

External magnetic field have significant effects on diversity of magnetotactic bacteria in sediments from Yangtze River, Chagan Lake and Zhalong Wetland in China

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ABSTRACT

Magnetotactic bacteria (MTB) can rapidly relocate to optimal habitats by magnetotaxis, and play an important role in iron biogeochemical cycling. This study aimed to evaluate the contribution of the external magnetostatic field to the diversity of MTB in freshwater sediments from Yangtze River (Changjiang River, CJ), Chagan Lake (CGH) and Zhalong Wetland (ZL). The magnetic field intensity was tightly associated with the community richness of MTB in CJ, whereas it was closely related to the diversity of MTB in CGH and ZL ($p < 0.05$), elucidating a significant variation in the community composition of MTB. Magnetic exposure time appeared more significant correlation with community richness than diversity for MTB in CJ and CGH ($p < 0.05$), while an opposite relationship existed in ZL ($p < 0.01$). *Herbaspirillum* (93.81–96.48 %) dominated in the sediments of these surfacewaters regardless of waterbody types, while it shifted to *Magnetospirillum* in ZL under 100 Gs magnetic field. The network connectivity and stability of MTB deteriorate with the increase of magnetic field intensity. Functional analysis showed that the Two-component system and ABC transporter system of MTB obviously responded to magnetic field intensity and exposure time. Our findings will pave the way to understanding the response mechanism of MTB community in freshwater sediments to the external magnetostatic field.

1. Introduction

MTB are motile, diverse group of ubiquitous gram-negative bacteria with the ability to mineralize dissolved iron into the magnetosomes, which are a kind of organelle consisting of magnetic crystals (Fe_3O_4 and/or Fe_3S_4) covered by cell membrane (Camp, 2023; Gareev et al., 2021). Generally, the magnetosomes are aligned in one or more chains parallel to the long axis of the MTB cell, which cause the cell to swim/move along the geomagnetic field lines and other applied external magnetic fields (Kotakadi et al., 2022). MTB are distributed worldwide in aquatic environments such as oceans, lakes, rivers, marsh, estuaries, drains and estuaries as well as in chemically stratified water columns or sediments of these environments (Lin et al., 2017; Xing et al.,

2020). They are usually found at and below the oxic–anoxic transition zone (OATZ) and occur at a relatively high cell density of approximately 10^4 cells/mL at the oxic–anoxic interface and the anoxic regions of the habitat (Amor et al., 2020; Wang et al., 2020). The morphotypes of MTB include vibrio, cocci, spirilla, rod, and multicellular forms (Wang et al., 2013). It has been reported that most discovered MTB belong to *Alphaproteobacteria*, *Deltaproteobacteria*, *Zetaproteobacteria*, *Gammaproteobacteria*, *Candidatus Lamdaproteobacteria*, *Candidatus Etaproteobacteria* classes of the *Proteobacteria* phylum, and the *Nitrospirae* phylum, *Candidatus Omnitrophica* phylum, the *Candidatus Latescibacteria* phylum, and the *Planctomycetes* phylum (Ying et al., 2022). Through the reconstruction of 168 MTB genome sketches (The reconstructed genomes are from NCBI and NMDC with serial numbers PRJNA400260 and NMD

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C10017683, respectively), MTB could be classified into 13 bacterial families, including *Alphaproteobacteria*, *Deltaproteobacteria*, *Gammaproteobacteria*, *Zetaproteobacteria*, *Etaproteobacteria*, *Lambdaproteobacteria*, *Nitrospirae*, *Candidatus Omnitrophica*, *Planctomycetes*, *Candidatus Riflebacteria*, *Fibrobacteres*, *Candidatus Latescibacteria*, *Oligoflexia* (Lin et al., 2020).

The Earth's magnetic field sensing ability provides the unique characteristic of MTB compared with other microbes (Satyanarayana et al., 2021). In 1963, Salvatore Bellini discovered that some microorganisms with various morphologies from different freshwater environments swam northward persistently when placed into the hanging droplet and understood that their direction of motion was controlled by the geomagnetic field (Bellini, 2009). Twelve years later, Blakemore rediscovered that some microbes migrated northward continually. He called this phenomenon "magnetotaxis" and named these bacteria as "Magnetotactic bacteria" (Blakemore, 1975). Phase contrast microscope observation indicates that MTB can swim to the magnet pole at 100 $\mu\text{m/s}$ speed when the magnet is close to the microscope (Blakemore, 1982). The proper magnetic field intensity (0–500 mT) boosted both coefficient of magnetism (C_{mag} , the ratio of scattering intensity to light beam at different magnetic field angles, can be used for the semiquantitative evaluation of magnetite formation) and iron content of *Magnetospirillum gryphiswaldense* MSR-1 cells, thereby increasing the proportion of magnetosome-containing bacteria. However, the high magnetic field intensity (700 mT) adversely affected cell growth and magnetosome beta diversity synthesis of *M. gryphiswaldense* MSR-1 (Leila et al., 2019). The previous study indicated that Earth's field, zero field and alternating field appeared different effect on the cell concentrations of two wild-type MTB (cocci and rod-shaped *Magnetobacterium bavaricum*) in the sedimentary environment (Mao et al., 2022).

It has been reported that the distribution of MTB may be significantly affected by the geomagnetic field (Li et al., 2020; Mao et al., 2022). The biodiversity can be described by alpha and beta diversity, the former refers to the level of diversity at focal research sites, while the latter indicates compositional differences between these research units of alpha diversity (Magurran, 2021). The beta diversity of the dominant MTB community was found to show a significant correlation with the gradient of the Earth's magnetic field intensity by analysis of surface sediment samples from 16 sites in China and America (Lin et al., 2013). Additionally, the tight correlation between the variation of the MTB community and the geographic distance of sampling sites were discovered by the analogy of the publicly available MTB data (Burrows et al., 2019). This finding indicated that the geographical pattern of MTB might be driven by magnetic field intensity because Earth's magnetic field intensity varies over the Earth's surface (Lin et al., 2013; Mao et al., 2022). Over the past 3 decades, information on the phylogenetic diversity of MTB and their relationship with physicochemical factors are available anywhere, and the study on the magnetic field response of MTB almost focused on a single bacterium or isolated strain. However, there are few studies or sparse data on the influence of magnetic field gradients on the MTB community.

This study investigated the effects of an external magnetic field on MTB diversity in freshwater sediments from three different surface water bodies (CJ, CGH and ZL) by employing a microcosm incubation experiment. The response of alpha diversity, community composition, co-occurrence patterns and community function of MTB to static magnetic field strength geomagnetic field (0.5 Gs, 50 Gs and 100 Gs) and magnetic exposure time (1, 5, 8 and 11 weeks) were systematically addressed, respectively. In addition, the statistically significant correlation between magnetic field intensity and MTB diversity indices were established. This study will provide new insights into the contribution of the magnetic field to the enrichment process and diversity of MTB in environmental samples.

2. Materials and methods

2.1. Sampling and microcosm setup

Freshwater sediment samples were collected from the middle reaches of the Yangtze River (29.29°–30.69°N, 111.30°–116.27°E) in the running-water ecosystems, the static-water/lentic ecosystem, including Chagan Lake (45.15°–45.5°N, 124.05°–124.57°E) and Zhalong Wetland (46.86°–47.53°N, 123.78°–124.61°E) (Fig. 1). At each site, three surface sediment samples (0–5 cm) were obtained, and each sediment sample was composed of 5 subsamples pooled together in equal proportions. Finally, three sediment samples were mixed with an equal mass ratio, and in-situ water samples above the sediment-water interface were collected and sealed in an aseptic sampling bottle. All samples were transported to the laboratory in darkness and kept at a low temperature.

Microcosms were set up using a 250 mL aseptic sampling bottle with a height of 8.3 cm and a diameter of 6.9 cm. Each sampling bottle was filled with 200 g of sediment mixed sample and 140 mL of in-suit water, then sealed and set aside. The static magnetic field was established by adjusting the distance between two ordinary magnets (84.6 × 64.8 × 18 cm) (Fig. S1). The magnetic field intensity of the center of the microcosm bottle is measured by a hand-held teslameter (Changsha Tianheng Measurement and Control Technology Co., Ltd., TD8620) to ensure that the sample is in a uniform magnetic field for the experiment. The microcosm experiments were carried out at room temperature in darkness under the external magnetic field intensity of 0.5, 50 and 100 Gs for 5 weeks, and under the external magnetic field of 0.5 and 50 Gs for 1, 5, 8 and 11 weeks, respectively. The microcosm without external magnets, i.e., under a geomagnetic field (0.5 Gs) is used as the control group. All microcosms are placed in the same dark room to isolate other parameters that may affect the composition of the population, and the microuniverses with different magnetic field intensities are shielded from magnetic field interference through larger metal cages. Three repeats of the microcosm culture experiment were conducted.

2.2. Magnetic enrichment and collection

The magnetic enrichment method and magnetic capillary racetrack technique are commonly used for studying MTB, which have the advantages of simplicity, convenience, speed and efficiency (Koziaeva et al., 2019). After exposure to the magnetostatic field, MTB were collected by these two methods according to previous reports (Koziaeva et al., 2019; Xing et al., 2020). Briefly, the surface sediment was stirred gently to homogenize with Pasteur pipette, then the sediment samples were enriched by closely placing a south pole permanent magnet (approximately 500 Gs, this higher magnetic field strength is beneficial for separating MTB with weaker magnetotaxis) to the mud-water interface of the microcosm sampling bottle surface for 30 min. The sediment-water mixture adjacent to the magnet was collected with a sterile pipette and further collected using a capillary racetrack and a 500 Gs magnet for 30 min. MTB migrated towards the top of the capillary were collected by intercepting the tip 2 cm. This process was repeated 6 times for each sample.

