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The effect of aboveground long-term low-dose ionizing radiation on soil microbial diversity and structure

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Studies investigating the diversity and structure of soil microbial systems in response to ionizing radiation are scarce. In particular, effects of long-term low-dose radiation is rarely studied because of its unique conditions. In this study, an area in Chengdu, China, which has been irradiated by the radionuclide thorium-232 for more than 10 years was investigated. Four groups of samples with absorbed dose rates ranging from 192.906 ± 5.05 to 910.964 ± 41.09 nGy/h were collected to analyze the compositional and functional changes of the soil microbial systems in the region. The diversity and structure of the soil microbial systems were determined using high-throughput sequencing. Our results showed that long-term low-dose ionizing radiation had no significant effect on soil bacterial diversity, but had a great impact on fungal diversity. Long-term ionizing radiation strongly affected soil microbial community structure. Long-term low-dose ionizing radiation was shown to have a promoting effect on iron-oxidizing bacteria and ectomycorrhizal fungi and have an inhibiting effect on predatory or parasitic fungi, further affecting the soil C/N ratio. This study is of great reference significance for future research on the impact of long-term low-dose ionizing radiation on soil ecosystems.

KEYWORDS

long-term gamma radiation, low-dose gamma radiation, soil microorganisms, soil microbial ecosystem, ionizing radiation pollution

1. Introduction

Ecological environment pollution has become a hot topic in recent years. Especially the environmental ionizing radiation problem that affects human life and health, such as lung cancer induced by radon emanation (Mariona et al., 2022), increasing the risk of lens opacity (Gao et al., 2021) and accelerating vascular aging (Su et al., 2016). With the development of science and technology, many projects with large-scale radiation effects have been established, and the surrounding ecosystems have been continuously affected by ionizing radiation. Certain doses of ionizing radiation result in pollution and damage to the environment, thereby affecting the ecological cycle, including soil ecosystems (Andrei et al., 2014). However, most studies on the effects of nuclear radiation on soil microbial communities have focused on long-term exposure to high doses. One study systematically

studied the community distribution and composition of fungi in the area around the Chernobyl nuclear power plant leakage and found that the area was rich in fungal diversity (Zhdanova et al., 2000). Distribution characteristics, namely composition and abundance, of the fungal community were significantly influenced by the radiation dose. The proportion of melanized fungi is larger in soil under long-term low-level ionizing radiation (Dighton et al., 2008). Most fungi exhibit amazing adaptability to radiation (Dadachova and Casadeval, 2008). Other studies have shown that radiation is a selective pressure that results in certain bacteria surviving in specific environments (Hoyos-Hernandez et al., 2019). Nevertheless, large-scale nuclear accidents involving short-term high-dose radiation are rare.

Short-term low-dose radiation generated by radioactive substances result in microorganisms reducing radiation damage by rapidly repairing damaged DNA fragments, forming spores to slow down their metabolic rate, generating superoxide dismutase to remove free radicals, and changing the carbon source utilized. These changes are made to adapt to the living conditions caused by nuclear radiation (Yang et al., 2021). Microorganisms develop resistance to radiation through adaptive reactions and can tolerate higher intensities of ionizing radiation over time (Fornalski et al., 2022). However, short-term and high-dose radiation has a sustained and irreversible impact on the composition, distribution, and metabolic pathways of microbial communities (Mohammad et al., 2019). The composition and functional integrity of biofilms are affected as the radiation causes single-strand or double-strand DNA breakages, denaturation of related proteins, and the reduction or inactivation of some enzymes (Romano et al., 2022). Few studies have investigated the effects of low-dose radiation on microorganisms. One study found that the main damage caused by irradiation of *Salmonella typhimurium*, *Escherichia coli*, and *Listeria monocytogenes* was intracellular enzyme inactivation and DNA damage (Cho and Ha, 2019). Another study showed that low-dose radiation increases the diversity of soil microbial communities and changes the metabolic capacity of carbon and nitrogen sources (Senatore et al., 2018). However, it still remains unclear that whether the composition and function of soil microbial systems are significantly affected in long-term low-dose radiation environment.

The exploitation of radioactive minerals, construction of fission reactor nuclear power plants, and research and development of nuclear fusion have all led to long-term radioactivity in the soil of some regions, causing the microorganisms in the soil to endure long-term radiation effects. Microorganisms play an important role in soil ecosystems (Zhang and Li, 2020). Therefore, if long-term low-dose radiation can significantly affect the composition and function of soil microbial systems, it will affect the material cycling processes of the entire ecosystem. To determine whether there is a quantifiable relationship between long-term low-dose ionizing radiation and soil microorganisms, this study analyzed the composition and functional changes of soil microbial systems in an area that has been irradiated by radionuclide thorium−232 for more than 10 years. The results may provide a new reference and basis for solving problems arising from long-term low-dose radiation of soil microbial systems.

2. Materials and methods

2.1. Experimental set-up and sampling

Samples were collected from a grassland in the Chengdu University of Technology campus in Chengdu, China (30°40′29″ North and 108°8′11″ East). A block (75 × 75 × 75 cm cube) of thorium mineral, an isotope of radioactive nuclide thorium−232, was present on the sample site, exposing the surrounding soil to radiation for more than 10 years. The mineral is a technical mineral, and it is exposed in the soil surface. The radioactivity of the thorium mineral is about 2.93×10^6 Bq. The thorium ore is placed in a relatively closed and independent ecological environment, and the *Tradescantia fluminensis* grows around the ore. After years of generational alternation, the *Tradescantia fluminensis* is the is the absolute constructive species. The soil type in the sampling location is the dark brown soil. No significant differences are found in other environmental factors such as soil moisture, pH (about 7.5), light and other environmental factors in the plots with different radiation intensity samples. Owing to the rapid propagation of microorganisms in soil, soil microorganisms in this region have formed stable communities that have adapted to the nuclear radiation present.

