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# Nurse role and mechanism of *Coriaria nepalensis* in abandoned land of Pb-Zn mining area

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Mining activities, while providing a huge material base for human society, have also caused great damage to the ecosystem. A large amount of mine waste is in urgent need of treatment and remediation. Phytoremediation, as a green and low-cost way of mine site restoration, has been researched by a large number of scholars. Ecological restoration, as a suitable alternative to phytoremediation, has also received extensive attention from scholars too. Field survey revealed that a native plant, *Coriaria nepalensis*, adapted to the abandoned sites of Pb-Zn mines for its adaptability to pollution and extreme habitats and its improvement of the surrounding microenvironment, with its formation of plant communities may contribute to the natural recovery of the abandoned sites of mines. For this reason, the present study was conducted on the nurse plant, *C. nepalensis*, which was naturally colonized in the abandoned land of the Pb-Zn mine in Mine Town, Huize County. The specific results of the study are as follows: *Coriaria nepalensis* promotes the stabilization of the soil structure under the canopy, and the local resources of the soil increase and the "fertilizer island" effect appears: (1) Improvement of physical properties: Compared with the herbaceous sample, the soil bulk density of the *Coriaria nepalensis* is significantly lower than that of the herbaceous sample. (2) Improve soil nutrition: the organic matter, total nitrogen and total phosphorus contents of the inter-root soil of the *Coriaria nepalensis* in large multi-diversity sites were higher than those of the herbaceous sample sites. (3) Reducing the toxicity of soil heavy metals to plants: although the total amount of heavy metals and the effective state of the *Coriaria nepalensis* were significantly higher than that of the herbaceous samples, the diversity and biomass of the plants under the *Coriaria nepalensis* were not affected, but were higher instead, which indicated that the *Coriaria nepalensis* mitigated the stress and toxicity of the heavy metals to the plants under the canopy, and allowed the plants to colonize and grow under the canopy. (4) *Coriaria nepalensis* in Pb-Zn mine abandoned sites can regulating soil microbial community structure, thus enabling plant community succession in degraded environments. Ascomycetes, Mycobacteriophages, Ascomycetes, and Stramenophages with higher abundance. (5) *Coriaria nepalensis* microbial community structure and increases the abundance of functions associated with nitrogen cycling and stress tolerance. There were higher abundances of bacterial functions related to nitrogen fixation, nitrate reduction, nitrogen respiration, nitrate respiration; and higher abundances of stress-tolerant, parthenogenetic

anaerobic, biofilm-forming, aerobic, mobile protozoa-containing, and Gram-negative bacteria in the *Coriaria nepalensis*. In sum: *C. nepalensis* can have a nurse effect on its sub-canopy plants by improving microhabitat soil properties and regulating soil microbial community structure in abandoned sites of Pb-Zn mines, thus enabling plant community succession in degraded environments.

#### KEYWORDS

nurse plant, heavy metal, Pb-Zn mine, *Coriaria nepalensis*, ecological restoration

## Highlight

- *Coriaria nepalensis* has a good nurse effect on plants and can help other plant species to colonize under its canopy.
- *Coriaria nepalensis* promotes the stabilization of the soil structure under the canopy, and the local resources of the soil increase and the “fertilizer island” effect appears.
- *Coriaria nepalensis* in Pb-Zn mine abandoned sites can regulate soil microbial community structure, thus enabling plant community succession in degraded environments.

## 1 Introduction

Mining activities provide basic physical energy security for humans and are one of the key sources of global economic growth (Zhu et al., 2018). Globally, approximately  $350 \times 10^9$  tons of mining waste will be generated annually (Adiansyah et al., 2016). The country has maintained a dominant position in global mineral resource production and consumption (Pokhrel and Dubey, 2013). Mineral resources as an important material basis for economic development, the development and utilization of mining areas is extremely important for the modernization of China (Pan et al., 2014). Yunnan is known as the “kingdom of non-ferrous metals”, and 143 kinds of minerals have been discovered in Yunnan, accounting for 83% of the discovered minerals in China, including lead and zinc, which are among the most abundant in China and the world (Li, 2006). Among them, the Pb-Zn mining area in Huize County, which has the richest Pb-Zn ore taste in China, has a history of zinc refining for hundreds of years (Lei and Duan, 2008). As a famous collection and distribution area for clay-based Zn refining in China, most of the mining processes of Pb-Zn mines in Huize are characterized by large-scale mining of metal deposits with high grade and associated useful elements; long mining history; and low metal recovery and comprehensive utilization, so many mining abandoned sites leave a large amount of tailings and abandoned low-grade ores, which make the release of toxic and harmful heavy metal elements in them (Li et al., 2014;

Chen et al., 2022), thus causing non-negligible secondary pollution to the local ecological environment.

Mining activities in Pb-Zn mines have led to the accumulation and gradual diffusion of large amounts of toxic and hazardous substances into the environment, making mine waste sites a source of toxic and hazardous heavy metal elements, thus causing different levels of pollution (Rieuwerts et al., 2014). Soil acidification due to the massive export of potentially toxic elements and the oxidation of sulfides in mine spoils has resulted in reduced turnover of organic matter, increased soil toxicity, and loss of biodiversity in mine soils (Rodriguez-Seijo et al., 2020), and has caused soil degradation, lack of vegetation cover, soil structural damage, poor soil and water conservation, high soil heavy metal content, and soil nutrient depletion in mine waste sites (Mi et al., 2019). and soil nutrient depletion (Mi et al., 2019). Heavy metal contamination of abandoned sites in Pb-Zn mines is a serious hazard to plants, animals, microorganisms and humans (Cui et al., 2020). Meanwhile, these extreme environments can also prevent natural plant recolonization, which can lead to ecological damage (Stylianou et al., 2020; Li et al., 2022). Therefore, heavy metal contamination of abandoned sites in Pb-Zn mines has caused serious harm to flora and fauna, ecosystems and human health, and the treatment and remediation of abandoned sites should be carried out without delay.

In recent years, in order to improve the ecological environment of mining areas, a large number of research on mine remediation technologies have been carried out, and the main common methods of heavy metal remediation of mine waste sites are physical remediation, chemical remediation, waste site reuse and bioremediation (Mahar et al., 2016; Wei et al., 2021). However, most of the above restoration methods are costly, and a low-cost restoration method becomes the key to mine restoration at this time due to the large number of mine abandoned sites in China, the remote location of mine abandoned sites, and their low economic value. Phytoremediation method is widely suggested by many as a low cost method suitable for general promotion (Mahar et al., 2016; Khalid et al., 2017). Ecological restoration, as a suitable alternative to phytoremediation, has also received extensive attention from scholars too. Plant species selection is the key to the success of ecological restoration in mine waste sites (Chen et al., 2020). Conventional ecological restoration methods are to screen