2.3. TEM observation

The in-situ water samples (IS), magnetic enrichment method treated samples (ME), and magnetic capillary racetrack technique treated samples (MCR) were collected from the CJ, CGH and ZL, respectively. After vortex shaking the sample, take 1–2 drops of the sample and rest on a copper mesh for 10 min. Then the excess suspension was sucked with the filter paper and dyed with 2 % phosphotungstic acid dye solution for 2 min, and the dye solution was absorbed by the filter paper. After drying, the morphology of MTB from different samples were

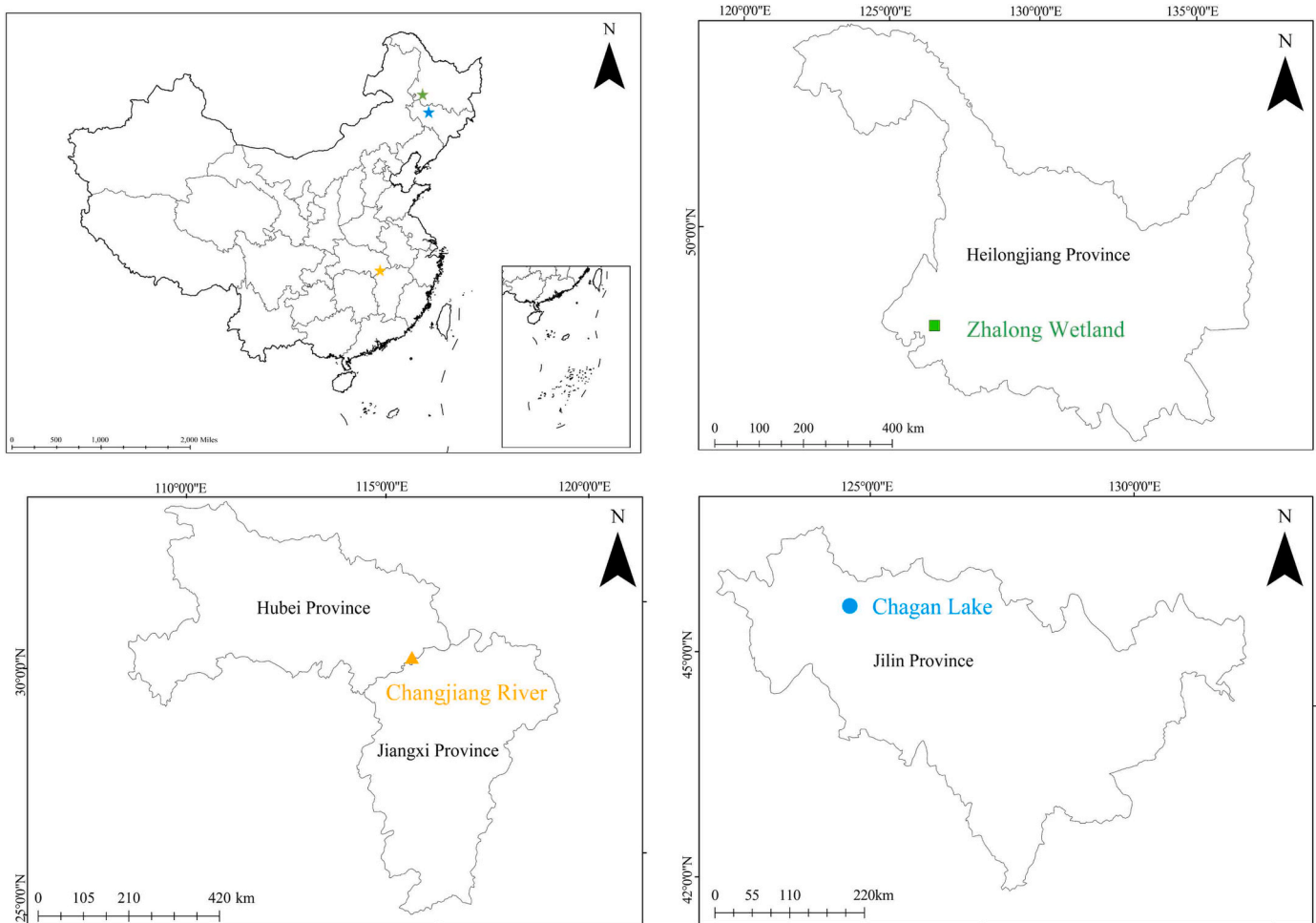


Fig. 1. Map indicating position of sampling site for sediments and in-situ waters.

examined with HT7700 transmission electron microscope (HITACHI, Tokyo, Japan) at 80 kV.

2.4. 16S RNA amplification and sequencing

The primers consisted of 515 F (5'-GTGCCAGCMGCCGCGGTAA-3') and 909 R (5'-CCCCGYCAATTCMTTTRAGT-3') were used to amplify hypervariable region V4 of 16 S RNA genes directly from magnetically purified MTB cells (Xing et al., 2020). The PCR reaction was carried out according to the protocol described (Liu et al., 2022). The PCR products were confirmed using electrophoresis in a 1.0 % agarose gel and purified by PCR Cleaning Kit (AP-PCR-50, Axygen, Jiangsu, China). The concentration and quality were determined by Nanodrop 2000 (Thermo Fisher Scientific, Co., Ltd. Shanghai, China). The gel-purified products were sequenced using Illumina Hiseq2500 (BioMarker Technologies, Beijing, China).

2.5. Analysis

The sequences of the operational taxonomic units (OTUs) were compared with the Genbank database (nt/nr) using the BLASTN algorithm (<http://www.ncbi.nlm.nih.gov/BLAST/>). The OTUs associated with the MTB were screened from the output sequence. The classification of all OTUs sequences was manually corrected, and a ≥ 85 % similarity threshold was used to screen the MTB related sequences (Liu et al., 2022; Xing et al., 2020).

The bioinformatics analysis was performed on the Biomarker Cloud platform (www.biocloud.net). The analysis of the bacterial diversity

frequently includes different estimates of the actual number of taxa, e.g., abundance-based coverage estimator (ACE), Chao1, Shannon, and Simpson index, whereas ACE and Chao1 indices are used to estimate community richness, and Shannon and Simpson indices were calculated based on observed species as a measure of community diversity. Chao1 is defined as $S_{Chao1} = S_{obs} + \frac{a^2}{2b}$, where S_{obs} is the number of detected taxa, a is the number of taxa containing one sequence (singletons), and b is the number of taxa containing two sequences (doubletons) (Chernov et al., 2015). ACE is defined as $S_{ACE} = S_{abund} + \frac{S_{rare}}{C_{ACE}} + \frac{F_1}{C_{ACE}} \gamma_{ACE}^2$, where S_{abund} and S_{rare} are the number of abundant and rare OTUs, respectively, C_{ACE} is the sample abundance coverage estimator, F_1 is the frequency of singletons, and γ_{ACE}^2 is the estimated coefficient of variation for rare OTUs (Kim et al., 2017). The Shannon index of diversity (SHDI) is defined as $SHDI = 1 - \sum_{i=1}^N Np_i \times \ln p_i$, where N is the number of land cover types and p_i the proportional abundance of the i th type. The Simpson index (SIDI) is defined as $SIDI = 1 - \sum_{i=1}^N Np_i \times p_i$ (Nagendra, 2002). These indexes were all calculated by Mothur (v.1.30, <https://mothur.org/>).

The Chao 1, Simpson, ACE and Shannon index were calculated by Mothur (v.1.30, <https://mothur.org/>). The significance analysis of diversity indexes using PASW Statistics 26.0 (SPSS, Chicago, Illinois, USA). Regression analysis of the relationship between diversity indices and magnetic field intensity or magnetic exposure time were performed using Origin 2022b (Origin Lab, Northampton, USA). The phylogenetic relationship of MTB from different samples were ascertained by the unweighted pair group method with arithmetic means (UPGMA) using the python 2 (<https://python.org/>). MTB community comparisons were visualized by nonmetric multidimensional scaling (NMDS) using the

QIIME 1.9.1 (<http://qiime.org>). The co-occurrence networks were presented and the topological properties (i.e., clustering coefficient and shortest average path length) were generated using the interactive platform Gephi (<http://gephi.github.io/>). The STAMP v2.1.3 (<http://kiwi.cs.dal.ca/Software/STAMP>) was used to predict the function of genes, and ANOVA of STAMP analyzed the data.

The variation of Alpha diversity index of MTB with magnetic field intensity and magnetic exposure time was fitted by Polynomial Fitting in Origin (version 2021b, OriginLab, USA), and the correlation and fitting situation between them were analyzed.

2.6. Nucleotide sequence accession number

The high-quality sequence data was deposited in the National Microbiology Data Center (<http://nmdc.cn>, NMDC Accession SUB1676633432424).

3. Results

3.1. Microbial morphology in different treated sediments

According to the TEM results, three morphological types of MTB can be observed in the samples, i.e., rod-shaped and oval-shaped and arc-shaped microbes (Figs. 2–4). The rod-shaped MTB was dominant in CJ, CG and ZL (Fig. 2d and h; Fig. 3c, d, h and i; Fig. 4d, g and i), and a small number of arc-shaped MTB were found only in CJ-ME (Fig. 2f). It was worth noting that no MTB was found in CJ-IS (Fig. 2a–c). In addition, the magnetosomes were mainly dispersed in the cells (Fig. 2d, f–i; Fig. 2d, e, g–i; Fig. 4c, e, g, h and i). Most magnetosomes are generally organized into single or multiple chains, which tend to be parallel to the long axis (Fig. 2g and h; Fig. 3c; Fig. 4d and i).

3.2. Alpha diversity responded to the magnetic field

The alpha diversity indices of MTB in three freshwater sediments under different external magnetic fields are shown in Table 1. Coverage, species richness and diversity indexes at different magnetic fields (0.5,

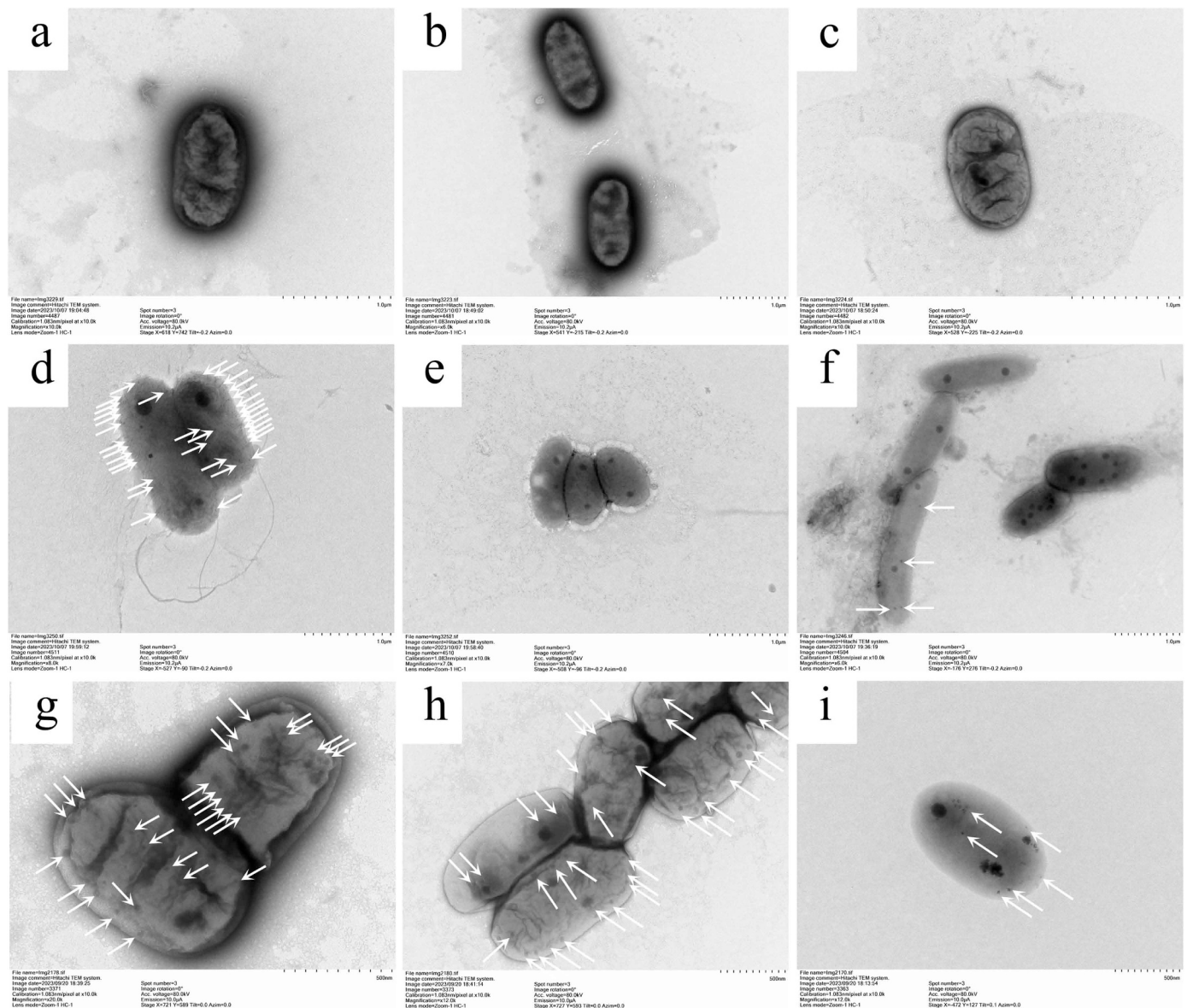


Fig. 2. Transmission electron microscope (TEM) images of CJ (a–c: CJ-IS; d–f: CJ-ME; g–i: CJ-MCR. a, c, e, g and i: oval-shaped; b, d, f and h: rod-shaped; e, f: arc-shaped. a–f: scale bars is 1 μ m, g–i: scale bars is 500 nm).