A plane coordinate system was established with the thorium mineral as the coordinate origin. A HPGe portable gamma-ray spectrometer trans-SPEC-DX-100T (AMETEK, San Diego, CA, United states) was used to measure the absorbed dose rate of thorium minerals at different distances. The relative measurement efficiency of this spectrometer was 40%, with the energy resolution at 122 and 233 keV being 1.6 and 2.3 keV, respectively. Sampling around the radioactive source is divided into 3 gradients based on the decay of the absorbed dose distance (2 ± 0.5, 7 ± 0.5, and 14 ± 0.5 cm). Their corresponding values were approximately four, three, and two times the maximum background-environmental radiation limit in Sichuan Province, and these will be referred to as High, Medium, and Low group, respectively (**Figure 1**). The highest absorbed dose rate was 910.964 ± 41.09 nGy/h (source) and the lowest was 192.906 ± 5.05 nGy/h (at 25 ± 0.5 cm away from the source). In addition, samples were collected at the maximum background-environmental radiation limit, referred to as the Blank group (**Figure 1**).

In soil sampling, each radiation dose gradient was used as the index, around the source of radiation and the soil core was obtained by 5-point sampling method and 20 samples in total are collected. 0−20 cm topsoil was excavated with a bamboo shovel. After removing stones, plant roots and other sundry materials, the soil was mixed, bagged, sealed and labeled, and stored in a 4°C ice box at low temperature, transported to the laboratory and stored in −20°C prior to analyses.

2.2. DNA extraction and PCR amplification

Soil microbiome DNA extraction was performed using the PowerSoil DNA Isolation Kit (MoBio Laboratories, Carlsbad, CA, United states) following the manufacturer's instructions. Each sample was weighed 0.25 g (fresh weight) soil sample

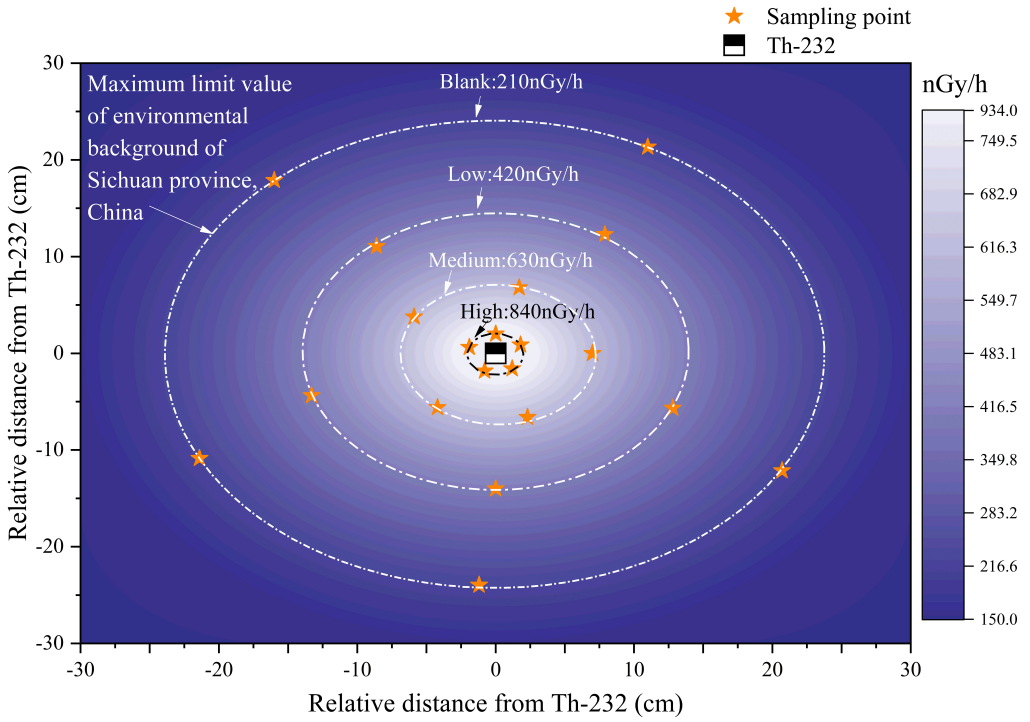

FIGURE 1
Schematic diagram of the sampling location and gamma radiation absorption dose rate.

