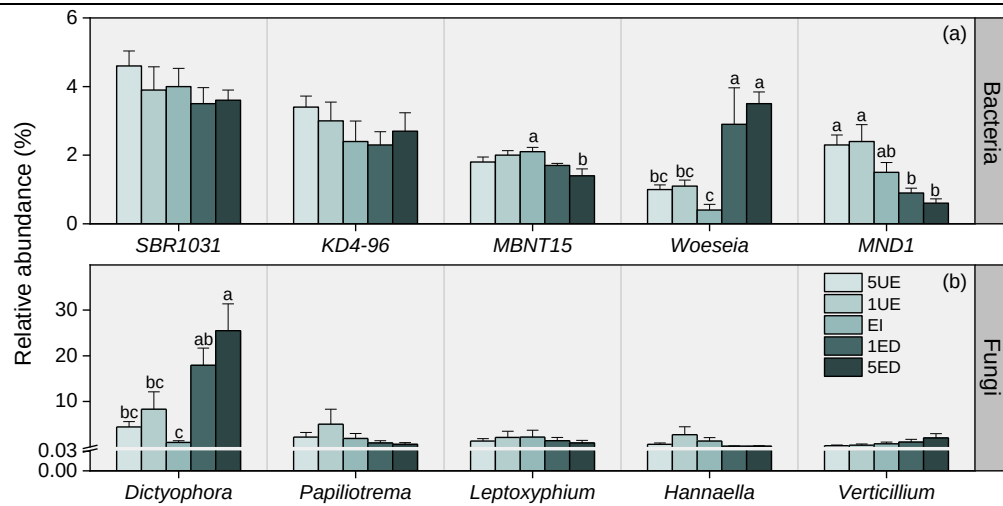


Figure S3. Relative abundance of the dominant bacterial (a) and fungal (b) genera (top 5 only) following marsh erosion. 5UE and 1UE represent 5 m and 1 m off the marsh edge up into the uneroded salt marsh, respectively; EI means eroding; 1ED and 5ED represent 1 m and 5 m off the marsh edge down into the eroded open bay, respectively. Different letters (a, b, c) on the bar indicate significant differences between sites.

3.4. Co-occurrence network analysis

Network analysis was performed to compare the complexity and stability of bacterial and fungal communities (Figure 6). Overall, soil bacterial and fungal community networks showed distinct co-occurrence patterns across all sites, although their network relationships responded differently to marsh erosion. More specifically, the co-occurrence network of the bacterial community did not change obviously with the erosion gradient, but the complexity and stability of the fungal networks increased distinctly with the gradient.

For bacteria, network analysis showed that Chloroflexi (*SBR1031* and *KD4-96*) and Proteobacteria (*MND1*, *MBNT15*, and *Woeseia*) were the key bacteria taxa, and the number of connections was large and occupied an important position, although the connections between nodes were both positively and negatively correlated (Figure 6 a–e).

For fungi, the number of nodes and connections gradually increased with the intensification of marsh erosion, and the dominant genus changed from uneroded sites to eroded sites (Figure 6 f–j). Specifically, *Papiliotrema*, *Leptoxylum*, and *Hannaella* were the dominant genera before erosion, and *Dictyophora* and *Verticillium*, after erosion.

These results clearly indicate that soil bacterial communities have greater network complexity and stability than fungi, and marsh erosion greatly increases intra-fungal community relationships and thus the complexity of fungal networks.