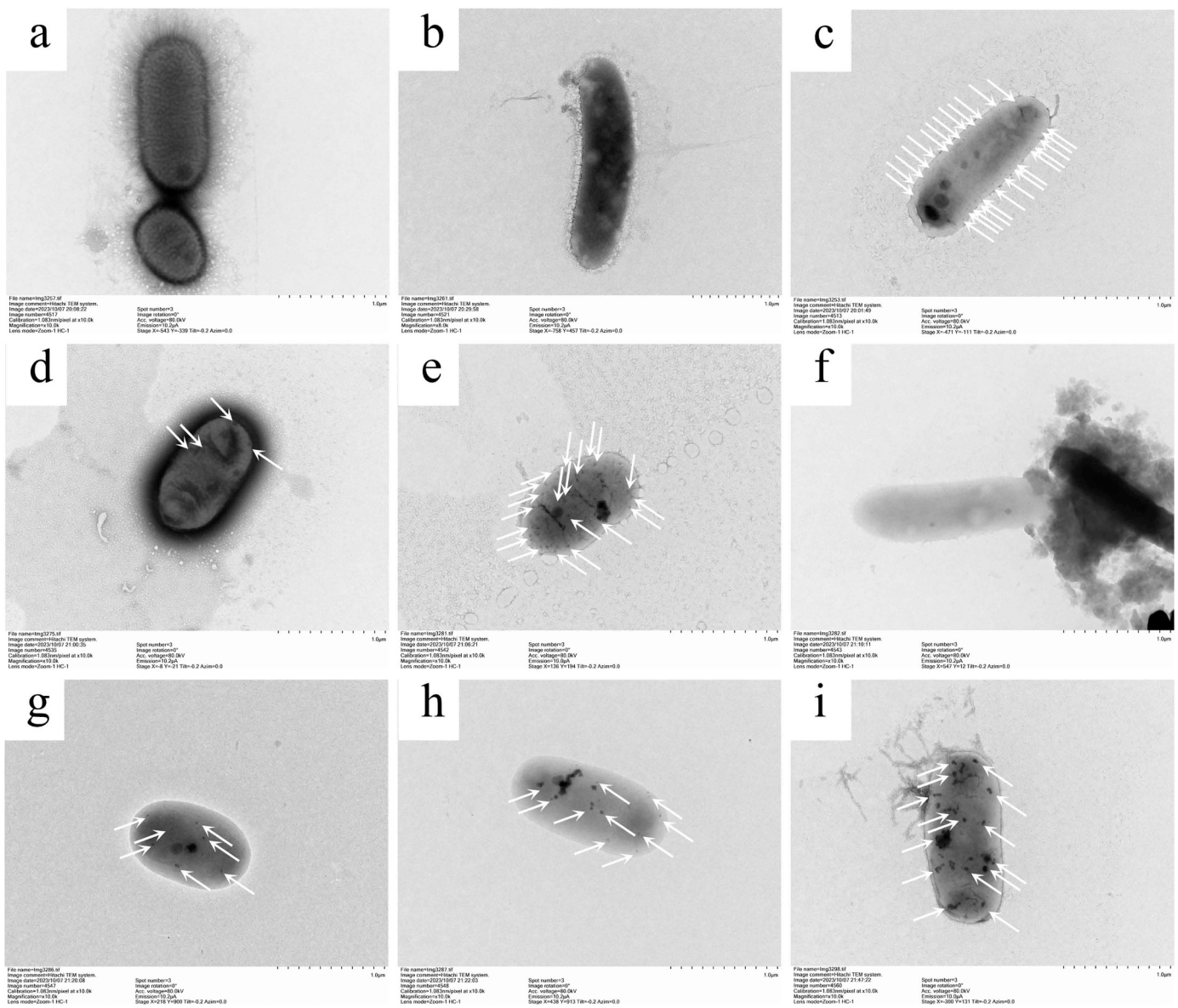


Fig. 3. Transmission electron microscope (TEM) images of CG (a-c: CG-IS; d-f: CG-ME; g-i: CG-MCR. a, e and g: oval-shaped; a, c, d, f, h and i: rod-shaped; b: arc-shaped. a-i: scale bars are 1 µm).

50, 100 Gs) were calculated for each sediment sample. The Good's coverage ranged from 97 % to 99 %, indicating that the rarefied sequencing depth was adequate to evaluate the phylogenetic diversity in each sample. The OTU numbers, ACE index and Chao 1 index of MTB in CJ under 0.5 Gs magnetic field were 34.67, 41.03 ± 3.04 and 39.73 ± 2.90 , respectively lowest in all samples, and the Chao 1 index and Shannon index are positively correlated with the magnetic field intensity. With the increase of magnetic field intensity, the Chao 1 index and Shannon index of MTB from CGH were first decreased and then increased, whereas an opposite trend appeared in Chao 1 index of MTB in ZL. The Shannon index of MTB in ZL was the lowest and declined gradually with increased magnetic field intensity. Generally speaking, the response of diversity and abundance of MTB in different water bodies to magnetic field change were different.

The relationships between the magnetic field intensity and diversity indices were assessed by regression analysis, where the Chao1 index and Shannon index represent the abundance and diversity of MTB in the sample, respectively (Liu et al., 2022) (Fig. 5). The results showed that the Chao1 index of MTB in CJ was closely associated with magnetic field intensity ($R^2 = 0.8030$, $p < 0.01$) (Fig. 5a) but weakly associated with

the Shannon index ($R^2 = 0.6708$, $p < 0.05$) (Fig. 5b). These indicated that the contribution of the external magnetic field intensity to community richness of sediment MTB was much greater than diversity. The highly significant correlation between the magnetic field intensity and Shannon index of MTB in CGH ($R^2 = 0.8411$, $p < 0.01$) (Fig. 5d) and ZL ($R^2 = 0.9026$, $p < 0.01$) (Fig. 5f) were observed, respectively, indicating that the contribution of magnetic field intensity to MTB community diversity was greater than their community richness.

The diversity indices of the MTB from three samples at different magnetic exposure times (1, 5, 8 and 11 weeks) under the 0.5 Gs and 50 Gs magnetic field are shown in Table 2. The lowest values for the OTU numbers (19.00), Chao1 index (21.01 ± 0.70) and Shannon index (2.20 ± 0.24) of MTB in CJ were presented, whereas their highest values appeared in CGH (Table 2). Under the intensity of 0.5 and 50 Gs magnetic field, the Chao1 index and Shannon index of MTB in CJ increased first and then decreased and reached the maximum at 5 weeks. The Chao1 index of MTB in CGH rose first and then decreased with the increase of time, whereas the Shannon index decreased continuously. The Chao1 index of MTB in ZL recovered rapidly after trough level at 5 weeks. With magnetic exposure time increase, the change of Shannon

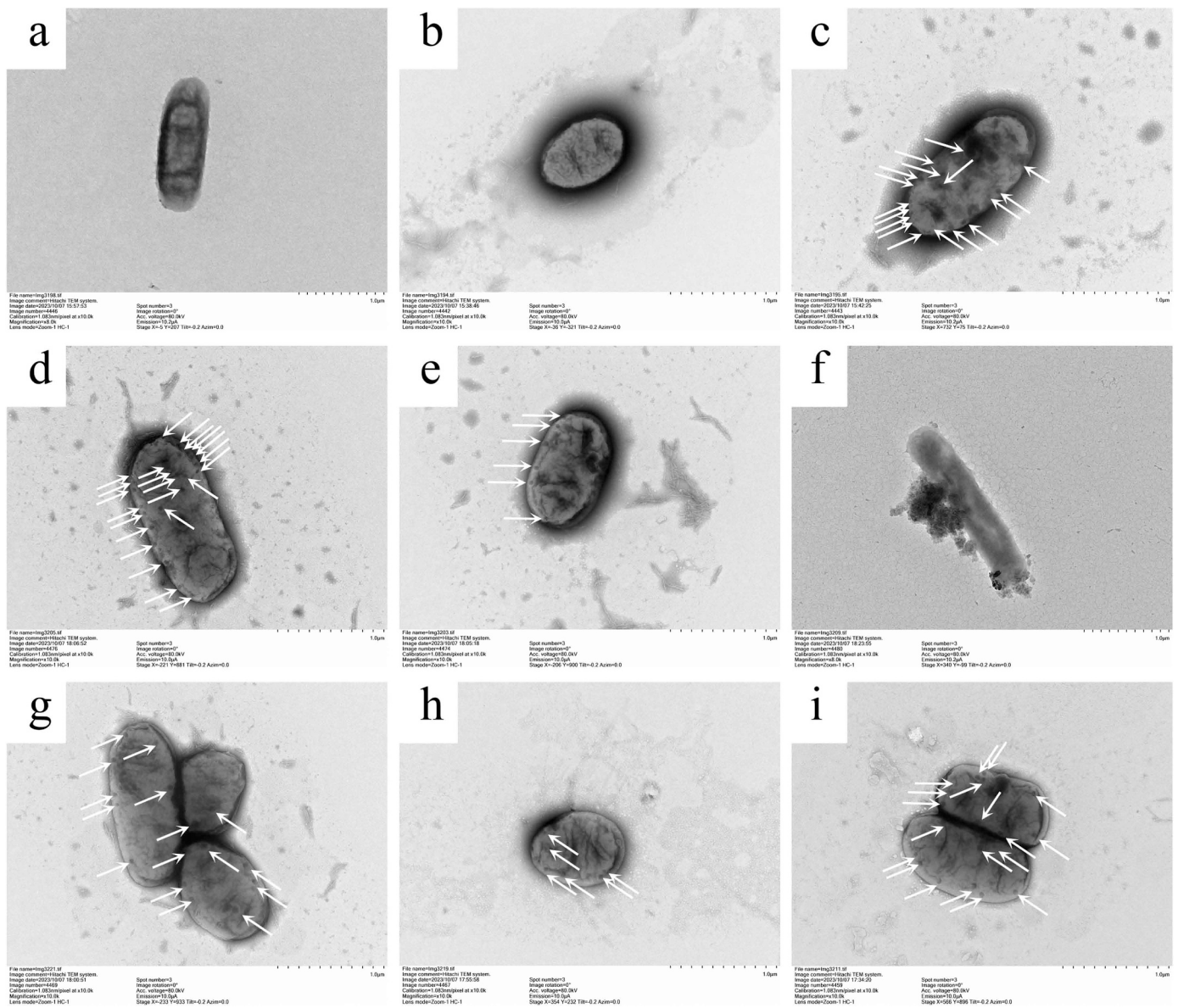


Fig. 4. Transmission electron microscope (TEM) images of ZL (a-c: ZL-IS; d-f: ZL-ME; g-i: ZL-MCR. a, d, f, g and i: rod-shaped; b, e, g and h: oval-shaped. a-i: scale bars are 1 μ m).