hyperaccumulator plants for large-scale planting, but hyperaccumulator plants generally have problems such as being confined to their native habitat, shallow roots, slow growth, small biomass, and metal selectivity (van der Ent et al., 2013; Sheoran et al., 2016), and are difficult to colonize mine waste sites. Even if it is colonized, its ability to form a long-term stable community and to continue succession has not been demonstrated (Saxena et al., 2020). In the past few years, the selection of ecological remediation plants has evolved from hyperaccumulation plants to native plant screening, but more studies have focused only on the uptake, transfer and accumulation effects of native plants on heavy metals and the short-term improvement of the soil environment, never on their effects on plant survival, plant community formation and plant colonization, and plant succession factors. Gastauer et al. (2018) said that perhaps native nurse plants can have greater ecological benefits relative to hyperaccumulation plants in extremely degraded environments such as mine waste sites. Nurse plants are stress-resistant species that not only grow rapidly in extremely degraded environments, but also trigger the restoration of essential ecosystem functions through ecological facilitation. In this study, a field survey at the abandoned site of Pb-Zn mine in Mine Town, Huize County, revealed that a native plant, *Coriaria nepalensis*, which is adapted to the abandoned site of Pb-Zn mine, may contribute to the natural restoration of the abandoned site of the mine by its adaptation to pollution and extreme habitats and its improvement of the surrounding microenvironment by forming a plant community. To this end, this study was conducted to investigate the effects of *C. nepalensis* on soil physicochemical properties, soil heavy metal storage characteristics, soil microbial community and plant colonization under the canopy under different years of abandonment by using field plant sample survey and soil physicochemical property determination. We also investigated the effects of *C. nepalensis* on soil physical and chemical properties, soil heavy metal fugacity, soil microbial community and under-canopy planting under different years of abandonment. It aims to provide a theoretical basis for restoration of abandoned land in Pb and Zn mining areas through ecological restoration.

## 2 Materials and methods

### 2.1 Description of the study area

Study area is located in the lead-zinc mining area of Mine Town, Huize County, Qujing City, Yunnan Province (103.70° E, 26.64° N, altitude 2500 m), which belongs to the Wumeng Mountain System. The region has a temperate highland monsoon climate with abundant rainfall, mild climate and unknown seasons, but a clear division between rainy and dry seasons. The average annual rainfall is 858.4 mm and the average annual temperature is 12.6°C. This Pb-Zn mining area is the richest area in China in terms of Pb-Zn ore taste and has a history of zinc refining for hundreds of years (Zhou et al., 2018), and it is a famous collection and

distribution area for clay-based zinc refining in China, which is now a mine abandoned area with sparse vegetation. The area is dominated by yellow-brown soils with weakly alkaline soils, and the main vegetation types are herbs and shrubs (Zhou et al., 2018), and the study area and sampling sites are shown in Figure 1.

### 2.2 Study site and soil sampling

In early September 2021, a field survey was conducted on abandoned sites of Pb-Zn mines in mining town of Huize County: representative sample sites of *Coriaria nepalensis* were selected, and the soil heavy metal element range of each sample site was delineated by a portable soil heavy metal analyzer and based on the plant inspection of each sample site and the narrative of the mine management personnel, etc., four (> 7 ha) different sample sites of *C. nepalensis* were selected for this study, representing four types of study sites that were abandoned for 10 years, abandoned for 20 years, abandoned for 30 years, and disturbed by mining, respectively. The four sample plots are described in detail as follows: abandoned 10-year sample plot (20 ha); abandoned 20-year sample plot (12 ha); abandoned 30-year sample plot (15 ha); and undisturbed by mining sample plot (7 ha). These four plots were identified as the study plots (Figure 1), labeled S1, S2, S3, and S4, respectively, and were selected based on the following criteria: similar topography and slope < 3%, distance between any two plots > 2 km, and distance between any two plots within 5 km for similar topography and soil types and similar climatic conditions.

### 2.3 Sample collection and handling

Five *C. nepalensis* plants of similar size (*C. nepalensis* canopy diameter of about 1.5~2 m) were randomly selected in each sample site. Each *C. nepalensis* plant was used as a small sample point for the study, totaling 20 sample points. A sample square (3 m × 3 m) was set up at each sample site with the *C. nepalensis* as the geometric center, and there were five sample squares in each sample site. Five herbaceous samples were randomly selected in the area without *C. nepalensis* around the sample plots, and five herbaceous samples (3 m × 3 m) were set up (Figure 2), for a total of 40 samples. The cover, plant height, vegetation cover, name of herbaceous species, number of species, frequency of each sample, and the cover and height of five randomly selected plants of each species in the sample were counted and taken back to the laboratory for biomass determination. Plant names and species delineation were identified by consulting the Yunnan Central Wild Plant Manual and seeking assistance from a plant taxonomist. Soil sample collection: Soil samples were collected from 0–45 cm of the *C. nepalensis* sample (Y) and the herbaceous samples (N) using the five-point sampling method, and stored in two parts: one in a –80°C refrigerator for soil microbiological determination, and one for natural air-drying for the study of soil physical and chemical properties and heavy metal distribution under *C. nepalensis*.

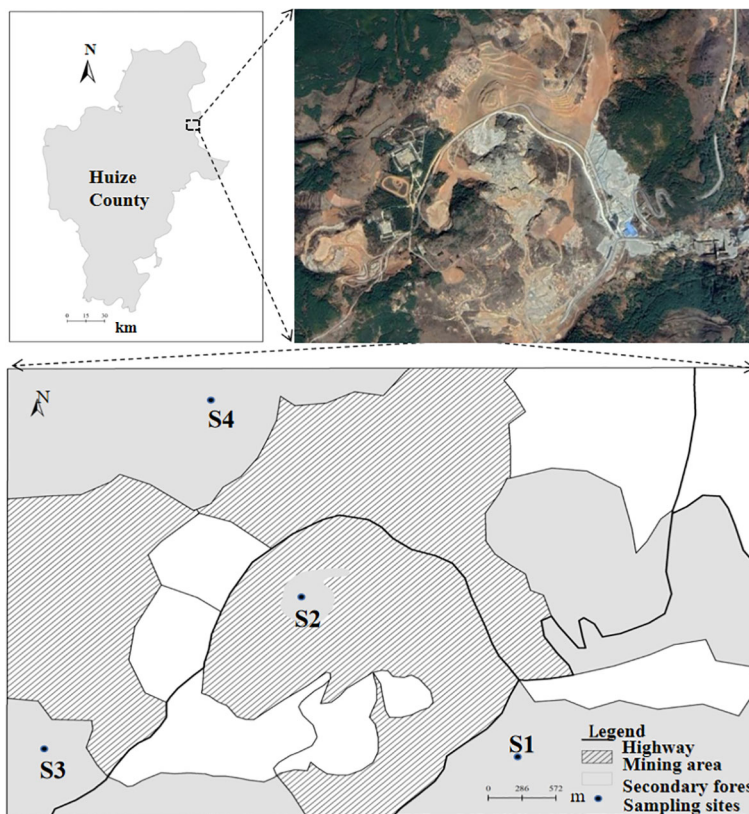


FIGURE 1 Geographical location of study sites (Drawing approval number is GS(2016)1600.), S1: 10 years of abandonment; S2: 20 years of abandonment; S3: 30 years of abandonment; S4: four types of study sites undisturbed by mining.