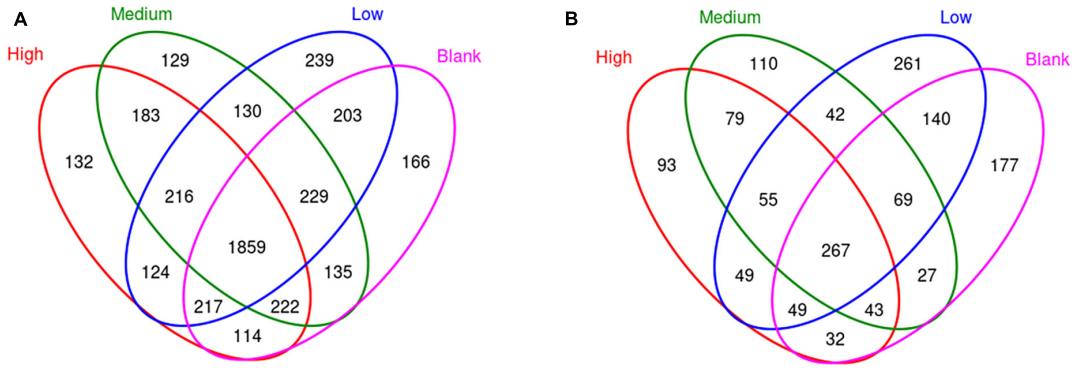

FIGURE 2
Venn diagram of panel **(A)** 16 S and **(B)** ITS OTUs under different radiation intensities.

for extraction. The quality and concentration of the DNA extracted was detected by 1% agarose gel electrophoresis and spectrophotometry. The mean of DNA concentration was 212.5 ng/μl with standard deviation of 42.33. Samples were stored at −20°C for subsequent experiments.

The bacterial and fungal species were identified by PCR amplification and sequencing. The v3-v4 region of the bacterial 16 S rRNA gene was amplified using the primers 338F (5′-ACTCCTACGGGAGGCAGCAG-3′) and 806R (5′-GGACTACNNGGGTATCTAAT-3′). The ITS1 region of the fungal ITS gene was amplified using the primers ITS1 (5′-CTTGGTCATTTAGAGGAAGTAA-3′) and ITS2 (5′-TGCGTTCTTCATCGATGC-3′). Barcode sequences 8 bp in length were added to the 5′ ends of the upstream and downstream primers to differentiate the different samples. The PCR reaction mixtures were comprised of: 12.5 μL 2xTaq Plus Master Mix, 3 μL BSA (2 ng/μL), 1 μL forward primer (5 μM), 1 μL reverse primer (5 μM), 2 μL DNA (30 ng), and 5.5 μL ddH_2O to equal a final volume of 25 μL. The thermocycling conditions of the 16 S rRNA reaction were as follows: pre-denaturation at 94°C for 5 min; 30 cycles of denaturation at 94°C for 30 s, annealing at 50°C for 30 s, and extension at 72°C for 60 s; and final extension at 72°C for 7 min. The thermocycling conditions of the ITS reaction were as follows: pre-denaturation at 94°C for 5 min; 34 cycles of denaturation at 94°C for 30 s, annealing at 55°C for 30 s, and extension at 72°C for 60 s; and final extension at 72°C for 7 min. The PCR products were visualized by 1% agarose gel electrophoresis and purified using an Agencourt AMPure

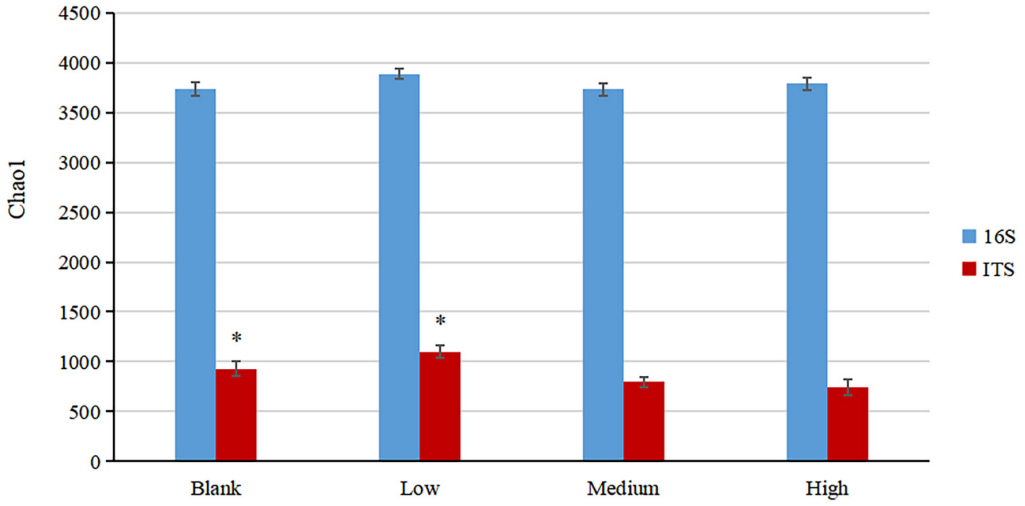

FIGURE 3
Soil microbial diversity index under different radiation intensities. *$P < 0.05$.

