

## Article

# Soil Bacterial Community Structure and Physicochemical Influencing Factors of Artificial *Haloxylon ammodendron* Forest in the Sand Blocking and Fixing Belt of Minqin, China

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**Abstract:** Microbial activity plays a crucial role in upholding the functional stability of vegetation–soil ecosystems. Nevertheless, there exists a paucity of studies concerning the impact of sand-fixing vegetation (*Haloxylon ammodendron*) on the structure and functional attributes of soil microbial communities. We employed Illumina high-throughput sequencing and PICRUSt2 functional prediction technology to investigate the characteristics of soil bacterial community structure, diversity, and metabolic functions in an artificial *H. ammodendron* forest, and RDA analysis and the Mantel test were used to reveal the main environmental factors affecting the structure and ecological functions of soil bacterial communities. The findings revealed a significant increase in the principal nutrient contents (organic matter, total nitrogen, total phosphorus) in the *H. ammodendron* forest soil compared to the mobile dune soil, while a reduction of 17.17% in the surface soil water content was observed. The *H. ammodendron* forest exhibited a significant enhancement in the diversity and richness index of soil bacteria. Specifically, Actinobacteria (24.94% ± 11.85%), Proteobacteria (29.99% ± 11.56%), and Chloroflexi (11.14% ± 4.55%) emerged as the dominant bacterial phyla, with Actinobacteria displaying significantly higher abundance compared to the mobile dune soil. PICRUSt2 analyses revealed that the predominant secondary metabolic functions of soil bacteria were carbohydrate metabolism, amino acid metabolism, and the metabolism of cofactors and vitamins. Additionally, the tertiary metabolic pathways exhibited greater activity in relation to enzyme function, nucleotide metabolism, energy metabolism, and antibiotics. The RDA results demonstrated that SOM, AK, and pH collectively accounted for 82.4% of the cumulative contribution, significantly influencing the bacterial community. Moreover, the Mantel test revealed that the metabolic function of soil bacteria primarily relied on five environmental factors, namely SOM, TN, AK, pH, and EC. This study significantly advances our understanding of the structural and functional changes in soil bacterial communities during the reclamation of sandy land through the establishment of artificial *H. ammodendron* forests.



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## 1. Introduction

The desert–oasis transition zone represents a pivotal ecological juncture wherein desert and oasis ecosystems converge under a shared influence [1]. The sand blocking and fixing belt at the edge of the oasis, which consists of the protective forest belt and the peripheral sealing and protection belt, is the core barrier belt of the artificial oasis, playing a key role in preventing the invasion of wind and sand, maintaining the stability of the transition zone ecosystem, and guaranteeing the oasis’s survival and development. At the same time, it is also an important part of the fragile ecosystem of the desert–oasis transition zone. However, the advent of global warming and irrational human activities has exacerbated the desertification process in this transition zone, rendering its ecological environment increasingly

fragile and susceptible [2,3]. Therefore, the region's ecological stability and sustainable economic development have been severely impeded [4]. Nevertheless, the introduction of artificial vegetation specifically designed to stabilize the sand in the transitional zone has proven to be an efficient and expeditious means of mitigating desertification [5–9]. This approach not only ensures the preservation of oasis ecosystem stability but also enhances land productivity. Over the course of approximately fifty years, experts and scholars have widely embraced this perspective as an effective technique for combating desertification.

Considering its structurally intricate and non-homogeneous nature, soil plays a pivotal role in sustaining terrestrial ecosystem functions and services [10]. Soil nutrients are limited within desert ecosystems, necessitating the implementation of ecological mechanisms that expedite the soil element cycling process, regulate soil fertility transformation, and enhance the absorption and utilization of plant nutrients [11]. These mechanisms are crucial for ensuring the sustainable restoration of desert vegetation productivity and effectively mitigating land desertification [12]. Soil microorganisms, often referred to as the “engines” of biogeochemical cycles, assume a pivotal position in facilitating the circulation of materials, the flow of energy, and the preservation of stable ecological functions within soil ecosystems [13–15]. On one hand, the participation of soil microorganisms in ecological processes comprises the decomposition of apoplastic material and humus, the breakdown of organic matter, and the facilitation of symbiotic nitrogen fixation through plant–microbe systems [16–18]. On the other hand, the soil microbial communities exhibit remarkable sensitivity to changes in environmental factors and harbor a wealth of information pertaining to regional soil environmental changes [19]. This information is frequently employed to evaluate the stability and vitality of soil ecological functions. Notably, bacteria represent the predominant constituents of the soil microbial community, owing to their abundant population, extensive diversity, and intricate complexity. In addition, they possess the ability to adapt to extreme habitats, rendering them valuable as indicator species for assessing the stability, quality, and functionality of soil ecosystems [20].