## 2.4 Soil nutrient and heavy metal content analysis

We measured and analyzed 40 soil samples collected for soil bulk density (SBD), total nitrogen (TN), organic matter (SOM), total phosphorus (TP), and soil heavy metals (TPb, TZn, TCd, TMn). Soil bulk density (SBD, g/cm<sup>3</sup>) was determined by the ring-knife method (Marc and Jacques, 2006). Total soil carbon and total nitrogen (TC/TN, g/kg) were determined by combustion method

(Zhang and Elser, 2017) using a vario TOC select type total organic carbon analyzer (Elementar Analysensysteme GmbH, Germany), and soil organic matter (SOM, g/kg) was derived by total soil nitrogen conversion. Soil organic matter (SOM, g/kg) was obtained by total soil nitrogen conversion. Soil total phosphorus (TP, g/kg) was determined by the sulfuric acid digestion-molybdenum antimony resistance method (Zhang et al., 2013). Total heavy metals in soil samples were determined by flame atomic absorption spectrometry (Moyan et al., 2017). The samples were

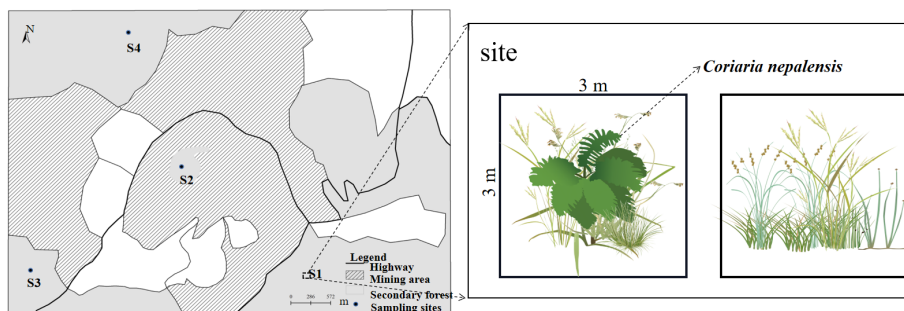


FIGURE 2 Plant Sample Layout, S1: 10 years of abandonment; S2: 20 years of abandonment; S3: 30 years of abandonment; S4: four types of study sites undisturbed by mining.

determined on a flame atomic absorption spectrometer (Agilent AA240 spectrometer, Agilent Technologies, CA, USA).

## 2.5 Soil microbiology determination

Total DNA was extracted from 0.5 g of soil sample per tube, and the composition of soil bacterial, fungal and actinomycete communities was analyzed using high-throughput sequencing (Li et al., 2023).

Amplified by PCR using primers 338F: (5'-ACTCCTACG GGGAGGCAGCA-3')/806R: (5'-GGACTACHVGGGGTWTCT AAT-3') for the V3+V4 region of the bacterial 16S rRNA gene.

Fungi PCR amplification of the ITS1 region of the fungal ITS rRNA gene was performed using the primer ITS1F: (5'-CTTGG TCATTTAGAGGAAGTAA-3')/ITS2: (5'-GCTGCGT TCTTCATCGATGC-3').

Actinomycetes were amplified by PCR using primer 960F: (GGCTTAATTTGACTCAACRCG) NSR1438: (GGGCA TCACAGACCTGTAT) for the V7 region of the Actinomycetes 18S rRNA gene.

The qualified products were subjected to Illumina Miseq sequencing, which was entrusted to Beijing Baimike Biotechnology Co. The measured data (Raw Reads) were filtered by Trimmomatic v 0.33 software, primer identification and removal were performed by cutadapt1.9.1 software, followed by splicing of the samples by overlap and length filtering by Usearch v10 software, and finally denoising and removal of the chimeric sequences were performed by QIIME2 2020.6. chimeric sequences to obtain the final valid data.

## 2.6 Plant characterization of the sample

(1) The relative interaction index (RII) and incremental species richness (ISR) for the *C. nepalensis* samples and surrounding herbaceous samples, (Cavieres et al., 2016) were calculated as follows:

$$RII = (\alpha_Y - \alpha_N) / (\alpha_Y + \alpha_N) \quad (1)$$

$$S_{Total} = \gamma_Y + \gamma_{Shared} + \gamma_N \quad (2)$$

$$S_N = \gamma_N + \gamma_{Shared} \quad (3)$$

$$ISR_Y = (S_{Total} - S_N) / S_{Total} \quad (4)$$

Where:  $\alpha_Y$ ,  $\alpha_N$  are mean values of species richness within the *C. nepalensis* samples and herbaceous samples, respectively;  $\gamma_N$  denotes species found only within the matsutake bush sample;  $\gamma_{Shared}$  denotes species found in two microhabitats.

(2) Plant diversity indices: richness index (R), Simpson diversity index (D), Shannon-Wiener diversity index (H), and Pielou evenness index (J) (Ma et al., 1997), calculated as follows:

$$\text{Richness index: } R = S \quad (5)$$

$$\text{Simpson diversity index: } D = 1 / \sum_{i=1}^S P_i^2 \quad (6)$$

$$\text{Shannon-Wiener diversity index: } H = -\sum_{i=1}^S P_i \ln P_i \quad (7)$$

$$\text{Pielou evenness index: } J = \sum_{i=1}^S P_i \ln P_i / \ln S \quad (8)$$

Where: S denotes the number of species occurring within the sample square;  $P_i$  is the relative importance value, which is the proportion of the number of the *i*th species to the total number of all species.

(3) Biomass determination: 5 plants of each species randomly determined in each sample square were dug out with roots, marked and bagged according to different species in different squares, returned to the laboratory, washed, divided into above-ground and below-ground parts and then killed in the oven at 105°C for half an hour, then dried at 65°C to a constant weight and weighed with an electronic balance with an accuracy of 0.01 g to determine total biomass.

## 2.7 Data analysis

Excel 2020 software was used to count and organize the data; IBM SPSS 26.0 software was used to perform statistical analysis of the data. One-way analysis of variance (ANOVA) was used to assess differences in soil physicochemical properties, microbial diversity, and plant diversity and biomass across the same parties. Finally, Origin 2021 software was used for plotting. Structural equation models (SEM) were constructed using the lavaan software package in R (Rosseel, 2012; Hong et al., 2021), and the model parameter estimation method was based on the maximum probability method. SEM was created to estimate the contribution of the main influences and pathways in the presence of *C. nepalensis* (Branco et al., 2016). All the above statistical tests and illustrations were performed in R 4.1.3 or R 4.2.0 (R Core Team, 2018).