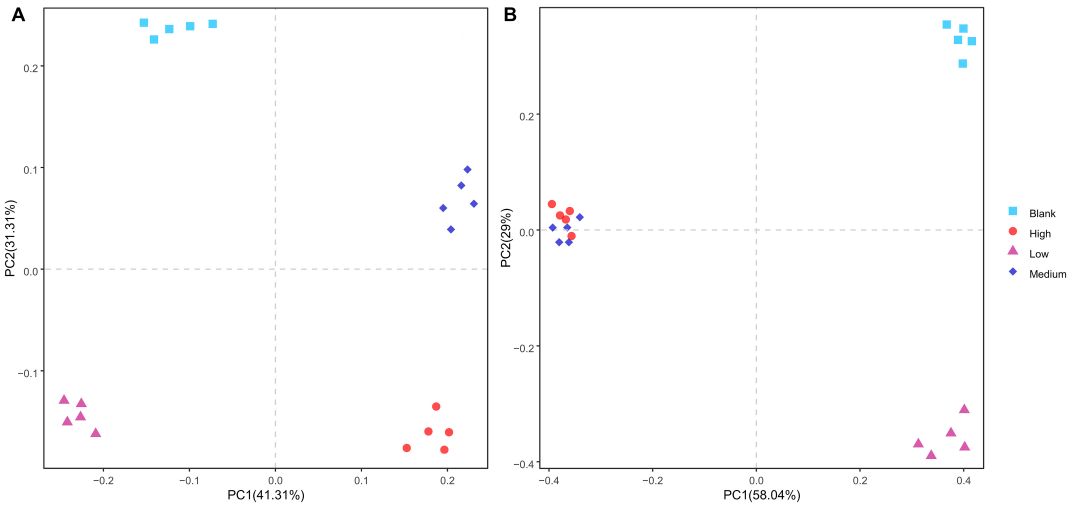

FIGURE 4
Principal components analysis of the β diversity of panel **(A)** bacteria and **(B)** fungi under different radiation intensities.

XP nucleic acid purification kit (Beckman Coulter, Brea, CA, United States) following the manufacturer's instructions.

2.3. Sequencing and data analysis

The PCR products were used to construct a microbial diversity sequencing library, and the Illumina MiSeq PE300 high-throughput sequencing platform (Illumina, Santiago, CA, United States) was used for paired-end sequencing. The original sequences were uploaded to the Sequence Read Archive database of the National Center for Biotechnology Information. The raw data were split using the QIIME 2^{TM} software (Bolyen et al., 2019) according to the barcode sequences, and the data were filtered and spliced using PEAR (v1.1) software. Sequences with scores lower than 20 and those containing non-standard bases and primer mismatch sequences were removed. The minimum overlap when splicing was set to 10 bp and the mismatch rate to 0.1. After splicing, sequences shorter than 230 bp were removed using VSEARCH (v2.8.1) (Edgar, 2010), and chimera sequences were removed using the UCHIME method according to the Gold Database downloaded from http://drive5.com/uchime/uchime_download.html. The VSEARCH (v2.8.1) software program was used to cluster high-quality sequences with operational taxonomic units (OTUs), with the sequence similarity threshold at 97% (Edgar, 2013). This was compared with the RDP classifier algorithm, which Silva and Unite databases use, set at a 70% confidence threshold and used to obtain the species classification data corresponding to each OTU. R (v4.0.2) software was used for data analysis of the species annotations and relative abundance results.

Venn diagrams were drawn using the R package, Venn Diagram (Fouts et al., 2012). The QIIME 2^{TM} software was used for α