Table 1
The Alpha diversity indices of MTB in three sediment samples under different magnetic field intensities.

Sample ID	OTUs	ACE	Chao1	Simpson	Shannon	Coverage (%)
CJ0	34.67c	41.03 $\pm$ 3.04b	39.73 $\pm$ 2.90b	0.84 $\pm$ 0.054abc	3.46 $\pm$ 0.36abcd	99.64
CJ50	37.33bc	49.47 $\pm$ 10.67b	44.00 $\pm$ 6.41b	0.86 $\pm$ 0.034ab	3.63 $\pm$ 0.25abc	99.61
CJ100	46.33abc	53.63 $\pm$ 7.22b	55.33 $\pm$ 8.85ab	0.90 $\pm$ 0.016ab	3.98 $\pm$ 0.15ab	99.57
CGH0	56.67a	61.66 $\pm$ 2.33ab	61.14 $\pm$ 2.31ab	0.94 $\pm$ 0.001a	4.51 $\pm$ 0.022a	99.58
CGH50	54.00a	58.69 $\pm$ 4.23ab	58.26 $\pm$ 4.39ab	0.94 $\pm$ 0.001a	4.45 $\pm$ 0.012ab	99.62
CGH100	53.67a	59.98 $\pm$ 1.22ab	61.52 $\pm$ 3.99ab	0.94 $\pm$ 0.001a	4.46 $\pm$ 0.019ab	99.56
ZL0	49.67ab	73.55 $\pm$ 3.24ab	64.78 $\pm$ 10.05ab	0.81 $\pm$ 0.033abc	3.39 $\pm$ 0.27bcd	99.29
ZL50	46.33abc	89.49 $\pm$ 25.52a	81.81 $\pm$ 21.70a	0.67 $\pm$ 0.121bc	2.67 $\pm$ 0.54 cd	99.09
ZL100	37.33bc	50.68 $\pm$ 13.21b	45.31 $\pm$ 8.44b	0.62 $\pm$ 0.151c	2.50 $\pm$ 0.61d	99.57

index of MTB in ZL showed a single peak curve under 0.5 Gs, whereas appeared an opposite trend under 50 Gs.

The relationship between the diversity indices and the magnetic exposure time of MTB was assessed by regression analysis (Fig. 6). The Chao1 index of MTB from CJ and CGH were strongly correlated with the magnetic exposure time, but weakly with the Shannon index, indicating

that the contribution of magnetic exposure time to MTB community richness was much greater than community diversity. However, the opposite results were present in the ZL.

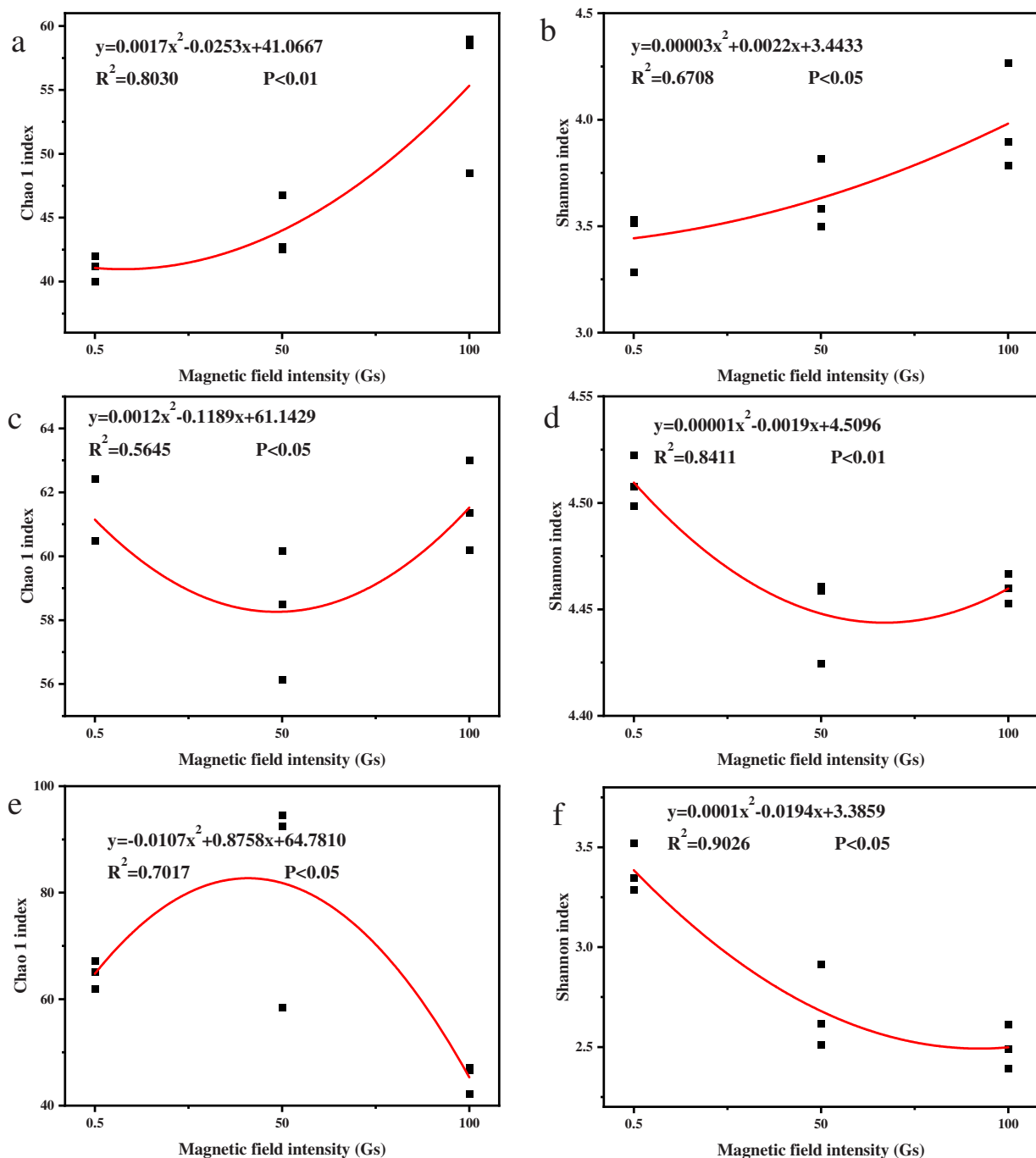


Fig. 5. Relationship between magnetic field intensity and Alpha diversity indices (a, c, e: Chao1 index; b, d, f: Shannon index) of MTB in freshwater sediment samples (a, b: CJ; c, d: CGH; e, f: ZL).

3.3. Community composition responded to the magnetic field

3.3.1. Cluster analysis

Many methods can be used for microbial beta diversity analysis, such as Principal Component Analysis (PCA), Principal coordinates analysis (PCoA), Nonmetric Multidimensional Scaling (NMDS), Unweighted Pair-group Method with Arithmetic Mean (UPGMA), Permutational Multivariate Analysis of Variance (PERMANOVA) and Analysis of Similarities (Anosim). Among, the model of NMDS is nonlinear and can better reflect the nonlinear structure of ecological data than that of PCA/PCoA (Xue et al., 2020). UPGMA is a straightforward approach to constructing a phylogenetic tree from a distance matrix, which could easily infer the evolutionary relationships of different samples (Oestreicher

et al., 2022). This paper mainly studies the influence of different magnetic fields on the diversity of MTB. Herein, the evolutionary relationship of MTB from different samples were inferred by UPGMA, and the difference in MTB community composition was visualized using NMDS (Figs. S2, S3).

The stress values of NMDS analysis in all samples were less than 0.2, indicating the reliability of this analysis. For MTB samples from CJ and ZL, 0.5 and 50 Gs magnetic field clustered together with 84.77 % and 21.36 % similarity, respectively (Fig. S2a,e). This result was supported by NMDS (Fig. S2b,d). It can be found that magnetic field intensity less than 50 Gs had a slight influence on the community structure of MTB and 100 Gs magnetic field strongly affected the MTB samples from CJ (Fig. S2a). Although the cluster analysis of MTB in CGH performed by

Table 2

The Alpha diversity indices of MTB in three sediment samples at different magnetic exposure times.