## 3 Results

### 3.1 Effect of *C. nepalensis* on soil physicochemical properties

#### 3.1.1 Effect of *C. nepalensis* on soil nutrition

*C. nepalensis* can change the native habitat and improve the soil properties in *C. nepalensis* sample (Y) compared with the surrounding herbaceous sample (N). This indicates that the *C. nepalensis* promotes the stabilization of the soil structure under the canopy and increases the local resources of the soil with a "fertilizer island" effect. As shown in Figure 3, the soil improvement effects were reflected in the following aspects: (1) the soil bulk weight of *C. nepalensis* samples was significantly lower than that of herbaceous samples; (2) the organic matter of *C. nepalensis* samples was significantly higher than that of herbaceous samples in all samples except for S3 samples; (3) except for S3 sample, the total nitrogen of the *C. nepalensis* samples was significantly higher than

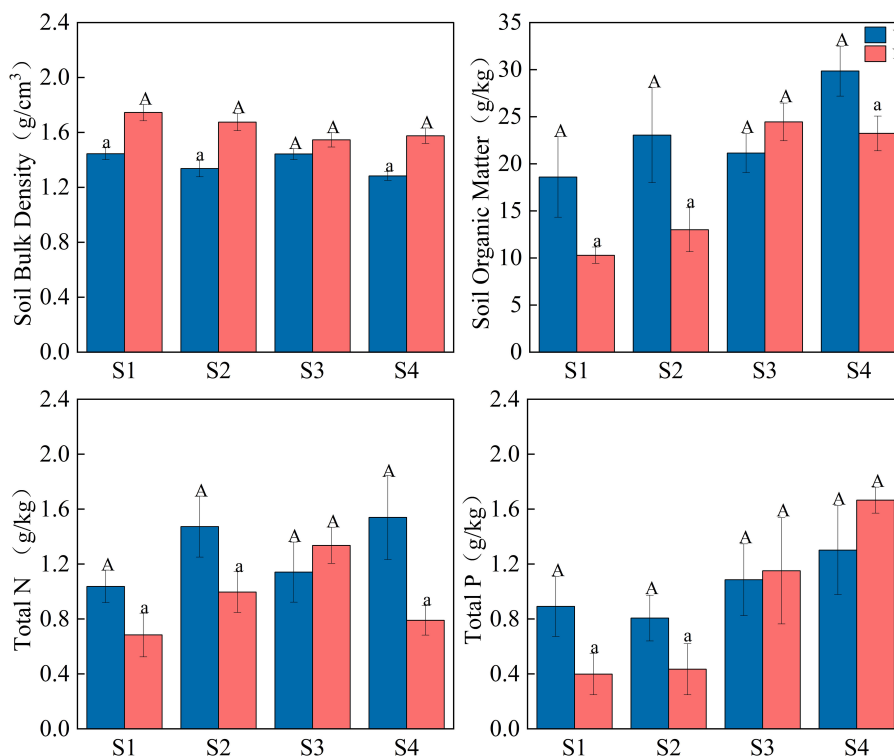


FIGURE 3

Effect of *C. nepalensis* on soil physicochemical properties; S1, S2, S3, S4 are different years of abandonment; Y is *C. nepalensis* samples; N is a herb samples; Different cases indicate significant difference between Y and N based on 95% confidence interval ( $p < 0.05$ ).

that of the herbaceous samples; (4) except for S3 and S4 samples, the total phosphorus of the *C. nepalensis* samples was significantly higher than that of the herbaceous samples.

### 3.1.2 Effect of *C. nepalensis* on soil heavy metals

As can be seen from Figure 4, total soil Pb in the *C. nepalensis* samples was not significantly different from that in the herbaceous samples. The total soil Zn and Cd in the *C. nepalensis* samples were significantly higher than that in herbaceous samples in the S1, S2, S4 samples, while the opposite was true in Sample S3. In the *C. nepalensis* samples, soil total Cd was significantly higher in S2 and S4 than in herbaceous samples, while the opposite was true in S3. In the *C. nepalensis* samples, soil total Mn was significantly higher in S1 and S2 than in herbaceous samples, while the opposite was true in S3.

## 3.2 Effect of *C. nepalensis* on soil microbial community structure

The results of NMDS analysis based on Bray-Curtis similarity coefficients for bacterial, fungal, and actinomycete community data from each site soil sample are shown in Figure 5.

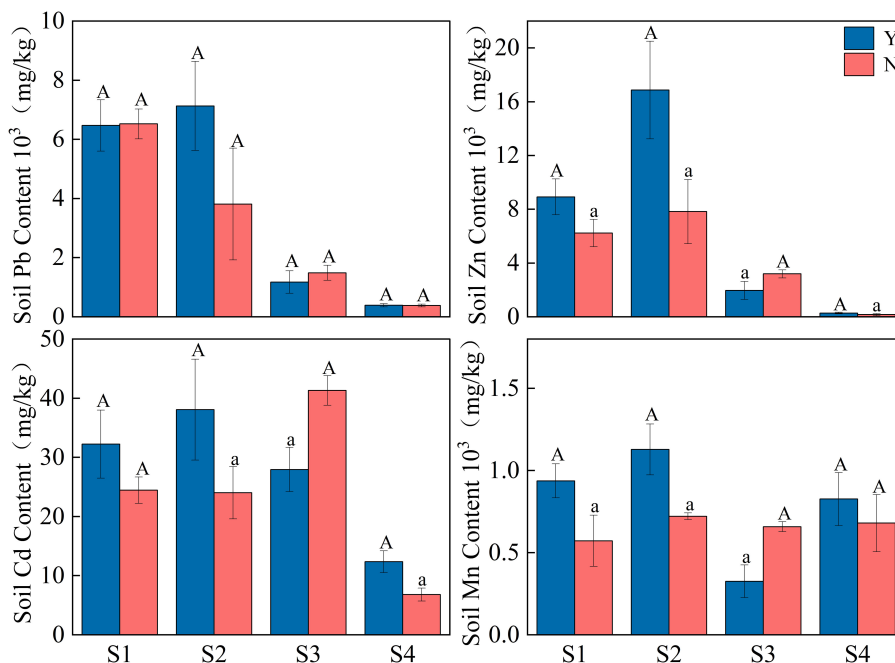
### 3.2.1 Effect of *C. nepalensis* on soil microbial diversity

As seen in Figure 6, For the bacterial community, Chao1 index was significantly higher in S1 and S3 samples for *C. nepalensis*

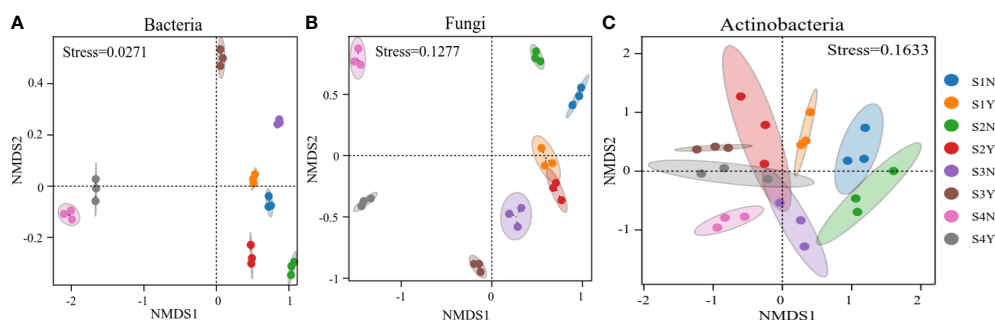
samples than for the herbaceous samples, while the opposite was true for S4 samples; Shannon index was significantly higher in S2 and S4 samples for *C. nepalensis* samples than for the herbaceous samples. For the fungal community, the fungal Chao1 index was significantly higher in the *C. nepalensis* samples than in the herbaceous samples in the S2, S3, S4 samples, and the fungal Shannon index was significantly higher in the *C. nepalensis* samples than in the herbaceous samples in the S3 and S4 sample sites. For actinomycetes, the Chao1 index and Shannon index of actinomycetes were significantly higher in the *C. nepalensis* samples than in the herbaceous samples in the three sample sites, except for the S3 sample site.