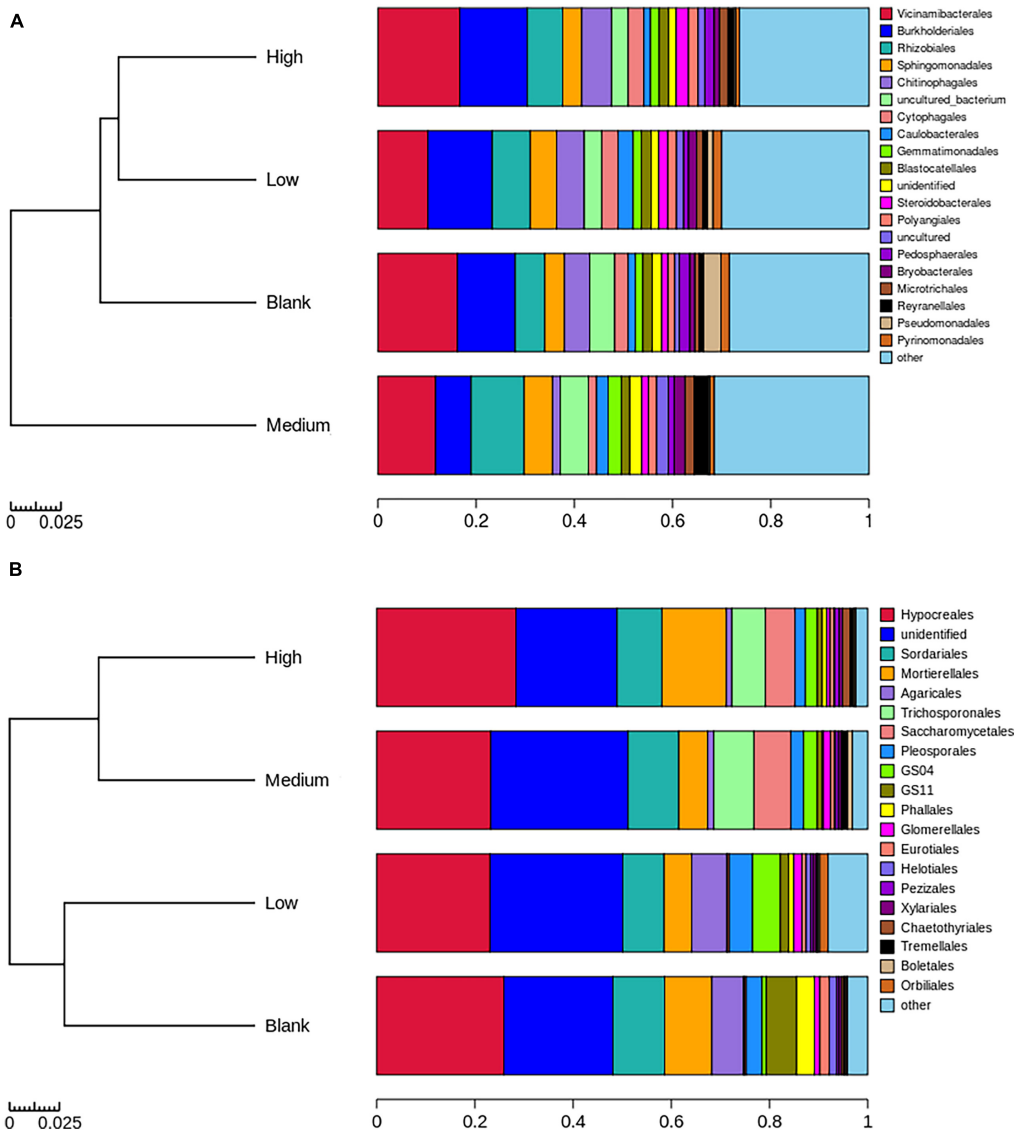

FIGURE 5
Relative species abundance and unweighted UniFrac distance of panel **(A)** bacterial and **(B)** fungal orders under different radiation intensities.

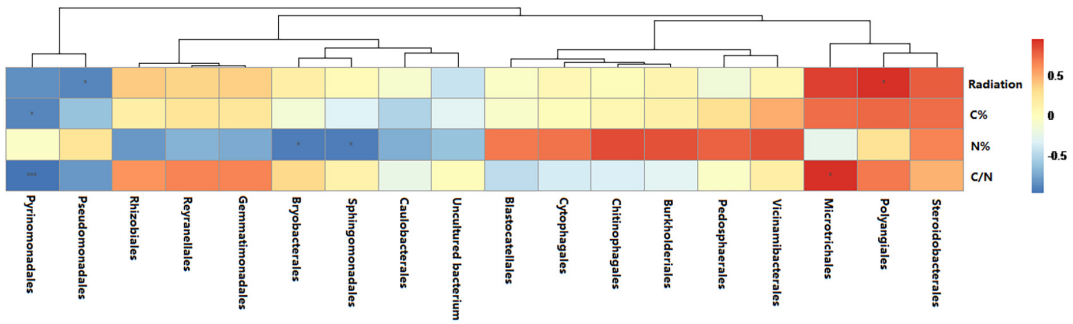

FIGURE 6
Relationships between the dominant species (at order level) that exhibited higher relative abundance and the radiation intensity, carbon content, nitrogen content, and C/N ratio. The lines represent the relationships from cluster analysis of species/OTUs. Color depth represents the level of correlation. Significance: * < 0.05; *** < 0.001. Distance algorithm: Bray-Curtis, clustering method: Pearson.

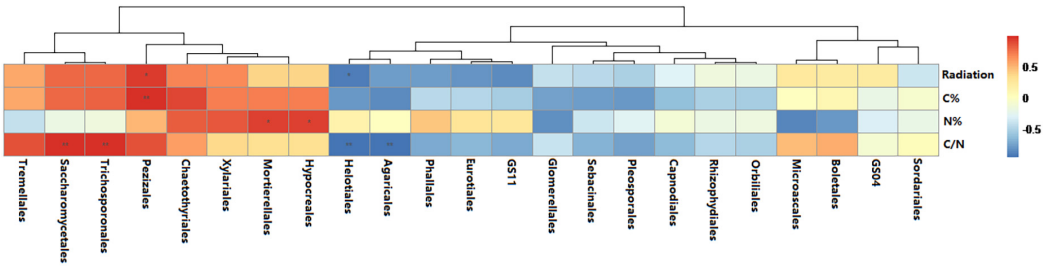

FIGURE 7
Relationships between the dominant species (at order level) that exhibited higher relative abundance and the radiation intensity, carbon content, nitrogen content, and C/N ratio. The lines represent the relationships from cluster analysis of species/OTUs. Color depth represents the level of correlation. Significance: * < 0.05; ** < 0.01. Distance algorithm: Bray-Curtis, clustering method: Pearson.