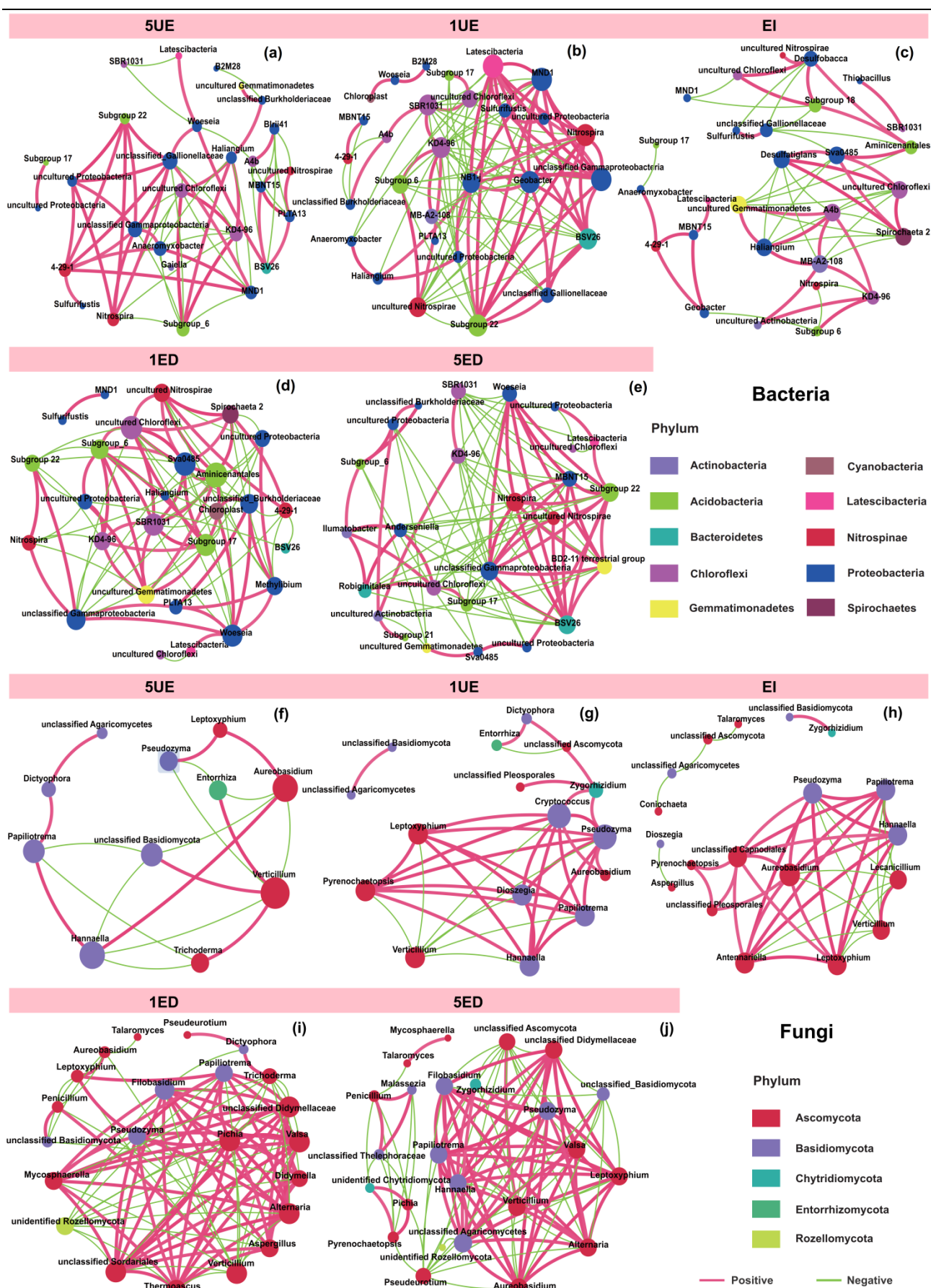