### 3.2.2 Effect of *C. nepalensis* on soil microbial composition

As shown in Figure 7, the composition of bacterial and fungal communities were similar for each site, but the abundance of each phylum differed. In the *C. nepalensis* samples, it could be found that the abundance of Proteobacteria was higher in each sample site than in the herbaceous sample sites; except for the S3 sample site, the abundance of Bacteroidetes was higher in the herbaceous sample sites; in each sample site, the abundance of Chloroflexi was higher in the herbaceous samples than in the *C. nepalensis* samples. For the fungal community composition, In the *C. nepalensis* samples, it could be found that the abundance of Ascomycota was higher than that of herbaceous sample sites in all sample sites except S4; the abundance of Basidiomycota was higher than that of herbaceous



**FIGURE 4** Effect of *C. nepalensis* on soil heavy metals; S1, S2, S3, S4 are different years of abandonment; Y is *C. nepalensis* samples; N is a herb samples; Different cases indicate significant difference between Y and N based on 95% confidence interval ( $p < 0.05$ ).



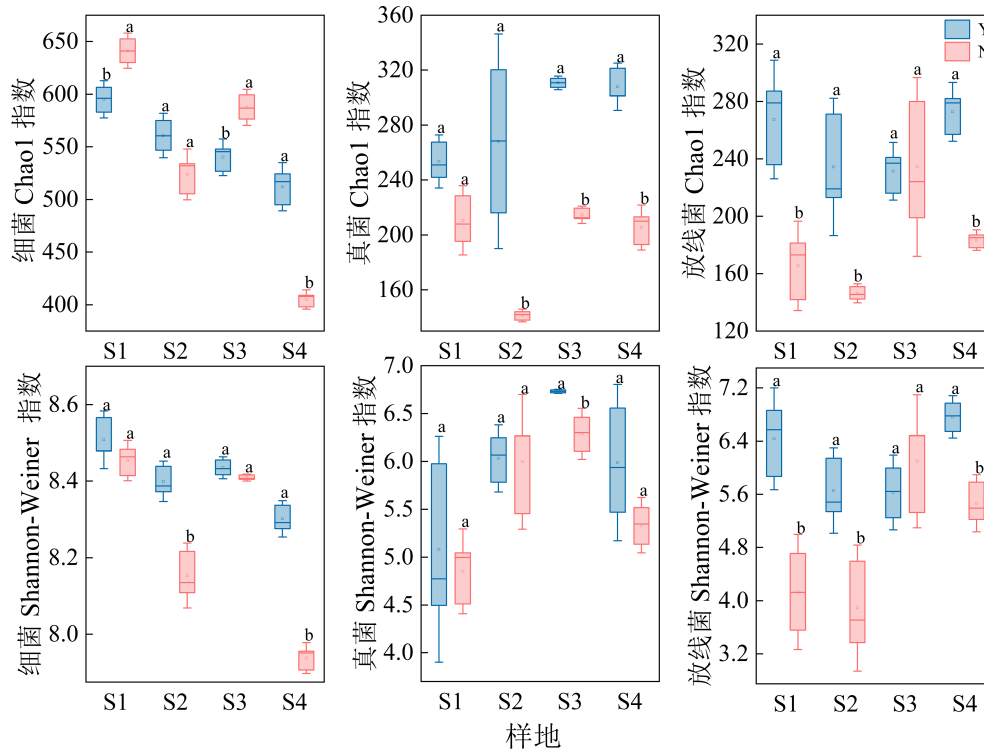
**FIGURE 5** Non-metric multidimensional scale (NMDS) ranking plots based on Bray-Curtis distances for (A) bacterial, (B) fungal and (C) actinomycete community samples for all loci.

samples in all sample sites except S3; and the abundance of Glomeromycota and Chytridiomycota was higher than that of herbaceous samples in all sample sites.

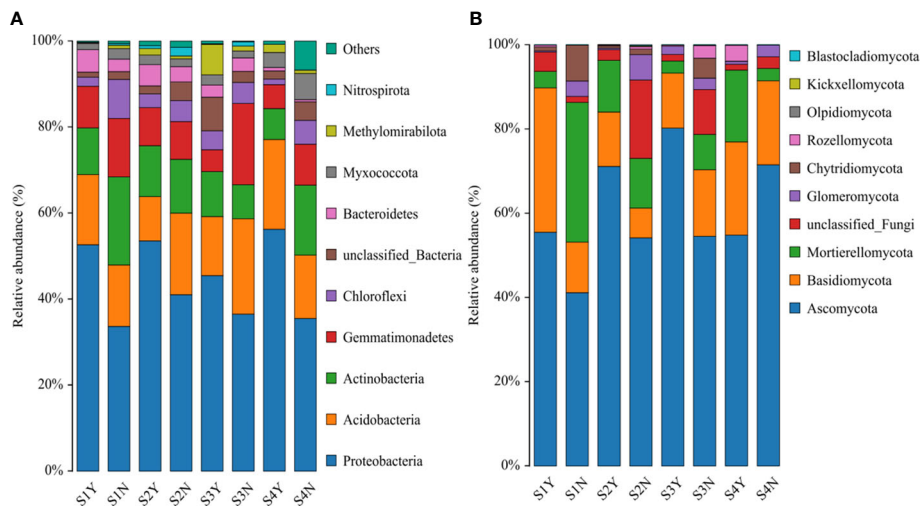
### 3.2.3 Effect of *C. nepalensis* on soil microbial functions

By comparing with the FAPROTAX database, we found that the bacterial functions related to nitrogen fixation and nitrate reduction were higher in the *C. nepalensis* samples than in the herbaceous samples in all the sample plots; the bacterial functions related to

nitrogen respiration and nitrate respiration were higher in the *C. nepalensis* samples than in the herbaceous samples except for the S4 sample plots; the bacterial functions related to predation or ectoparasitism were higher in the herbaceous samples than in the *C. nepalensis* samples except for the S3 sample plots (Figure 8). The bacterial functions related to predation or ectoparasitism were higher in the herbaceous samples than in the *C. nepalensis* samples except for S3 (Figure 8). By comparing with the Bugbase database, we found that more parthenogenic anaerobic bacteria and stress tolerance were present in the *C. nepalensis* samples in all the sample plots; greater



**FIGURE 6** Alpha diversity indices of bacteria, fungi and actinomycetes in different loci. Top: Chao1 indices of bacteria, fungi and actinomycetes. Bottom: Shannon indices of bacteria, fungi and actinomycetes. Different lowercase letters indicate significant differences ( $p < 0.05$ ) based on 95% confidence intervals for *C. nepalensis* samples and herbaceous samples.