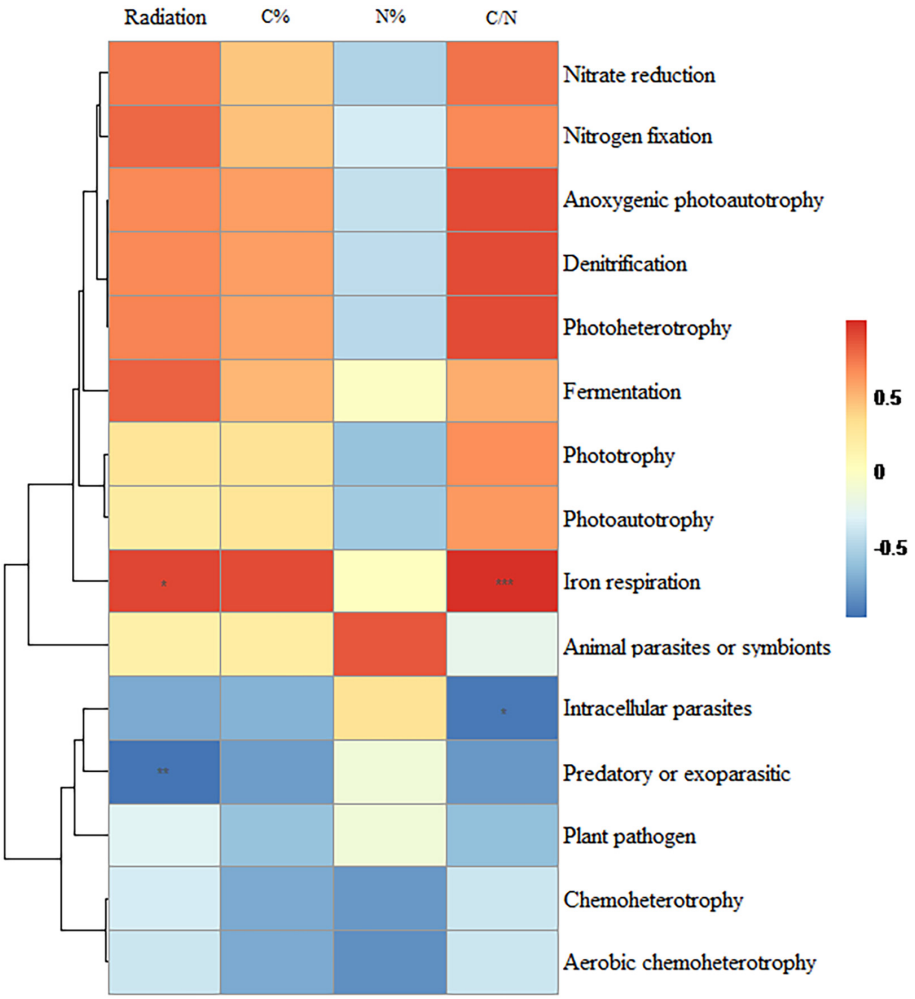

FIGURE 8
Relationships between bacterial functional taxa and radiation intensity, carbon content, nitrogen content, and C/N ratio. The lines represent the relationships from cluster analysis of species/OTUs. Color depth represents the level of correlation. Significance: * < 0.05; ** < 0.01; *** < 0.001. Distance algorithm: Bray-Curtis, clustering method: Pearson.

diversity index analysis (Bolyen et al., 2019). The β diversity distance matrix was calculated using QIIME 2^{TM} and cluster analysis was performed using the UPGMA method within R (v4.0.2), based on the unweighted UniFrac distance. A principal component analysis (PCA) which was previously described was used (Wang et al., 2012). Histogram analysis of species composition was performed, and a correlation heat map was drawn using the R packages psych and pheatmap. Functional guilds of bacteria and fungi were divided using FAPROTAX and FungalTraits (Louca et al., 2016; Põlme et al., 2020). Structural equation models (SEM)

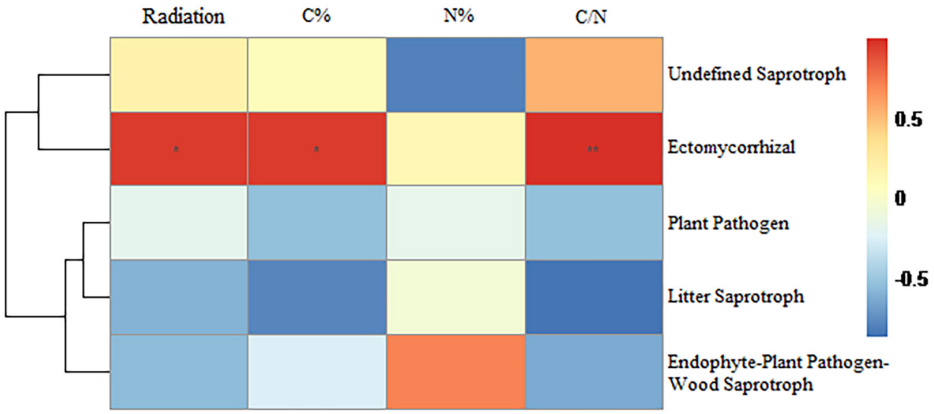

FIGURE 9
Relationships between bacterial functional taxa and radiation intensity, carbon content, nitrogen content, and C/N ratio. The lines represent the relationships from cluster analysis of species/OTUs. Color depth represents the level of correlation. Significance: * < 0.05; ** < 0.01. Distance algorithm: Bray-Curtis, clustering method: Pearson.