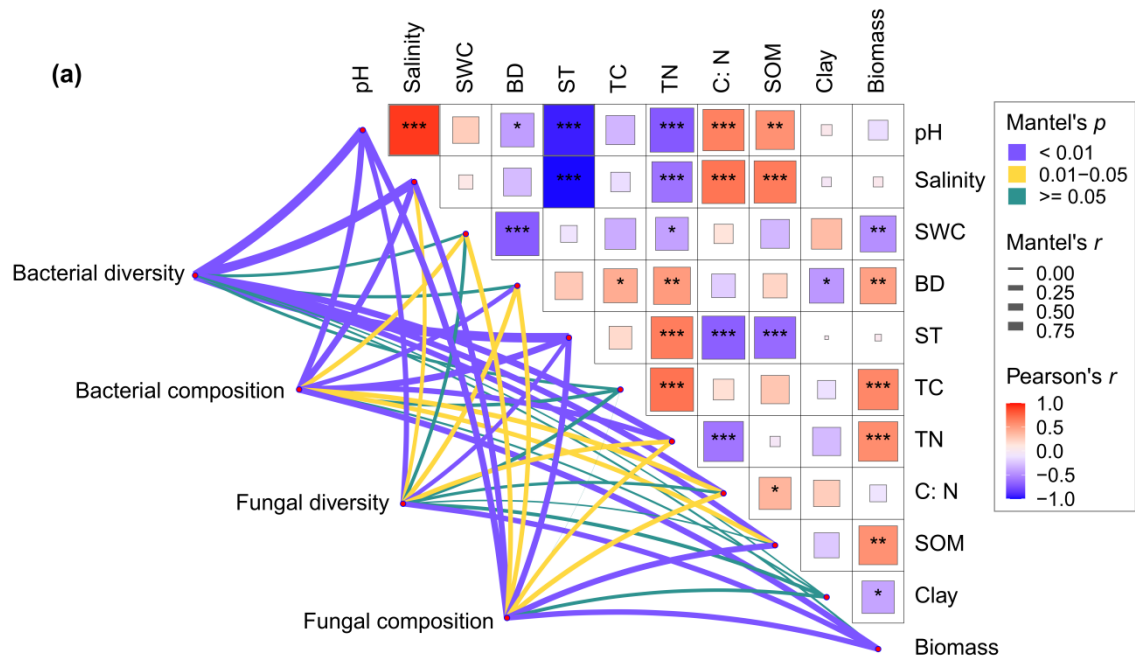