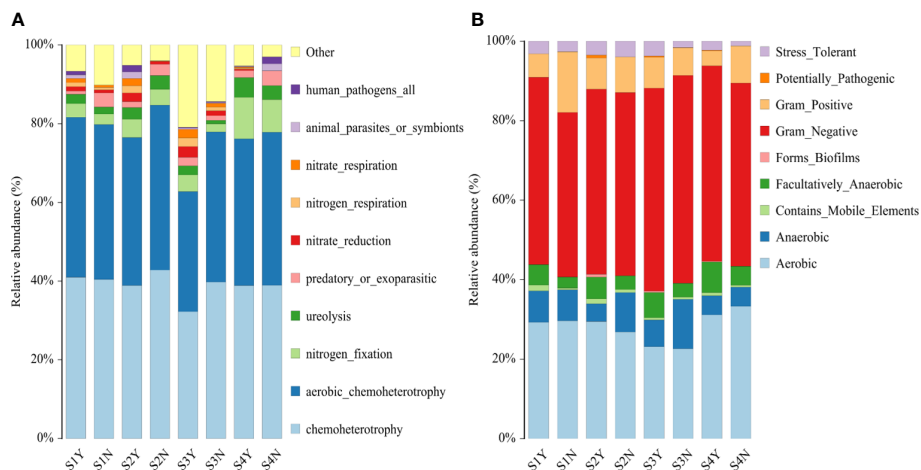


**FIGURE 7** Relative abundance (%) of bacterial and fungal taxa at the phylum level in different equations. (A) Bacterial taxa; (B) fungal taxa.

abundance of potentially pathogenic bacteria and biofilm formation were present in the *C. nepalensis* samples in all the sample plots except S1; greater abundance of stress tolerance function was present in the *C. nepalensis* samples in all the sample plots except S2; greater

abundance of aerobic bacteria and Gram-negative bacteria were present in the *C. nepalensis* samples in all the sample plots except S3; and greater abundance of aerobic bacteria was present in the *C. nepalensis* samples in all the sample plots except S4. In addition to S3,





**FIGURE 8** Microbial function prediction in different parties (A) based on bacterial function prediction in different parties of FAPROTAX; (B) based on bacterial function prediction in different parties of Bugbase.

*C. nepalensis* samples had greater abundance of mobile elements and Gram-negative bacteria; except for S4, *C. nepalensis* samples had greater abundance of aerobic bacteria. In contrast, higher abundance of Gram-positive bacteria was found in herbaceous samples in all the plots except S3 (Figure 8).

**TABLE 1** Composition of unique species in each sample.

Sample site	Sample point	Species found in one of the sample squares
S1	Y	<i>Juncus effusus</i> , <i>Rorippa indica</i> , <i>Cyperus iria</i> , <i>Cynoglossum amabile</i> , <i>Sonchus oleraceus</i> , <i>Erigeron canadensis</i>
	N	<i>Cirsium japonicum</i>
S2	Y	<i>Anemone vitifolia</i> , <i>Juncus effusus</i> , <i>Pseudognaphalium affine</i> , <i>Tradescantia sillamontana</i> , <i>Stellaria media</i> , <i>Oxalis corniculata</i> , <i>Galium asperifolium</i> , <i>Rosaomeiensis pteracantha</i> , <i>Chenopodium album</i> , <i>Artemisia stechmanniana</i>
	N	<i>Oenanthe javanica</i>
S3	Y	<i>Plantago asiatica</i> , <i>Cynoglossum amabile</i> , <i>Geranium wilfordii</i> , <i>Cirsium japonicum</i> , <i>Rosaomeiensis pteracantha</i> , <i>Duchesnea indica</i> , <i>Eupatorium fortunei</i> , <i>Lespedeza juncea</i> , <i>Cotoneaster hissaricus</i> , <i>Imperata cylindrica</i> , <i>Vaccinium fragile</i>
	N	<i>Cyperus iria</i> , <i>Incarvillea arguta</i> , <i>Arthraxon hispidus</i> , <i>Cynodon dactylon</i>
S4	Y	<i>Plantago asiatica</i> , <i>Erigeron canadensis</i> , <i>Oxalis corniculata</i> , <i>Oenanthe javanica</i> , <i>Duchesnea indica</i> , <i>Lespedeza juncea</i> , <i>Arthraxon lanceolatus</i> , <i>Vaccinium fragile</i> , <i>Aster tataricus</i> , <i>Leontopodium dedekensii</i> , <i>Elaeagnus pungens</i> , <i>Populus yunnanensis</i> , <i>Tradescantia fluminensis</i>
	N	<i>Peristylus coeloceras</i>

S1 is a 10-year abandoned sample plot; S2 is a 20-year abandoned sample plot; S3 is a 30-year abandoned sample plot; S4 is a mining-disturbed sample; Y is a *C. nepalensis* sample plot; N is a herbaceous sample.

### 3.3 Effects of *C. nepalensis* on plant community structure

#### 3.3.1 Effect of *C. nepalensis* on the colonization of sub-canopy plants

As shown in Table 1, the number of species unique to the *C. nepalensis* samples were significantly higher than that of the herbaceous sample in all the sample sites, and *C. nepalensis* had more of its endemic species under its canopy. This indicates that in the abandoned sites of Pb-Zn mines, *C. nepalensis* has a good nurse effect on plants and can help other plant species to colonize under its canopy.

As shown in Figure 2, the relative interaction index (RII) and incremental species richness (ISR) were calculated for each sample site based on the number of species and unique species in each sample site (Table 2). As shown in Table 2, the relative interaction index (RII) was greater than 0 for each site, indicating that the

**TABLE 2** Relative interaction index (RII) and incremental species richness (ISR) of sample.

Sample site	Sample point	RII index	ISR index
S1	Y	0.1923; > 0	23.08%
	N		3.85%
S2	Y	0.2500; > 0	28.57%
	N		2.86%
S3	Y	0.3235; > 0	35.29%
	N		11.76%
S4	Y	0.4137; > 0	44.82%
	N		3.44%

S1 is the abandoned 10-year sample site; S2 is the abandoned 20-year sample site; S3 is the abandoned 30-year sample site; S4 is the sample site disturbed by mining; Y is the sample site of *C. nepalensis* sample; N is the surrounding herbaceous sample.

species richness increased at the patch scale in each sample site. At the community level, the proportional increase in species richness from the *C. nepalensis* can be expressed by the incremental species richness (ISR) index, which was greater than 20%.

### 3.3.2 Impact of *C. nepalensis* on plant $\alpha$ -diversity

As shown in Figure 9, In *C. nepalensis* sample, the Shannon diversity index and Simpson index were higher in the S2 and S4 samples than in the herbaceous sample. The Pielou index of the herbaceous sample without *C. nepalensis* sample was significantly higher than that of the *C. nepalensis* sample in the S1 sample.

### 3.3.3 Effect of *C. nepalensis* on subcanopy biomass

The biomass of each sample was measured and the results are shown in Figure 10. For the same site, the biomass of the *C. nepalensis* sample was found to be significantly higher than that of the surrounding herbaceous samples in all four sample sites.

## 3.4 Nurse role of *C. nepalensis* in abandoned sites with different ages of Pb-Zn mines

In this study, structural equation modeling was used to explore the key factors affecting plant biomass within the sample plots (Figure 11). The herbaceous sample square (SN) was used as a control. In the SY sample, the effects can be divided into four main pathways: (i) TN→Bio ( $\lambda = 0.28$ ), (ii) ACT-S→Bio ( $\lambda = 0.40$ ) and (iii) SBD→Bio ( $\lambda = -0.50$ ), (iiii) SBD→ACT-S ( $\lambda = 0.35$ )→Bio ( $\lambda = 0.40$ ). In the SN sample, there is a major pathway: (i) ACT-S→Bio ( $\lambda = 0.62$ ), while there is a nitrogen recharge pathway: SOM→TN ( $\lambda = 0.56$ ) in the SN sample due to nitrogen deficiency. In the *C. nepalensis* complex, TN, ACT-S and SBD are direct factors affecting plant biomass within the sample, while the effect of SBD on ACT-S also affects plant biomass within the sample as an indirect factor. When in herbaceous samples, ACT-S can directly affect plant biomass within the sample, while herbaceous samples will increase N content through SOM due to N deficiency, but have no significant effect on biomass. Overall, N may be the main factor limiting plant colonization and survival in degraded habitats in mining areas.