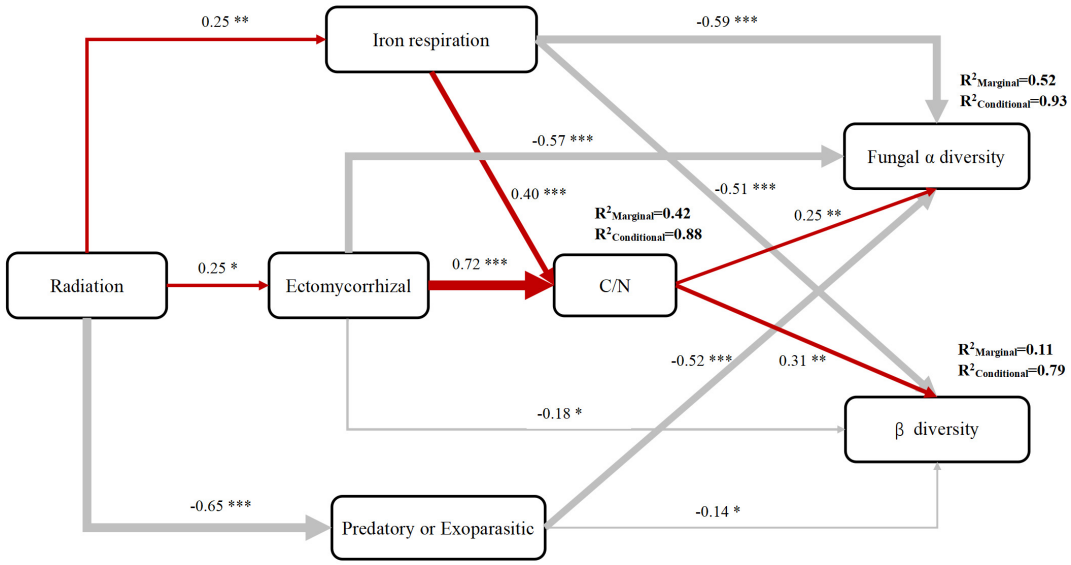

FIGURE 10
Structural equation model explaining the effect of gamma radiation on the soil microbial community (Fisher's *C* = 27.23, *P* = 0.257, DF = 20, AIC = 73.230). Red and gray arrows indicate positive and negative relationships, respectively. Numbers next to the arrows indicate the normalized path coefficients. *Represents its significance: * < 0.05; ** < 0.01; *** < 0.001. The SEM explained 56% of C/N ratio, 52% of fungi α diversity, and 41% of microorganisms β diversity.

were constructed using the R-packages lavaan and piecewiseSEM to investigate the relationships between nuclear radiation, C and N nutrition, microbial groups, and diversity (Lefcheck and Freckleton, 2016). The goodness of fit of the model was evaluated using Fisher's C statistic method (Bowd et al., 2021).

3. Results

3.1. Soil microbial diversity

A total of 4,298 bacterial and 1,493 fungal OTUs were identified from the soil samples, of which 1,859 and 267 OTUs were common in each group (Figure 2). The numbers of bacterial OTUs specific to the High, Medium, Low, and Blank groups were 132, 129, 239, and 166, respectively (Figure 2 and Supplementary Table 1), and the respective number of fungal OTUs was 93, 110, 261, 177 (Figure 2 and Supplementary Table 2). There was no significant difference in the bacterial α diversity among the groups, but the fungal α diversity in the Low and Blank groups was significantly higher than that in the High and Medium (Figure 3).

The PCA analysis showed that the bacterial β diversity in each group differed. However, the fungi from the High and Medium groups clustered together whereas those from the Low and Blank groups were dispersed (Figure 4). The unweighted UniFrac distance of the bacterial community in the Medium clustered separately from that of the bacterial community in other groups,

whereas the fungal communities in the High and Medium groups clustered together, and Low and Blank groups clustered together (Figure 5).

3.2. Composition structure of soil microorganisms

Vicinamibacterales, Rhizobiales, and Burkholderiales were the dominant bacterial orders present in the High, Medium, Low, and Blank groups (Figure 5). The dominant fungal order present in the High, Medium, Low, and Blank groups was Hypocreales (Figure 5). The dominant phyla of endemic bacteria in the High, Medium, Low, and Blank groups were Proteobacteria; Proteobacteria and Bdellovibrionota; Bacteroidota and Proteobacteria; and Verrucomicrobiota and Patescibacteria, respectively (Supplementary Table 1). The dominant phyla of endemic fungi in the High, Medium, Low, and Blank groups were Basidiomycota; Chytridiomycota, Basidiomycota, and Ascomycota; Ascomycota; and Ascomycota, respectively (Supplementary Table 2).

Among the highly abundant bacterial orders present, the relative abundance of Polyangiales was significantly positively correlated with radiation intensity whereas that of Pseudomonadales was significantly negatively correlated with radiation intensity (Figure 6). Among the highly abundant fungal orders present, the relative abundance of Pezizales was significantly positively correlated with radiation intensity and carbon content whereas that of Helotiales was significantly negatively correlated with radiation intensity and C/N ratio (Figure 7). In bacterial functional groups, the relative abundance of iron-oxidizing bacteria was positively correlated with radiation intensity and C/N ratio whereas that of predatory or exoparasitic bacteria was negatively correlated with radiation intensity (Figure 8). In fungal functional groups, the relative abundance of ectomycorrhizal fungi was significantly positively correlated with radiation intensity, carbon content, and C/N ratio (Figure 9). The SEM showed that iron-oxidizing bacteria, predatory or exoparasitic bacteria, and ectomycorrhizal fungi had negative effects on fungal α diversity and microbial community β diversity, but the C/N ratio had positive effects on fungal α diversity and microbial β diversity. The SEM explained 52% of fungal α diversity and 41% of microorganisms β diversity (Figure 10).

4. Discussion

4.1. Effect of gamma radiation on soil microbial diversity and structure

There was no significant difference in bacterial α diversity among the groups; however, the fungal α diversity in the Low and Blank groups was significantly higher than that in the High and Medium groups. The PCA analysis revealed that fungi from the High and Medium groups clustered together, away from the Low and Blank groups, indicating that the threshold value was reached when the radiation dose was approximately 480 nGy/h, the effect of gamma radiation on fungal diversity was greater than that on bacterial diversity. Under natural conditions, fungal communities are relatively less efficient in recovering from harsh environmental conditions than bacterial communities (Gao et al., 2022). Therefore, it is difficult to recover species lost in environments due to strong radiation (Franciska et al., 2018; Song et al., 2020; Coban et al., 2022). This results in a significant decrease in fungal α diversity in the High and Medium groups and the significant changes in community structure of the Low and Blank groups.