Figure 6. Co-occurrence network analysis of bacterial (a–e) and fungal (f–j) communities as affected by marsh

erosion. The red and green lines represent positive and negative relationships between microbial taxa, respectively; 5UE and 1UE represent 5 m and 1 m off the marsh edge up into the uneroded salt marsh, respectively; EI means eroding; 1ED and 5ED represent 1 m and 5 m off the marsh edge down into the eroded open bay, respectively.

3.5. Linking microbial communities with environmental variables

The Mantel test and redundancy analyses were performed to explain the association between microbial communities and environmental variations along the erosion gradient. Overall, the diversity and composition of the bacterial and fungal communities can be explained by soil pH, salinity, soil temperature, plant biomass, and total C and N concentrations (Figure 7a). Furthermore, RDA explains 61.7% and 62.5% of the relationship between bacterial and fungal communities and environmental variables, respectively (Figure 7b–c). More specifically, bacterial communities are strongly associated with plant biomass, soil temperature, and soil TN concentration (together they explain 64.7% of the total variation); fungal communities are mainly associated with plant biomass, soil C:N ratio, and bulk density (explained 52.7% of the variation) (Figure S4). These results suggest that a combination of soil nutrient availability and plant biomass explains most of the variation in microbial communities.



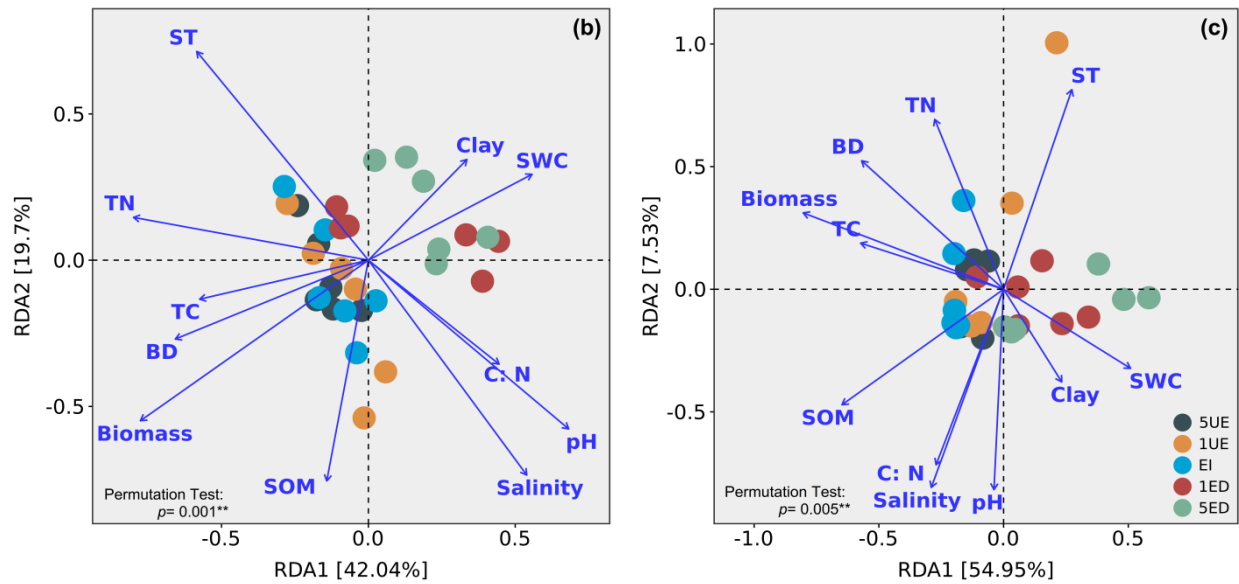


Figure 7. Relationships between bacterial (b) and fungal (c) communities and environmental variables along the marsh erosion gradient according to the Mantel test (a) and redundancy analysis (RDA) (b, c). (a) Heatmap shows a pairwise comparison between environmental variables based on Pearson correlations. (b, c) The arrows indicate the types of environmental variables and their relative effects on microbial communities (top 10 most abundant genera). * represents $p < 0.05$; ** represents $p < 0.01$; *** represents $p < 0.001$. 5UE and 1UE represent 5 m and 1 m off the marsh edge up into the uneroded salt marsh, respectively; EI means eroding; 1ED and 5ED represent 1 m and 5 m off the marsh edge down into the eroded open bay, respectively. EC is electric conductivity; SWC is soil water content; BD is bulk density; TC is total carbon; TN is total nitrogen; C:N is carbon to nitrogen ratio; SOM is soil organic matter; ST is soil temperature.