## 4 Discussion

### 4.1 Effect of *C. nepalensis* on soil properties

The promotion of sub-canopy species by conservation plants is primarily through intermediates (soils) (Hunter and Price, 1992). Soil nutrient sharing may provide long-term benefits to nurse plants and may be a neglected mechanism for maintaining plant community coexistence and increasing phylogenetic diversity (Anthelme et al., 2017; Montesinos-Navarro et al., 2017). Wright et al. (2017) showed that in degraded systems, the impact of nurse plants on soil characteristics was mainly in the form of improved microhabitat (Tapella et al., 2021) through microclimate changes induced within the canopy by nurse plants and in the form of nutrient enrichment. In the *C. nepalensis* sample soil properties outside the canopy were also improved compared to the herbaceous sample, indicating that the *C. nepalensis* sample contributed to the stabilization of the sub-canopy soil structure and the increase of local soil resources and the “fertilizer island” effect. Firstly, the soil tolerance of *C. nepalensis* sample was significantly lower than that of herbaceous sample sites, which is consistent with Tapella et al. (2021). As a symbiotic nitrogen-fixing actinomycete, *C. nepalensis* fixes nitrogen in the air and increases the soil total nitrogen content of *C. nepalensis* sample, thus improving the soil nutrition of the patches, which is consistent with the study of Wang et al. (2017), and *C. nepalensis* sample enriches nitrogen near *C. nepalensis* due to its strong nitrogen fixation ability, thus promoting plant growth and increasing community biomass. Meanwhile, it was found that the organic matter in the *C. nepalensis* sample in large diverse sites was significantly higher than that in herbaceous sample sites. This may be due to the greater plant biomass under the *C. nepalensis* sample, the accumulation of apoplastic material from the plants under the cluster and the *C. nepalensis*'s own apoplastic material, which made the organic matter content significantly higher than that of the bare ground, thus contributing to the increase of soil nutrients.

The presence of *C. nepalensis* can increase soil nutrients, Meanwhile significantly reduce heavy metal spillage. Soil organic matter easily forms complexes with metals and acts as a sorbent (Pezzarossa and Petruzzelli, 2003), and high molecular weight humic acids form very stable complexes with metals, removing toxic and hazardous metals from the environment and reducing

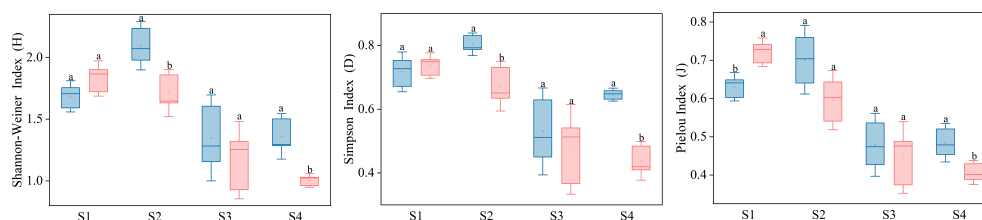
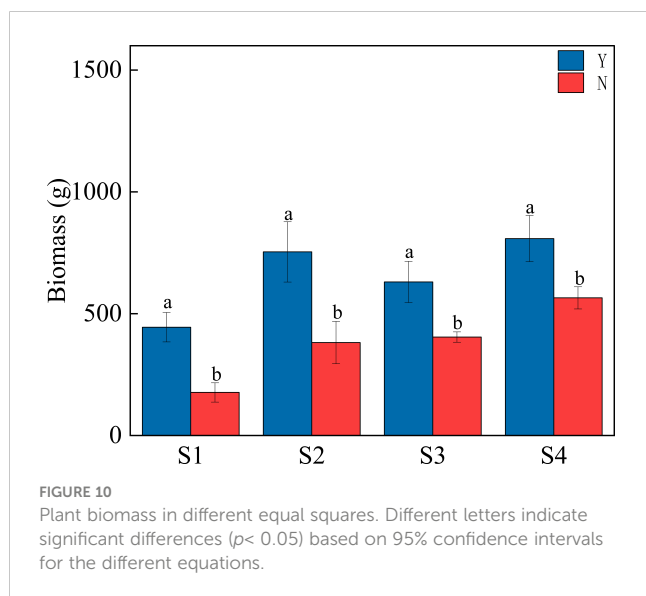


FIGURE 9

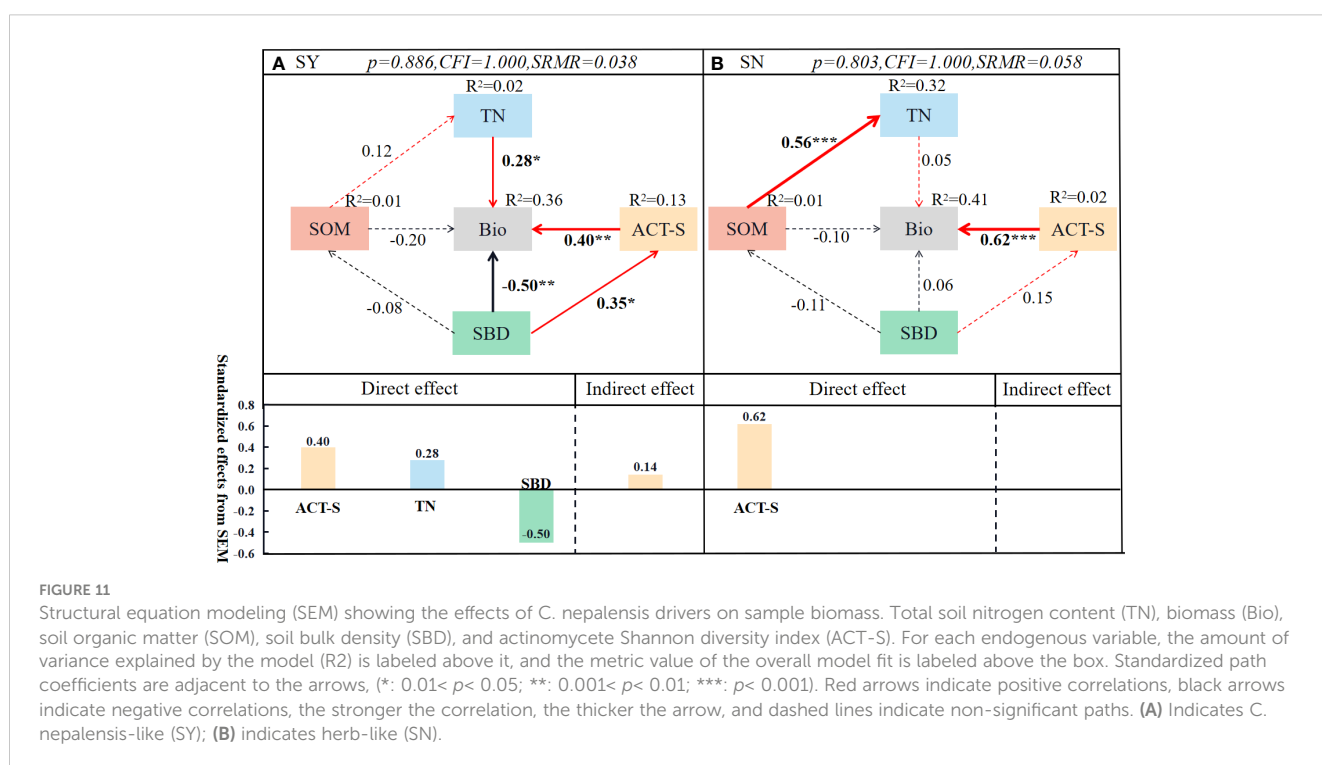
Plant diversity indices for the different equal sides. Different letters indicate significant differences based on 95% confidence intervals for different squares ( $p < 0.05$ ).