Although there was no significant difference in the α diversity of bacteria in each group, PCA and unweighted UniFrac analysis showed that gamma radiation had a significant effect on bacterial community structure. The regulatory capacity of bacterial communities is usually stronger than that of fungal communities (Liu et al., 2021). Therefore, under radiation conditions, although some bacteria are eliminated because of their inadaptability to the environment, new bacterial groups maintain the stability of the whole community's diversity, making the bacterial community structure of each group different; however, the biodiversity is not significantly different (Wang et al., 2016). In addition, owing to the existence of a moderate interference effect, the unweighted UniFrac distance of the fungal community in the medium group differs significantly from that of the other groups (Ma and Geng, 2012; Zhang et al., 2018).

4.2. Effect of gamma radiation on soil microbial community

The radiation intensity in this study was not sufficient to change the dominant soil microbial groups, but it was sufficient to change the community composition of these groups. Compared with the control group, the microbial groups in the high, middle and low groups all died out, in the mean time other microbial groups also filled the niche. Proteobacteria, which exhibit strong adaptability, was the predominant group which filled the niche vacated by the extinction of microorganisms not adapted to radiation environment; therefore, the bacterial community remained stable and its diversity was not changed (Souza and Procópio, 2021). The main phyla of endemic fungi in the irradiated areas, namely Basidiomycota, was shown to gradually replace Ascomycota in these areas. Ionizing radiation also inhibited the pathogenic and parasitic bacteria, namely Pseudomonadales and Helotiales bacteria, which indirectly promoted the growth of other fungi such as Polyangiales and Pezizales. This promoted the stability of ecosystem productivity and affected the change in soil nutrients, especially the C/N ratio (Ning et al., 2021). The change in the C/N ratio further affects the biodiversity of the microbial community by the adaptability of microorganisms to soil nutrient changes (Zhou et al., 2017).

It is worth noting that radiation intensity was positively correlated with the relative abundance of iron-oxidizing bacteria, which has not been previously reported. Iron-oxidizing bacteria

are involved with the circulation of nutrient elements, such as nitrogen and phosphorus, in the soil. These bacteria utilize large amounts of nitrogen and phosphorus and reduce the loss of organic carbon, thereby increasing the C/N ratio (Weber et al., 2006; Giesler et al., 2012; Cai et al., 2022). Studies have shown that iron-oxidizing bacteria can promote pollutant degradation, protect steel from erosion, and improve ecological resistance (Herrera and Videla, 2009; Qin and Shi, 2017; Zhang et al., 2021). However, there is no clear answer as to whether iron-oxidizing bacteria can improve the resistance of ecosystems to ionizing radiation. This issue needs to be addressed in future research.

In addition, the relative abundance of ectomycorrhizal fungi was significantly positively correlated with radiation intensity, which may be because the hyphae of ectomycorrhizal fungi wrap around the root cells to form a biomembrane. This biofilm not only protects plants from pathogens and chemical pollutants (Martino and Perotto, 2010; Clasen et al., 2018) but also from ionizing radiation. Ectomycorrhizal fungi may function as anti-radiation agents. Plants in high-radiation environments are more inclined to choose ectomycorrhizal fungi as partners, which increases the abundance of ectomycorrhizal fungi (mainly Basidiomycota) significantly. This was clearly observed in the Blank group where the abundance of ectomycorrhizal fungi was zero. Additionally, ectomycorrhizal fungi can help plants absorb soil nutrients, such as nitrogen and phosphorus (Liu et al., 2022), and are beneficial for carbon fixation (Zak et al., 2019). Thus, ectomycorrhizal fungi improve the nutritional status of plants damaged by radiation (Li et al., 2022), increase the soil C/N ratio, and change the soil microbial diversity and community composition (Zheng and Song, 2022). However, more research is needed to prove that ectomycorrhizal fungi have the function of resisting radiation.

5. Conclusion

Long-term ionizing radiation had no significant effect on soil bacterial diversity but had a significant effect on fungal community diversity. High and medium radiation significantly reduced the soil fungal diversity and significantly affected the fungal community structure. Long-term ionizing radiation had a significant promoting effect on iron-oxidizing bacteria and ectomycorrhizal fungi and a significant inhibitory effect on predatory and parasitic fungi. The relative abundances of iron-oxidizing bacteria and ectomycorrhizal fungi were positively correlated with the soil C/N ratio, and the increase in the soil C/N ratio promoted the α diversity of soil fungi and β diversity of microorganisms. The increase in the relative abundance of iron-oxidizing bacteria, ectomycorrhizal fungi, and predatory and parasitic bacteria had a negative effect on soil fungal α diversity and microbial β diversity. The SEM can explain the 56% of C/N ratio, 52% of fungal α diversity, and 41% of microorganisms β diversity. The results of this study thus provide direction for future research on the effects of long-term ionizing radiation on soil ecosystems.

Data availability statement

The datasets presented in this study can be found in online repositories. The names of the repository/repositories and accession number(s) can be found below: https://www.ncbi.nlm.nih.gov/, PRJNA950186.

Author contributions

FL and WS provided the conceptualization and framed the methodology. XH wrote and prepared the original draft. XH and QQ did the review and editing. FC and ZJC provided the validation. All authors made significant contributions to this study and contributed to the article and approved the submitted version.

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Conflict of interest

The authors declare that the research was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

Publisher's note

Supplementary material

The Supplementary Material for this article can be found online at: https://www.frontiersin.org/articles/10.3389/fevo.2023.1184582/full#supplementary-material

SUPPLEMENTARY TABLE 1
Endemic 16 S OTUs and their relative abundance in each group.

SUPPLEMENTARY TABLE 2
Endemic ITS OTUs and their relative abundance in each group.

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