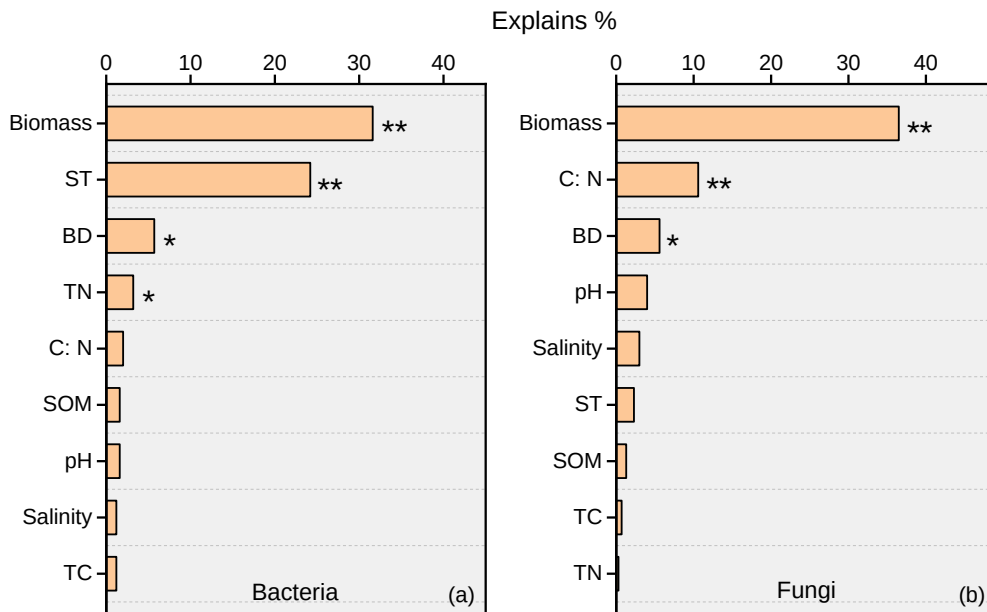


Figure S4. Percentage of variation of soil bacterial (a) and fungal (b) communities explained by environmental variables based on the results of redundancy analysis (RDA). ST is soil temperature; BD is bulk density; TN is total nitrogen; C:N is carbon to nitrogen ratio; SOM is soil organic matter; TC is total carbon.

4. Discussion

4.1. *Distinct responses of soil bacterial and fungal diversity to erosion*

Numerous studies in terrestrial ecosystems have showed that erosion can evidently alter soil physicochemical parameters, reduce soil C and N pools, and thus regulate the nutrient budget balance (Qiu et al., 2021; Steinmuller et al., 2020; Xiao et al., 2018). In line with these studies, our data demonstrated clear differences in the variations of soil properties, environmental variables, and plant biomass along the marsh erosion gradient, where at the eroded sites, the levels of soil TC, soil TN, SOM concentrations, and plant biomasses were lower, and soil water content were higher than at the uneroded sites (Table 1).

A lack of plant cover and associated root exudates and decomposition of residues at eroded sites usually result in reduced soil nutrients and organic matter, as well as inhibited microbial activity and nutrient conversion capacity (Cline and Zak, 2015; Qiu et al., 2021; Zhang et al., 2018). Furthermore, the collapse and wetland subsidence caused by marsh erosion also releases previously sequestered sediment and nutrients by converting marsh into mudflats and changing the redox environment (Sapkota and White, 2021; Steinmuller and Chambers, 2019).

Taken together, our findings indicate that the combination of plant loss and wetland subsidence following marsh erosion could strongly regulate the soil physicochemical parameters and plant biomass, which we found was accompanied by a decrease in the soil nutrient availability and primary productivity of the coastal marsh.

In the present study, the abundance of the bacterial community (mean $1.66\text{E}+08$ copies g^{-1} soil) was significantly higher than that of the fungi (mean $3.81\text{E}+06$ copies g^{-1} soil) in the coastal salt marsh. This difference was likely predominantly due to the different erosion responses of soil bacterial and fungal communities in coastal marshes. On the one hand, it is well known that fungi prefer the well-aerated acidic soil and play a critical role in organic matter conversion in terrestrial ecosystems; fungi are less active in anoxic wetland environments (Ipsilantis and Sylvia, 2007; Mohamed and Martiny, 2011). On the other hand, the freshwater from runoff mixed with saltwater from the ocean in the estuary creates a special habitat that increases the abundance of bacteria by providing additional resources and ecological niches (Hu et al., 2022a). Moreover, because fungi (3–8 μm) usually have larger individuals than bacteria (0.5–1 μm), fungi take up more space and are more restricted by the porosity of soil aggregates (Finlay, 2002; Xiao et al., 2018).