Sample ID	OTUs	ACE	Chao1	Simpson	Shannon	Coverage (%)
CJ01	19.00 ± 0.58a	24.18 ± 1.95ab	21.01 ± 0.70b	0.57 ± 0.06 cd	2.20 ± 0.24bc	98.27
CJ05	25.33 ± 0.33a	31.35 ± 2.38ab	30.88 ± 3.56ab	0.87 ± 0.03a	3.59 ± 0.20a	97.53
CJ08	18.67 ± 0.67a	31.10 ± 1.50ab	28.45 ± 1.89ab	0.74 ± 0.05abc	3.10 ± 0.32ab	98.64
CJ011	24.00 ± 2.31a	21.27 ± 0.49b	19.98 ± 0.45b	0.78 ± 0.06ab	2.79 ± 0.25abc	97.53
CJ51	18.67 ± 6.17a	32.11 ± 4.72ab	26.23 ± 6.27ab	0.66 ± 0.07bcd	2.20 ± 0.59bc	97.29
CJ55	26.33 ± 0.88a	39.37 ± 9.32a	36.50 ± 7.00a	0.86 ± 0.03a	3.65 ± 0.23a	97.29
CJ58	20.00 ± 2.89a	33.27 ± 4.88ab	30.17 ± 4.92ab	0.73 ± 0.04abc	2.60 ± 0.23abc	97.16
CJ511	16.67 ± 4.18a	21.06 ± 4.86b	20.33 ± 5.84b	0.53 ± 0.09d	1.95 ± 0.44c	98.15
CGH01	59.33 ± 0.67a	64.73 ± 0.78a	64.88 ± 2.07a	0.91 ± 0.01a	4.39 ± 0.13a	99.20
CGH05	54.33 ± 2.33a	61.91 ± 2.62ab	59.53 ± 3.43ab	0.92 ± 0.004a	4.34 ± 0.001a	99.11
CGH08	27.00 ± 7.51bc	39.85 ± 13.10 cd	34.67 ± 8.03de	0.44 ± 0.21b	2.25 ± 0.29bc	99.26
CGH011	21.67 ± 5.86c	26.47 ± 2.79d	26.74 ± 4.17e	0.69 ± 0.06a	1.75 ± 0.81c	99.47
CGH51	51.00 ± 1.15a	55.76 ± 0.42abc	55.23 ± 0.50abc	0.93 ± 0.003a	4.39 ± 0.04a	99.32
CGH55	52.00 ± 1.73a	58.41 ± 2.86abc	60.23 ± 3.88ab	0.93 ± 0.001a	4.34 ± 0.005a	99.14
CGH58	31.67 ± 3.79bc	42.16 ± 4.39bcd	45.44 ± 9.58bcd	0.70 ± 0.06a	2.49 ± 0.26bc	99.14
CGH511	33.00 ± 2.52b	46.05 ± 9.21abcd	39.62 ± 4.83cde	0.79 ± 0.002a	3.12 ± 0.04b	99.23
ZL01	58.67 ± 2.96a	64.29 ± 0.57a	61.67 ± 1.29a	0.65 ± 0.09b	2.76 ± 0.38b	99.87
ZL05	52.67 ± 8.84a	56.34 ± 8.70a	55.50 ± 8.78a	0.81 ± 0.04ab	3.38 ± 0.34ab	99.89
ZL08	50.33 ± 1.45a	54.19 ± 1.83a	54.89 ± 2.63b	0.79 ± 0.001ab	3.34 ± 0.05ab	99.88
ZL011	55.67 ± 2.33a	58.49 ± 2.11a	61.08 ± 2.76b	0.81 ± 0.01ab	3.09 ± 0.03b	99.90
ZL51	59.33 ± 2.73a	61.26 ± 2.30a	60.83 ± 2.19a	0.82 ± 0.04ab	3.67 ± 0.29ab	99.92
ZL55	52.00 ± 5.51a	65.09 ± 4.33a	59.23 ± 2.52a	0.68 ± 0.12b	2.75 ± 0.56b	99.85
ZL58	62.67 ± 2.08a	65.05 ± 0.56a	61.28 ± 2.11a	0.89 ± 0.007b	3.64 ± 0.20ab	99.58
ZL511	58.00 ± 2.65a	61.21 ± 2.00a	65.12 ± 0.83a	0.85 ± 0.03ab	4.09 ± 0.08a	99.90

the UPGMA method showed high similarity between the two clades (50 and 100 Gs), they only shared 27.53 % similarity (Fig. S2c), suggesting that the MTB community in CGH sample was strongly affected by the magnetic field.

The changes in the MTB community were monitored by high-throughput sequencing under the external magnetic fields of 0.5 and 50 Gs for different weeks (1, 5 and 8, 11 weeks) (Fig. S3). The community composition of MTB in CJ varied under the 0.5–50 Gs external magnetic field, the branch clustered together of 1 and 11 week samples changed to 1 and 5 week samples, respectively (Fig. S3a,c). The MTB community in CGH sample at 1 week and 5 weeks clustered together with the increase of the magnetic field intensity (Fig. S3e,g), while an opposite trend occurred in ZL samples (Fig. S3i,k). Additionally, the samples at 8–11 weeks still gathered together regardless of magnetic field intensity changes (Fig. S3g,k).

3.3.2. Community composition

The structure of the MTB community under different magnetic field intensities was investigated based on a comparative analysis of 16 S rRNA gene sequences (Table 3). Results showed that the MTB were affiliated with the classes of *Alphaproteobacteria*, *Betaproteobacteria* and *Deltaproteobacteria*, including the genera of *Herbaspirillum*, *Magnetovibrio*, *Magnetospira* and *Magnetospirillum*. It can be seen that *Alphaproteobacteria* and *Betaproteobacteria* classes existed in all sediments from three surface bodies, while *Deltaproteobacteria* only appeared in ZL. *Herbaspirillum magnetovibrio* was dominant in all samples, whereas its relative abundance decreased with increased magnetic field intensity in ZL. The abundance of *Magnetovibrio blakemorei* increased first and then declined in CJ, while showing an opposite trend in CGH. The relative abundance of *Magnetospirillum marisnigri* in ZL in CJ gradually increased with the increase of magnetic field intensity from 0.5 to 100 Gs. Additionally, the relative abundance of *Magnetospirillum moscoviense*, *Magnetospirillum caucaseum*, *Desulfovibrio magneticus* and other genera is low, and variation significantly with the change of magnetic field intensity.

We further studied the community structure of MTB at different magnetic exposure times (1, 5, 8 and 11 weeks) under the external magnetic fields of 0.5 and 50 Gs (Table S2). During 11-week incubation, *Herbaspirillum* sp. always dominated in CJ and ZL, and the bacterial community composition did not change in ZL, whereas *M. gryphiswaldense* only appeared at 5 weeks in CJ. It can be observed that *Herbaspirillum* sp. was dominant in CGH at 1 and 5 weeks under 50

Gs, with a relative abundance of 86.55 % and 90.59 %, respectively. After incubation for 8 weeks, the relative abundance of *M. marisnigri* (52.43 %) increased and became the dominant bacterium. Thereafter, *Herbaspirillum* sp. (72.85 %) became the dominant bacterium again at 11 weeks. It also appeared that the relative abundances of *M. thiophila*, *M. blakemorei*, *M. moscoviense* and *M. marisnigri* in CGH and ZL significantly changed at 8 weeks.

3.3.3. Co-occurrence patterns

The co-occurrence network framework was constructed by the Spearman correlation matrix ($R^2 > 0.1$, $p < 0.05$, Spearman's rank correlation test) to analyze the correlation of the MTB in three sediment samples under different magnetic field intensities (Fig. 7). The OTUs in the networks were represented by nodes and the edges represented correlations between OTUs. The results showed that with the increment of the magnetic field intensity the edge numbers first decreased and then increased in CJ, while appeared an inverse trend in CGH and a gradual increase in ZL. The network connectivity measured by the average number of connections per OTU gradually decreased in three sediments under the magnetic field treatment. The changing trend of positive connections to the total number of edges was consistent with the edge numbers of the co-occurrence network of MTB in three freshwater sediments. The ratios of negative and positive correlations (neg/pos) were used to evaluate the stability of the MTB network, higher neg/pos proportion represents greater network stability. After magnetic field treatment, the stability of the network of MTB becomes worse in three sediment samples. The greater the degree of node, the higher degree centralization, and the more important the node is in the network. The different high degree centralization OTUs of co-occurrence network of MTB was caused by different magnetic field intensities and samples (Table S2). Six OTUs with high degree concentration were found in CJ under an external magnetic field of 0.5 Gs. Among them, OTU7 was classified into *Magnetospirillum* and OTU8-OTU11 and OTU15 were affiliated with *Herbaspirillum*. OTU3 under 50 Gs and OTU10 and OTU12 under 100 Gs were grouped into *Magnetospira*. In the CGH sample, OTU8, OTU10 and OTU13 were clustered into *Magnetospira* with high degree concentration and only OTU11 was identical to *Magnetospirillum* under 0.5 Gs; OTU2 under 50 Gs and OTU4 under 100 Gs were affiliated to *Magnetospira*. For ZL sample, OTU6 under 0.5 Gs, OTU3 under 50 Gs, OTU2 under 100 Gs were grouped into *Magnetospira*. The OTU number of *Magnetospirillum* was more than that of *Herbaspirillum*. Furthermore,