their bioavailability (Wang et al., 2010). Therefore, the increase of soil organic matter under the *C. nepalensis* sample further avoids the escape of toxic and harmful metals from the soil and reduces their toxic effects on organisms. It has also been shown that *C. nepalensis* can form complexes with heavy metals due to its own functional groups such as carboxyl or hydroxyl groups, and it can be used as the best detergent for remediation of heavy metal soils when the pH is acidic, while in the present study, the mine waste site is mainly alkaline, and *C. nepalensis* mainly shows complexation for heavy metals, and *C. nepalensis* can form complexes with heavy metals to reduce the toxicity of heavy metals to plants under the canopy (Cao et al., 2017).

## 4.2 Effect of *C. nepalensis* on microbial community structure

In microbial ecology, it is generally believed that co-nutritional microorganisms are closely associated with r-strategies, while oligotrophic microorganisms are associated with k-strategies (Zhou et al., 2017; Loayza et al., 2018). Microbial trophic partitioning may help to understand the results of this study (Ken et al., 2009; Mihoc et al., 2016). Both Proteobacteria and Bacteroidetes belong to the r-strategic bacteria (Zeng et al., 2018). Previous studies have suggested that an increase in easily decomposable organic matter such as glucose and root secretions in soil stimulates a rapid increase in the abundance of r-strategic bacteria (Bashan et al., 2017), which in turn initiates an excitation effect to accelerate soil organic matter decomposition (Bernard et al., 2007). In the study, the abundance of Proteobacteria and Bacteroidetes was found to be higher in each sample site than in the herbaceous sample sites, which justified the higher organic matter in the *C. nepalensis* sample in this study, and the increase in organic matter led to the increase in the abundance of r-strategic bacteria and the faster decomposition of organic matter in the *C. nepalensis* sample sites. Meanwhile, the presence of *C. nepalensis* increased the abundance and diversity of soil actinomycetes, probably mainly due to high inter-root organic matter content, faster decomposition, loose soil and good moisture conditions, which allowed more actinomycetes to colonize. Ascomycota and Basidiomycota have the ability to decompose cellulose and hemicellulose. Among them, Ascomycota belongs to r-strategic fungi, and the abundance of Ascomycota in *C. nepalensis* sample was greater than that of herbaceous samples in the abandoned sites of metal mining areas, which may indicate that *C. nepalensis* sample are significantly more



prone to decompose organic matter than herbaceous samples, and *C. nepalensis* sample decompose organic matter more rapidly. In contrast, Basidiomycota plays a major role in the decomposition of refractory organic matter, and an increase in the abundance of refractory organic matter in the composition of apoplankton will lead to an increase in Basidiomycota abundance (Yan et al., 2020). In the study, the abundance of Basidiomycota was greater in the *C. nepalensis* sample than in the herbaceous sample sites because of the high plant species richness and biomass of the *C. nepalensis* sample, which resulted in a complex composition of the *C. nepalensis* sample with a higher content of refractory organic matter than in the herbaceous sample sites. It was also found that the abundance of Chloroflexi in the bacterial community and Glomeromycota and Chytridiomycota in the fungal community was higher in the herbaceous sample sites than in the *C. nepalensis* sample, reflecting their ability to tolerate extreme conditions and support lower substrate utilization (Eilers et al., 2010).

Meanwhile, in this study, it was found that N was significantly higher in the *C. nepalensis* sample than in the herbaceous sample in a large diversity of sites, and the prediction of bacterial functions based on FAPROTAX revealed that the abundance of bacterial functions related to nitrogen fixation, nitrate reduction, nitrogen respiration, and nitrate respiration was higher in the *C. nepalensis* sample in a large diversity of sites, so *C. nepalensis* may have recruited more functional genes related to nitrogen cycling to improve the inter-root soil nitrogen cycle, which needs to be Further studies are needed to prove this. Bugbase's prediction of bacterial functions revealed that more biofilm-forming, parthenogenic anaerobic, stress-tolerant, aerobic, mobile progenitor-containing and Gram-negative bacteria were present in the *C. nepalensis* sample in a large diversity of sites. The inclusion of mobile elements could play an important role in horizontal transfer, thereby increasing microbial adaptation to the environment, while Gram-negative bacteria were shown to be more metal-tolerant, so *C. nepalensis* may recruit more well-adapted and tolerant microorganisms.

### 4.3 Effects of *C. nepalensis* on subcanopy plants

Nurse plants (e.g., leguminous shrubs and trees, matted plants, etc.) can induce microenvironmental changes within the canopy that provide a benign environment more conducive to seed germination and/or seedling recruitment than the surrounding environment, promoting the colonization, growth, and development of other plant species under their canopy, thereby increasing species richness, diversity, and species coexistence (Ellison, 2019). The present study showed that *C. nepalensis* could improve sub-canopy soil nutrition, reduce the toxicity of heavy metals to sub-canopy plants and recruit microorganisms that favor plant growth, resulting in more species and biomass under the canopy. This is in agreement with the findings of Joshi et al. (2001) in eroded sites and Mourya et al. (2019) in central Himalaya on *C. nepalensis*. In conclusion, *C. nepalensis* has a good nurse role in mining waste sites and *C. nepalensis* can help the establishment of other plants, thus restoring species populations and ecological interactions, which in turn makes it possible to restore the relevant ecosystem functions.

## 5 Conclusions

In summary, *C. nepalensis* has a good nurse role as a naturally colonized plant in Pb-Zn mine waste sites. It can improve the microhabitat soil properties and regulate the soil microbial community structure to conserve the under-canopy plants in the abandoned areas of Pb-Zn mines, thus enabling plant community succession in degraded environments. A comprehensive analysis of the environmental improvement effectiveness and mechanism of mulberry in Pb-Zn mine abandoned sites aims to provide a theoretical basis for revegetation and restoration of Pb-Zn mine abandoned sites.

## Data availability statement

The original contributions presented in the study are included in the article/supplementary material. Further inquiries can be directed to the corresponding author.

## Author contributions

JY: conceptualization, methodology, software, writing –original draft, visualization, and investigation. HT: investigation and software. C-QD: methodology, validation, revision, review and editing, supervision, and funding acquisition. X-QY, S-CW, LH, and L-YL: investigation and methodology. All authors 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.

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