Intriguingly, after marsh erosion occurred, contrasting patterns of responses to marsh erosion were observed for the diversity of bacterial and fungal communities, with a decrease in bacteria and an increase in fungi with erosion (Figure 3). This finding is consistent with previous reports showing that bacteria and fungi occupy different niches and exhibit contrasting responses to substrate availability and changes in environmental variables (Alfaro et al., 2017; Bahram et al., 2018; Jiang et al., 2021). Abundant root exudates and plant residues at uneroded sites (with plant cover) can provide a sufficient organic substrate and suitable environment for the growth of soil microorganisms, thereby promoting the abundance and diversity of bacteria (Fujii et al., 2021; Yarwood and Högborg, 2017). Our results corroborated this finding: the Mantel test and redundancy analysis indicated a significant positive correlation between bacterial diversity and soil TN, C:N ratio, and plant biomass across all samples (Figure 7). Nevertheless, plant communities may inhibit fungal diversity by limiting microbial biomass caused by litter changes (Jiang et al., 2021). Mohamed and Martiny (2011) also confirmed that salinity, rather than vegetation cover, primarily influences fungal communities in

4.2. Erosion changes in the composition of soil bacterial and fungal communities

In our study, marsh erosion resulted in marked alternations in the composition (beta-diversity) of the soil bacterial and fungal communities and shifted the microbial taxonomic composition along the erosion gradient. Soil microbial communities are closely related to environmental variables; therefore, changes in soil physicochemical properties and reduced plant biomass and associated resource availability following erosion (Table 1) may result in selective stress on microorganisms and exclude many microorganisms from erosion sites (Lozupone and Knight, 2007). For example, different dominant vegetation often has specific bacterial and fungal communities, and plant loss caused by erosion will directly or indirectly alter the microbial community by affecting residue decomposition and resource availability (Hinshaw et al., 2017; Wang et al., 2021; Yarwood and Högborg, 2017). This scenario is corroborated by a strong relationship between bacterial and fungal composition and plant biomass along the erosion gradient in our study (Figure 7).

In addition, the composition of the bacterial community showed obvious clustering at different erosion sites, emphasizing that bacteria was more sensitive to marsh erosion than fungi. This reasonable discrepancy was driven mainly by the different responses of bacteria and fungi to environmental changes combined with their direct or indirect substrate competition (Jiang et al., 2021; Rousk et al., 2010). Interestingly, we also observed that microbial network complexity was higher in bacteria than in fungi (Figure 6). Higher microbial network complexity generally implies the simultaneous presence of different freshwater and saltwater bacterial communities at this coastal estuarine confluence; the result is a richer and unique microbial community, consistent with the higher bacterial abundance and diversity we observed (Figures 2–3). This observation further validates the widely established concept of microbial biogeography that habitat specificity determines the type and distribution of microorganisms, leading to a heterogeneous distribution of microorganisms across different ecosystems (Bahram et al., 2018; Lozupone and Knight, 2007; Wu et al., 2013).

Soil bacterial and fungal communities, especially their functional groups, play a crucial role in regulating nutrient cycling and maintaining soil productivity. Our data clearly indicates that erosion affects microbiome complexity and keystone taxa (Figure 5; Figure S3). For instance, the bacteria *Chloroflexi* (*SBR1031*, *KD4-96*) and *Proteobacteria* (*MND1* and *MBNT15*) were widely distributed at the uneroded sites. The *Anaerolineae* *SBR1031* are the dominant taxa involved in nitrosation and anammox processes under anoxic conditions, and has potential impacts on N conversion and soil fertility (Chen et al., 2013; Zhu et al., 2022). *Proteobacteria* *MBNT15* exist in a broad range of mostly organic-rich environments (Begmatov et al., 2022). Although *Proteobacteria* *Woeseia* is ubiquitous in marine ecosystems, we found that it was dominant at the eroded sites, indicating that its wetland habitat was affected by marine erosion. *Woeseia* plays an important role in nutrient biogeochemical cycles, such as inorganic C assimilation, sulphur oxidation, and denitrification (Dyksma et al., 2016; Mußmann et al., 2017). In addition, we noted that considerable uncultured *Nitrospirae* are widely distributed in various habitats. *Nitrospirae* is a common nitrite oxidizing bacterium capable of complete nitrification and possessing a wide range of metabolic diversity, including the use of various compounds, nitrification, and chemical autotrophic aerobic hydro-oxidation (Wu et al., 2021).