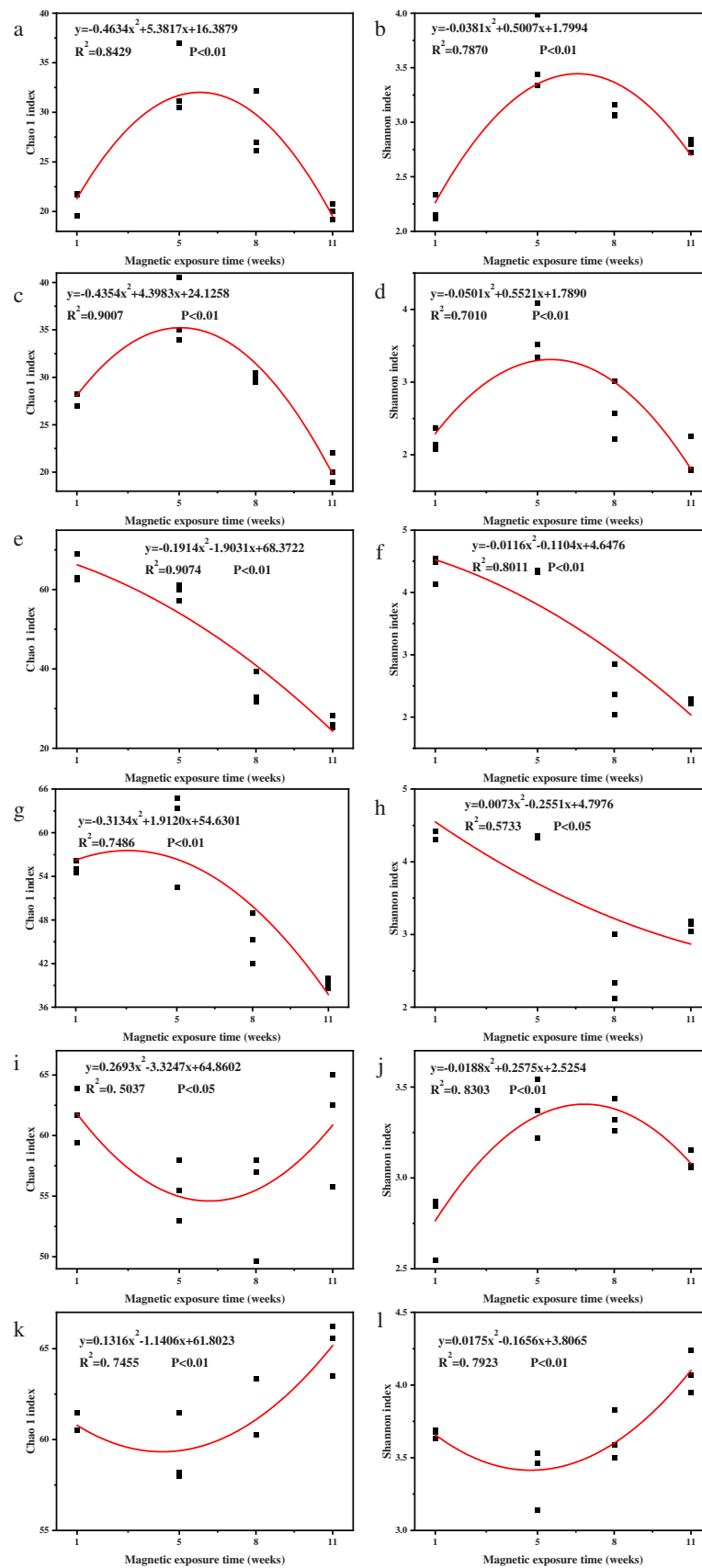
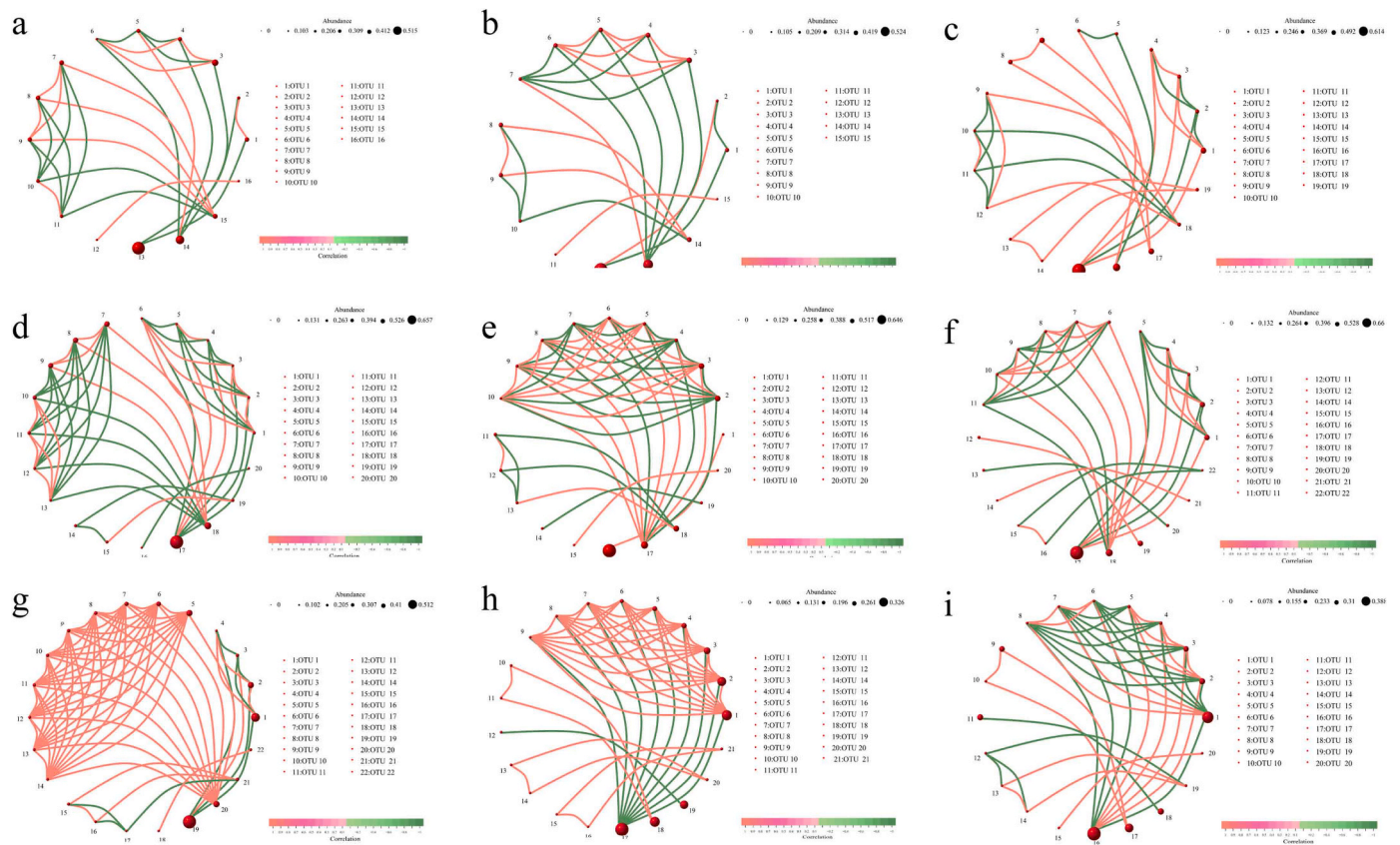


Fig. 6. Relationship between magnetic exposure times and Alpha diversity indices (a, c, e, g, i, k: Chao1 index; b, d, f, h, j, l: Shannon index) of MTB in freshwater sediment samples (a-d: CJ; e-h: CGH; i-l: ZL) under magnetic field intensity of 0.5 Gs (a, b, e, f, i, j) and 50 Gs (c, d, g, h, k, l).

Table 3

Statistical results of the abundance of MTB in sediments under different magnetic field intensities.

Related sequence	Related sequence	Cluster	Class	Relative abundance (%)								
				CJ0	CJ50	CJ100	CGH0	CGH50	CGH100	ZL0	ZL50	ZL100
<i>Herbaspirillum magnetovibrio</i> TK-2	DQ103258	<i>Herbaspirillum</i>	Betaproteobacteria	94.25	94.36	95.20	93.81	97.18	96.39	96.48	86.45	32.79
<i>Magnetovibrio blakemorei</i> MV-1	AF442518	<i>Magnetovibrio</i>	Alphaproteobacteria				0.57	0.86	1.05	0.15	0.04	0.12
<i>Magnetospira thiophila</i> MMS-1	NR_116475	<i>Magnetospira</i>		2.99	4.03	0.91	3.92	1.23	1.58	0.34	0.70	1.10
<i>Magnetospirillum moscoviense</i> BB-1	NR_121771	<i>Magnetospirillum</i>					0.11	0.14	0.16			
<i>Magnetospirillum marisnigri</i> SP-1	NR_149241						1.25	0.05	0.09	2.54	12.62	65.39
<i>Alpha proteobacterium</i> LM-1	JF490044			0.08	0.30	2.39	0.34	0.54	0.74			
<i>Magnetospirillum gryphiswaldense</i> MSR-1	NR_121771			1.09	1.11	1.27						
<i>Magnetospirillum caucaseum</i> SO-1	NR_149241			0.75	0.06					0.21	0.03	0.07
<i>Alpha proteobacterium</i> UT-4	JF490034			0.84	0.13	0.22				0.24	0.04	0.37
<i>Desulfovibrio magneticus</i> RS-1	NR_074958		Deltaproteobacteria							0.04	0.10	0.17

**Fig. 7.** The co-occurrence network interactions of MTB in freshwater sediment samples (a-c: CJ; d-f: CGH; g-i: ZL) under different magnetic field intensities (a, d, g: 0.5 Gs; b, e, h: 50 Gs; c, f, i: 100 Gs).

the OTUs of *Magnetospirillum* were more than that of *Herbaspirillum*.

We further assessed the relationships between MTB in sediment samples at 1, 5, 8 and 11 weeks under different magnetic field intensities. We found more edges in the 50 Gs network than in 0.5 Gs in CJ and ZL, while the number of edges did not change in CGH (Fig. S4). In the co-occurrence network of MTB, the proportion of positive connections to the total number of edges in 50 Gs was larger than that of 0.5 Gs in CJ and CGH, while appeared an opposite trend in ZL. The high-degree

centralization OTUs were all identical to *Herbaspirillum* in CJ and ZL (Table S2). OUT7 and OUT14 occurred in 0.5 Gs in CGH were grouped into *Magnetospira* and *Herbaspirillum*, respectively, while the OTUs of higher degree centralization only belonged to *Herbaspirillum* in 50 Gs.

3.4. Community function responded to the magnetic field

The predicted functional genes of MTB from three sediment samples

under different external magnetic field intensities enriched 180,136, 208 genes in 364 KEGG metabolic pathways. We explored functional potential within individual functional groups to the distribution and metabolism of MTB. On this basis, we did a heat map analysis between the main functional genes and the level 3 KEGG pathway, which were divided into 17 categories (Fig. 8a). It can be found that Microbial metabolism and Mineral absorption were respectively the highest and lowest categories, and appeared invariant with the changes of magnetic field intensity. Although the Sulfur metabolism, Biosynthesis of siderophore group nonribosomal peptides and other functional genes showed a relative abundance less than 1 %, they might also closely relate to MTB distribution. The abundance of ABC transporters increased in CJ with increased magnetic field intensity. For the functional group abundances of ZL, with increased magnetic field intensity, ABC transporters were inhibited. Interestingly, the abundances of functional groups were unchanged for CGH sample.

The metabolic functional structure of the bacterial community in sediment samples under an external magnetic field of 0.5 and 50Gs for different weeks (1, 5, 8 and 11 weeks) were analyzed (Fig. 8b, c, d). The main functional genes related to the distribution of MTB in three sediment samples were divided into 15 categories. The metabolic functional structure of MTB communities was quite different from diverse sediment

samples. All samples were significantly rich in functional genes for Two-component system, ABC transporters, Carbon metabolism and Quorum sensing. Although the Mineral absorption and Biosynthesis of the siderophore group nonribosomal peptides involved in iron uptake and cell motion showed a relatively low abundance (<1 %), they might also be associated closely with MTB response to the magnetic field. For the CJ samples, under the magnetic field intensity of 0.5 Gs, with the increase of incubation time, Two-component system and Carbon metabolism were first inhibited and then enhanced, while their abundance showed a gradual increase under the magnetic field intensity of 50 Gs. The ABC transporters and Quorum sensing in the 0.5 and 50Gs magnetic field increased first and then decreased and continued to decrease, respectively (Fig. 8b). For CGH samples, the ABC transporters under the 0.5 and 50Gs magnetic field continuously increased and reached maximum values of 23.455 % and 22.429 %, respectively. Quorum sensing rose first and then decreased with the highest values of 10.1 % and 10.051 % under the 0.5 and 50Gs magnetic field, respectively (Fig. 8c). For ZL samples, it can be seen from Fig. 8d that with the increase of magnetic exposure time the abundance of Carbon metabolism of ZL samples continually rose under 0.5 Gs, whereas first inclined and then declined under 50 Gs. The ABC transporters increased first and then decreased at 0.5 Gs, which was consistent with the results of CJ samples, but it first