Regarding fungi, *Papiliotrema* and *Leptoxylum* were dominant at the uneroded sites, and *Dictyophora* and *Verticillium*, at the eroded sites (Figure S3). These genera have been reported to be involved in the residue decomposition and organic matter conversion, and are indispensable for the C and N cycles in soil (Mohamed and Martiny, 2011; Wu et al., 2013). More precisely, *Papiliotrema*

is distributed in nutrient-rich ecosystems, such as farmland and artificial ponds, and is closely related to soil C and N cycles (Nevins et al., 2022). These conclusions and causality were also confirmed by the presence of higher soil TC, TN, and SOM concentrations at the uneroded sites relative to the eroded sites (Table 1).

Our observations, combined with previous findings, confirm that soil bacterial and fungal communities (especially bacteria) are sensitive to coastal marsh erosion, and changes in soil and plant properties affect microbial communities and, in turn, nutrient cycling and soil function.

4.3. Implications and future works

This study sheds light on the potential impact of marsh erosion on soil microbial communities by focusing on the dynamic changes of the abundance, diversity, and composition of the bacterial and fungal communities along an erosion gradient. Our findings suggest that coastal marsh erosion eliminated vegetation cover and reduced soil TC, TN, and SOM concentrations.

These effects are associated with lower levels of soil nutrient availability and plant productivity at the eroded sites (Figure 8). Marsh erosion had opposite effects on bacterial and fungal diversity: fungal taxonomic diversity increased and bacterial taxonomic diversity decreased with the erosion gradient. Further, both bacterial and fungal community compositions responded visibly to erosion and were reshaped along the erosion gradient, especially bacteria. This finding indicates that bacteria and fungi have different survival abilities in poor soils. In addition, the fungal community adapted better to stress conditions; the poorer C and nutrient resources, the stronger the stress of fungi. Additionally, a lower F:B ratio at the eroded sites is associated with an increased C turnover rate through reduced soil C retention (Xiao et al., 2018).

Together, these findings emphasize that erosion-induced changes in soil properties and plant loss alter the abundance, diversity, and composition of bacterial and fungal communities, but their responses were inconsistent in our study. Therefore, the relative contributions of these bacterial and fungal taxa to nutrient cycling and soil function differed with marsh erosion.

Future research should consider several uncertainties when the results are expanded from the local to a regional or global scale. First, coastal marshes are an open system whose edge erosion is a dynamic process because of the constant effects of waves caused by tides and runoff. Further research on erosion-induced changes in microbial communities and functions and their effects on ecosystem services and functions should be carried out at longer time and broader spatial scales. Second, frequent extreme climatic events such as typhoons and rainstorms, especially in subtropical regions, will alter hydrological dynamics. This will exacerbate the erosion and collapse of the marsh edge and alter the habitat environmental parameters, potentially regulating microbial activity and nutrient cycling.

Additionally, although in this study the effects of plant biomass on microbial diversity and composition have been observed, the role of plant rhizosphere activity and decomposition of residues has not been directly identified. Future research should focus on the temporal, spatial, or site-specific coupling of the driving forces regulating soil microbial community dynamics (e.g., redox environment, coastal management, and plant succession) to elucidate the role of marsh erosion on regional microbial communities and their function.

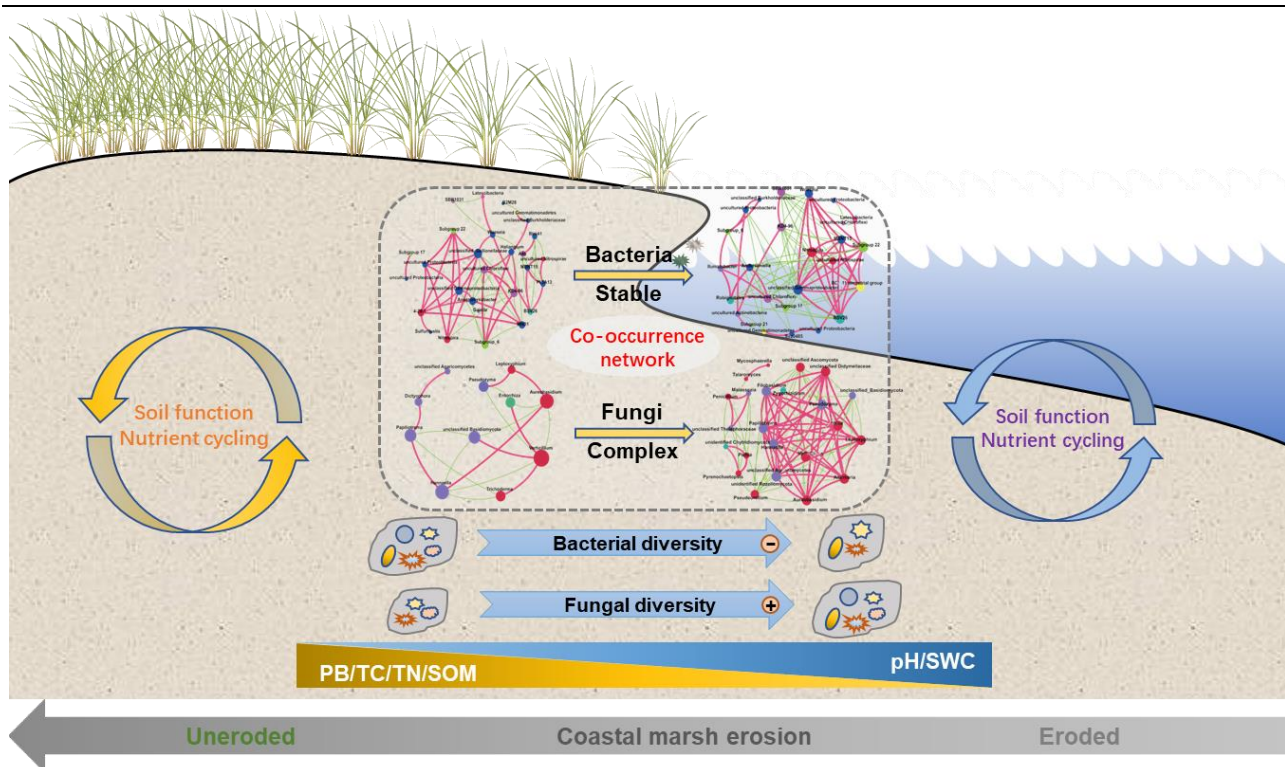


Figure 8. The conceptual framework showing the effects of marsh erosion on soil bacterial and fungal communities along an erosion gradient. Positive sign indicates an increase, and negative sign indicates a decrease. PB is plant biomass; TC is total carbon; TN is total nitrogen; SOM is soil organic matter; SWC is soil water content.

5. Conclusions

Our study demonstrated that marsh erosion caused substantial changes in the abundance and diversity of soil bacterial and fungal communities at the investigated sites by changing soil properties and plant biomass, which decreased bacterial diversity but increased fungal diversity along the erosion gradient. Our findings also showed that marsh erosion can reshape the structure of bacterial and fungal communities, particularly by clustering bacterial communities into three groups: uneroded, eroding, and eroded. This observation suggests that the shift in microbial composition is closely related to the response of soil properties (such as soil nutrient availability and plant biomass) to erosion. Bacteria and fungi have different ecological niches, so they have a different response ability and model to changes in substrate availability and environmental variables.

These results support our hypothesis that the transition from uneroded to eroded drove the decrease in bacterial and fungal abundance, and the decrease in bacterial diversity and increase in fungal diversity. These changes are associated with an increased complexity and stability of the fungal network, because relative to bacteria, fungi responded differently to changes in soil and plant properties.

Further studies considering multi-factor interactions are urgently needed to reveal how marsh erosion affects microbial processes and their functional characteristics at broader spatiotemporal scales. The gained knowledge will be key for a sustainable management of these habitats.

Acknowledgments

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