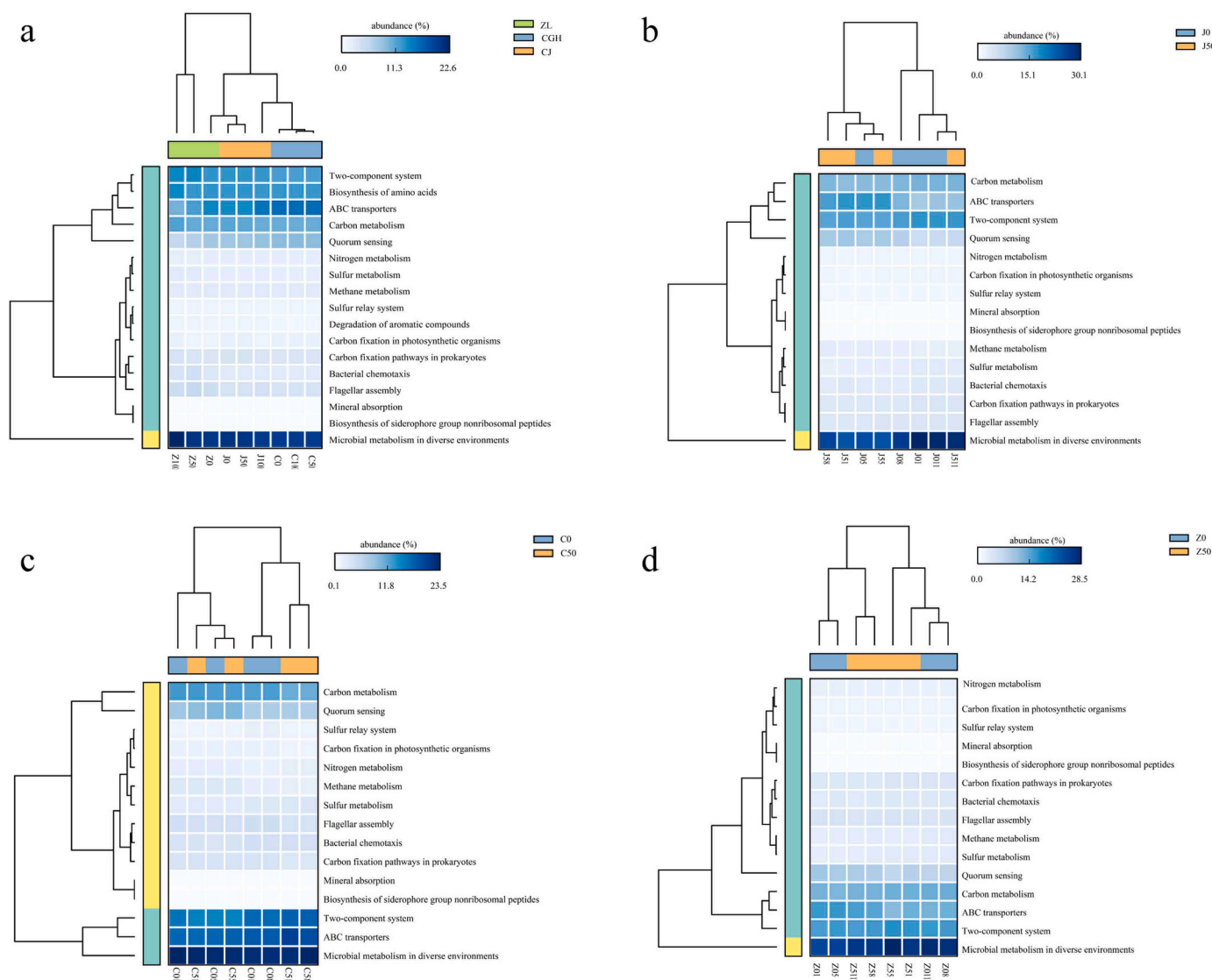


Fig. 8. The community function clustering analysis of MTB under the different magnetic field intensities (a) and magnetic exposure times to freshwater sediment samples (b, CJ; c, CGH; d, ZL).

decreased and then increased at 50 Gs. The Quorum sensing for CGH samples first decreased and then increased under 0.5 and 50 Gs, and the highest value appeared under 0.5 Gs at 1 week of magnetic exposure time.

4. Discussion

Many natural organisms, including birds, mammals, fish, and insects, can use Earth's magnetic field for navigation (Goswami et al., 2022). Therefore, the origin of the effect of magnetic orientation on organisms is a subject of extensive research. The MTB were (probably) the earliest case of magnetoreception on Earth and had wide ecological distribution, simple structure and various types of nutrition, so they were considered as a typical organism for the study of magnetic response (Barr et al., 2022). Magnetic capillary racetrack technique is useful for isolating large, fast-moving MTB (such as large magnetotactic spirilla and magnetotactic cocci), but for slower-moving MTB (such as *M. blakemorei*), it may take longer to be collected. When the time exceeds 30 min, movable non-magnetotactic pollutants may appear at the end of the seal (Lefèvre et al., 2013). As shown in Figs. 2–4, non-magnetotactic bacteria were gradually screened out with ME and MCR. And *M. blakemorei* was found in our samples after collecting 30 min, indicating that our experimental results are reliable. It has been reported that Revathy and Salam are used capillary racetrack technique and magnetic separation to isolate MTB from saline lagoon and Banjosa Lake, respectively. It proved that this systematic procedure is fast and effective (Revathy et al., 2016; Salam et al., 2023). The morphological and phylogenetic diversity of uncultivated MTB was revealed using this approach.

Some studies have shown that the forms of MTB in freshwater environment are rod-shaped, arc-shaped, oval, spherical and so on. And the rod-shaped, oval-shaped, and arc-shaped of MTB were found in our study. The sequencing results show that the abundance of *Herbaspirillum*, *Magnetovibrio* and *Magnetospirillum marisnigri* is relatively high. Nevertheless, this study found that the more rod-shaped of MTB may be associated with the rod-type MTB has a strong resistance and some arc-shaped of MTB experienced water loss and shrinkage (Fig. 2b, c and g; Fig. 3d; Fig. 4b, c, e, h and i). It has been reported that the iron content of freshwater sediments is more than 1.00 mg/L in CG and ZL, and the highest iron concentration was close to 8.0 mg/L in water-deficient period of ZL (Li et al., 2011; Zhu et al., 2021). However, the iron content of CJ was 0.03–0.08 mg/L (Duan et al., 2021). Based on the results of TEM, we found that no magnetotactic bacteria were found in CJ-IS (Fig. 2a–c), and MTB of CJ have fewer magnetosomes than ZL and CG. We speculated that it might be due to the low iron content in the environment.

This study aimed to explore the influence of static magnetic field on the community composition of MTB in freshwater sediments of three surface water bodies. In addition, some MTB existed ubiquitously in freshwater sediment with different water body types, including *Alphaproteobacteria*, *Betaproteobacteria* and *Deltaproteobacteria*. *Alphaproteobacteria* (0.56–10.64 %) and *Betaproteobacteria* (89.36–99.44 %) were the dominant MTB, which is consistent with the previous reports on MTB community composition in freshwater, marine environments and lakes (Table S1) (Dieudonné et al., 2019). *Magnetococcus*, *Magnetospirillum* and (or) *Nitrospirae* were mainly detected in freshwater and marine environments in the previous studies on MTB diversity (Liu et al., 2022). However, we found that *Herbaspirillum* genus also existed widely in the present sediment samples from surface water bodies. This inconsistency might be because the MTB 16 S rRNA gene classification was limited by the limited number of MTB sequences in the available databases, making it difficult to identify novel MTB by blasting comparison to describe the diversity (Xu et al., 2018). It has been reported that *Herbaspirillum* sp. TK-2 isolated from the surface soil of the mines at iron mountain exhibits strong tolerance to oxygen and metals (Yan et al., 2017). Therefore, the high dissolved oxygen and certain content metals in CJ, CGH and ZL might largely explain the high abundance of

Herbaspirillum sp. (Liu et al., 2021; Luo et al., 2021; Zhang et al., 2014). In addition, the number of *Herbaspirillum* sp. TK-2 is more than twice that of other MTB strains in a certain culture environment (Yan and Xing, 2018).

Magnetospira thiophila MMS-1 is an obligate microaerophile capable of chemoorganoheterotrophic and chemolithoautotrophic growth (Fang et al., 2019). The maximum abundance of *M. thiophila* MMS-1 under 50 Gs is higher than that under 0.5 Gs, suggesting that the magnetic field intensity of 50 Gs is conducive to the growth of *M. thiophila* MMS-1. *M. blakemorei* MV-1 is a microaerophile that requires seawater with a salinity greater than 10 ‰ for its growth (Correa et al., 2022). *Magnetospirillum marisnigri* SP-1 strictly micro anaerobically grow (Ryzhov et al., 2023). CJ is the running-water ecosystems with lower salinity and higher dissolved oxygen compared to the static-water/lentic ecosystem, possibly resulting in the undiscovery of *M. blakemorei* MV-1 and *M. marisnigri* SP-1.

MTB have been globally detected in the sediments of freshwater or seawater from Asia, Europe, North and South America, Africa, Australia, and Antarctica (Goswami et al., 2022; Lin et al., 2014). The previous study showed that the strength of the geomagnetic field possibly played an essential role in the biogeographic distribution of MTB (Mao et al., 2022). The present study monitored the magnetic field response of MTB in sediments from freshwaters with different water body types. The abundances of MTB in the samples from three different regions are different, the minimal and maximal values respectively appeared in CJ and ZL, which may be related to the above-inferred water flow type and human disturbance (Liu et al., 2022). The Shannon index of MTB with the highest value under 0.5 Gs decreased with increased magnetic field intensity in CGH and ZL, while the Shannon and Chao 1 index of MTB in CJ exhibited an opposite trend. This might be attributed to the different responses and adaptability of different MTB to the magnetic field. It has been reported that the growth of *M. magneticum* AMB-1 and *M. gryphiswaldense* MSR-1 were inhibited by 700 mT and 200 mT magnetic field intensity, respectively (Le Nagard, 2018; Leila et al., 2019). The magnetic field intensity of less than 500 nT was found to up-regulate or down-regulate the magnetosome synthesis gene of *M. magneticum* AMB-1 (Wang and Liang, 2009). Previous studies have shown that environmental factors could significantly impact MTB distribution (Xu et al., 2018). The magnetic field can change physiochemical factors in water, including temperature, pH, salinity, nitrate and sulfides, which suggests that the magnetic field could indirectly affect the growth of MTB (Zaidi et al., 2014). The Chao 1 index in ZL was consistent with the previous report that the proper magnetic field intensity tended to promote bacterial growth, whereas the high-level magnetic field had inhibited the growth or led to the death of the cell (Ren et al., 2018). Similarly, it has been reported that the microbial diversity in sludge samples was inconsistent under different magnetic field intensities, and the diversity index first increased and then decreased with the increase in magnetic field intensity (Ji et al., 2010). The Chao 1 index in CGH first decreased and then increased was consistent with the previous studies on *Streptococcus* and *Staphylococcus* mutants, suggesting that the magnetic field might execute growth inhibition, not bactericidal effect (Kohno et al., 2000). Although the action mechanism of the magnetic field on MTB is still unclear, the external magnetic field can inevitably change the yield of magnetosome formation and size and affect the linearity arrangement of magnetosome (Leila et al., 2019). These might lead to the different swimming speeds of MTB that affect the magnetic enrichment, thus changing the diversity and abundance of MTB in sediment samples.

Generally, the total numbers of MTB increased within several weeks in the freshwater microcosms and were stable for several years without noticeable change (Flies et al., 2005). In the present study, the varying trends of the relative abundance of MTB in CJ, CGH and ZL under 0.5 Gs (geomagnetic field) during incubation were different, which might attribute to the difference in water body types and geographical environment. It has been reported that the MTB population in indoor

microcosm were susceptible to the changes in microenvironments due to the no-disturbance incubation in the laboratory (Lin and Pan, 2010). We found that the Chao 1 index of MTB in CJ and CGH rose first and then decreased with time. These implied that an appropriate exposure time can promote the growth of MTB under certain intensity magnetic field, while longer magnetic exposure time might inhibit the growth or led to the death of MTB. The Chao 1 index and Shannon index of MTB in ZL decreased and then increased with time, suggesting that the magnetostatic field can inhibit or kill a part of MTB that might be more sensitive to the magnetic field. Similar results were also observed in *Salmonella enterica* and *Saccharomyces cerevisiae*, which were inhibited in the early stage of static magnetic field exposure and promoted later (El May et al., 2009; Novák et al., 2007).

It can be seen from Fig. 5 that the MTB diversity was more correlated with magnetic field intensity than species richness in CGH and ZL. The results agreed with the previous report, in which the magnetic field might affect the diversity and biogeography of MTB (Lin et al., 2013). The community composition of MTB was also affected by the local magnetic field magnitude (Lin et al., 2013). The correlation between magnetic exposure time and diversity index of MTB in CJ, CGH and ZL were different (Fig. 6), which might support the previous study that river flow rate and temperature were the best predictors of temporal patterns in microbial community structure (Mark Ibekwe et al., 2012). The fitting results showed that the Chao1 index correlated more with time than the Shannon index in CJ under 0.5 Gs (Fig. 6a, b), while the correlation coefficient increased under 50 Gs. The correlation pattern between the MTB diversity index and magnetic exposure time in three samples was unchanged under 0.5 and 50Gs, indicating that magnetic exposure time might affect MTB community diversity more than magnetic field intensity. It has been proposed that the distribution of MTB groups might depend on the incubation time of the microcosm (Koziaeva et al., 2020). In the present study, the incubation time of MTB was correlated to the Shannon index rather than the Chao1 index in ZL under 0.5 and 50 Gs magnetic fields. In addition, the high Chao 1 index under 50 Gs magnetic field (Fig. 6i, k) suggested that long-term magnetic field exposure would affect the abundance and diversity of MTB.

The community composition of MTB in CGH and ZL were significantly affected by magnetic field intensity ranging from 0.5 to 100 Gs (Fig. S2b,c). It is evident from Fig. S2a that the MTB community composition in CJ under 0.5 and 50 Gs were similar but observably different from that under 100 Gs. The cluster analysis showed that the external magnetic field changed the community of MTB at different weeks. With the increase of magnetic exposure time, the community of MTB in CJ at 11 weeks was very different from that at other weeks, suggesting that the long-time magnetic exposure might negative affect the growth of MTB. For the CGH samples, the community composition of MTB in the early stage of magnetic exposure treatment were similar, then changed and gradually became stable, indicating that MTB appeared different responses to the magnetic exposure time. The community composition of MTB in ZL at 11 weeks was similar to that at 1 and 8 weeks, implying that the magnetic field might first inhibit and then promote the growth of MTB.

We found four genera of MTB in freshwater sediments in the present study, including *Herbaspirillum*, *Magnetospirillum*, *Magnetospira*, *Magnetovibrio*. The relative abundance of *Herbaspirillum* decreased with the decrease of magnetic field intensity in ZL, while *Magnetospirillum* increased and became the dominant MTB genus under 100 Gs. It has been reported that *Herbaspirillum* can survive in the pH range of 6.0–7.5 and has a high requirement of nutrients for growth (Yan and Xing, 2018). The chemoorganoheterotrophic *Magnetospirillum* can survive in pH range of 5.8–8.2, utilize organic acids as carbon source and electrons, and can autotrophic and mixotrophic growth using reduced sulfur compounds as the source of electrons (Lefèvre et al., 2013). It has been reported that the magnetic field changed the pH value, electrical conductivity and dissolution rate of organic matter of water (Ponomarev et al., 2023; Wu and Brant, 2020). It is well known that chemical

parameters of the microenvironment significantly affect the community composition and abundance of MTB. Thus, the response of MTB in different locations to the magnetic field are different.

It has been found that the obligate microaerophile *Magnetospira* can promote the cycle of iron and sulfur in nature. In the present study, the relative abundance of *Magnetospira* changed under a magnetic field, which might be attributed to dissolved oxygen in water (Amor et al., 2020). It has been reported that oxygen is a paramagnetic substance and dissolved oxygen in the water existing effect metal ions such as ferric iron and cupric ion (Kohn et al., 2000). Therefore, the magnetic field also may directly affect the dissolved oxygen in the water and indirectly regulate the concentration of metal ions. *Magnetovibrio*, a gram-negative MTB, lives in sulfide-rich sediments in a salt marsh. It grows chemolithoautotrophically using reduced sulfur compounds, nitrate and Fe (III) as the terminal as an electron source (Bazyliński et al., 2013). Our results showed that *Magnetovibrio* not existed in the CJ and had a relatively low abundance in CGH and ZL. This might be attributed to the inhibition of the growth of *Magnetovibrio* by excessive sulfide. It has been reported that the sulfide content in the CJ sediments was 2.5–411.9 $\mu\text{mol/L}$ (Yan et al., 2021). Previous studies were consistent with our findings, in which the abundance of *Magnetovibrio* was negatively correlated with sulfide in sediments of volcanic lakes (Liu et al., 2022). Furthermore, frequent nonmagnetic mutants were observed in cultures of *Magnetovibrio* (Correa et al., 2022). The magnetic field may affect the hydrogen bond in DNA, which leads to the genetic variation of some lower organisms.

In this study, we used correlation analysis to delineate networks of MTB community in sediment samples (Fig. 7). Results indicated that the magnetic field was more facilitation than antagonism for MTB in CJ and CGH, while an opposite result appeared in ZL. The positive correlation might indicate a shared preference for a particular combination of environmental conditions (Das et al., 2018). However, the correlation change of MTB in ZL might be due to the different community compositions (Li et al., 2022). Negative interactions might weaken the competitive relations of the bacterial community, while positive interactions might strengthen competitive relations. Therefore, a higher neg/pos ratio represents weaker competition between microbial communities and a more stable microbial network structure (Wei et al., 2021). In this study, the stability of the MTB network gradually increased in CJ and CGH, while gradually weakening in ZL. In addition, the network connectivity gradually decreased in all networks of MTB in three samples, which indicated that the interaction between MTB weakened. Most keystone bacterial nodes belonged to the genus *Herbaspirillum*, the most abundant genus. With increased magnetic field intensity, *Magnetospira* became keystone bacteria in the CJ; the proportion of *Magnetospira* in CGH gradually decreased, while *Magnetospirillum* increased gradually in CGH; *Magnetospirillum* became the most keystone species in ZL. This might be due to the change in the electron transfer process between MTB. It has been reported that a magnetic field could enhance electron movement efficiency through extracellular electron transfer mechanisms (Lay et al., 2022). The magnetic field can also affect the exchange of information and substances between microorganisms by influencing the activity of microbial enzymes (Ren et al., 2018). Additionally, previous studies have shown that organic matter and iron affected the topological features of co-occurrence networks of microorganisms, which may also explain the change in the MTB symbiotic network (Ma et al., 2016).

MTB are widely distributed and play an important role in the geochemical cycle, so it is crucial to study the metabolic pathway of MTB. Among them, the relative abundance of ABC transporters changed with the increases in magnetic field intensity (Fig. 8a). It has been reported that the ABC transporters system related to the iron uptake of Gram-negative bacteria was one of the ubiquitous transport systems. The high abundance of ABC transporters system may be caused by the high abundance of MTB in CGH. Additionally, the magnetic field can affect iron solubility and lead to the difference of iron compounds in the

sediment, which might explain the difference in the abundance of ABC transporters (Delepeleire, 2019). The relative abundance of Mineral absorption and Biosynthesis of siderophore group nonribosomal peptides were low, which might be because MTB tended to grow in relatively low concentrations of nutrients (Ma et al., 2016). Similarly, we found that the variation trend of the metabolic pathway with time under 50 Gs was different from that under 0.5 Gs, which might be mainly related to the change in community composition. In addition, Two-component system, Carbon metabolism and Quorum sensing increased under the 50 Gs magnetic field, indicating that MTB would reduce the effect of the magnetic field on growth by improving the metabolic pathways under long-term magnetic exposure.

Under the action of the geomagnetic field, MTB will swim along the magnetic line to the preferred habitat with appropriate oxygen concentration. This indicates that the direction of the magnetic field may have an impact on the growth and development of MTB. It has been reported that the direction of the applied magnetic field may affect the magnetic microstructure, which may be caused by small disruptions in particle alignment along a chain (Simpson et al., 2005). However, MTB can solve this problem by swimming and relying on aerotaxis and chemotaxis to find areas of locally higher nutrient concentration (Frankel and Bazylinski, 2009). Alternating magnetic fields can lead to the death of some MTB by long-term observations of magnetotactic bacteria in Earth's field, zero field and alternating field (Mao et al., 2022). These studies indicate that the direction of the magnetic field will have a significant impact on the growth and development of MTB, and the influence of the magnetic field direction will be our research direction in the future.

5. Conclusions

We studied the effects of intensity and exposure time of magnetic field on MTB diversity in freshwater sediments of three different waterbodies. Magnetic field intensity is closely associated with the diversity of MTB in CGH and ZL, while magnetic exposure time is tightly related to the richness of MTB in CJ and CGH, and their diversity in ZL. The community composition of MTB in CGH and ZL was significantly affected by magnetic field intensity ranging from 0.5 to 100 Gs. MTB community composition in CJ under 0.5 and 50 Gs were similar but observably different from that under 100 Gs. The dominant genera of *Herbaspirillum* exist in three waterbodies, while the dominant taxa shifted to *Magnetospirillum* in ZL under 100 Gs external magnetic field. An increase of magnetic field intensity led to an adverse change in the network connectivity and stability of the network of MTB in three sediment samples. The community functions of MTB in sediments of surfacewater responded to the intensity and exposure time of the magnetostatic field, including Two-component system and ABC transporter system. Our finding would provide a basis for further study of the response mechanism of the MTB community to the magnetic field.

CRediT authorship contribution statement

Guojing Zhang: Conceptualization, Writing – original draft, Data curation, Methodology, Software, Visualization. **Tao Liu:** Collect samples, Validation, Investigation, Writing – original draft. **Dan Zhao:** Collect samples, Methodology, Writing – review & editing. **Xindi Sun:** Writing – review & editing. **Weijia Xing:** Collect samples, Methodology, Validation, Investigation. **Shuang Zhang:** Collect samples, Conceptualization, Funding acquisition. **Lei Yan:** Conceptualization, Supervision, Project administration, Funding acquisition, Writing – review & editing.

Declaration of Competing Interest

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

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Appendix A. Supporting information

Supplementary data associated with this article can be found in the online version at doi:10.1016/j.ecoenv.2023.115604.

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