The burgeoning popularity of the high-throughput sequencing of 16S rRNA and the utilization of PICRUSt2 macrogenomic function prediction technologies present innovative methodologies for unraveling the intricate microbial community structure that underlies the functional equilibrium of diverse soil ecosystems [21,22]. The study determined that the introduction of desert flora exerts a momentous influence on the micro-ecological rehabilitation of arid and semi-arid desert soils [9,11,17,19]. For instance, in the Horqin sandy land, the rehabilitation process involving *Caragana microphylla* vegetation not only contributed to enhancements in vegetation coverage and diversity but also entailed a significant enrichment of the soil microbial community structure [23]. Following two decades of growth and development in the Mu Us Sandy Land, *Pinus sylvestris* var. *mongolica* has demonstrably impacted the microbial diversity in the rhizosphere soil, thereby liberating an array of ecologically functional metabolites, thereby improving the metabolic functionality of soil bacteria [24]. The cultivation of *Artemisia ordosica* has not only ameliorated soil microbial enzyme activity and biomass but has also enhanced the abundance of Actinobacteria and Proteobacteria [25]. *Haloxylon ammodendron*, a diminutive tree belonging to the Chenopodiaceae family, has emerged as the favored and extensively implemented windbreak and sand-fixing vegetation in arid desert regions [26]. This phenomenon can be primarily attributed to its inherent characteristics of drought resistance, minimal water requirements, and significant capacity for carbon sequestration [27]. Therefore, it has garnered significant scholarly attention in sand control. The analysis conducted on the soil of the Urad natural *H. ammodendron* forest revealed a marked improvement in bacterial diversity, with surface vegetation and pH exerting a significant influence on said diversity [28]. In addition, the introduction of *H. ammodendron* vegetation induced changes in the spatial heterogeneity of microbial communities within desert ecosystems [29]. A study into the long-term impact of *H. ammodendron* forests on soil bacteria in sandy regions unveiled a significant enhancement in the bacterial richness index and the abundance of dominant bacteria, such as Actinomycetes, during a finite period of ecological succession [30]. Additionally, it has

been demonstrated that vegetation not only impacts soil bacterial communities and their diversity but also shapes the functional composition of soil bacteria [15,17].

An exploration of the soil bacterial community and its associated influencing factors in *H. ammodendron* forests offers valuable insights into the underlying mechanistic principles governing the adaptation of *H. ammodendron* to arid environments. However, the existing literature on the impact of artificially planted *H. ammodendron* forests on the bacterial composition and functional attributes of sandy soils, as well as their correlation with physicochemical properties, remains limited and inconclusive. Therefore, this study is centered on the soil composition of an artificial *H. ammodendron* forest situated in the sand blocking and fixing belts on the periphery of the Minqin oasis. The purpose of this study was to investigate the effects of *H. ammodendron* forest planting on the structure and function of desert soil bacterial communities and to reveal the main environmental variables affecting the structure and function of soil bacterial communities in *H. ammodendron* forest. We hypothesized that (1) the planting of artificial *H. ammodendron* forest significantly affects the structure, diversity, and metabolic function of soil bacterial communities, and (2) soil physical and chemical properties are the key driving factors affecting soil bacterial community structure and potential metabolic functions. This research seeks to enhance the existing body of knowledge pertaining to the impact of planting artificial sand-fixing vegetation (*H. ammodendron*) on the micro-ecological functions of sandy land.

## 2. Materials and Methods

### 2.1. Study Site Description

This study was carried out in the sand blocking and fixing belt (Laohukou Desert Control and Prevention Demonstration Area), situated on the periphery of the Minqin Oasis in Northwest China (38°39'14" N–38°55'23" N, 103°02'86" E–103°12'37" E). The geographical location of this region places it in the transitional zone between two major deserts, namely the Badain Jaran Desert to the west and the Tengger Desert to the east. These natural characteristics render the area an optimal field research site for the study of desertification prevention and control [31]. The average annual precipitation in this area is approximately 113.5 mm, while the average annual evaporation exceeds 2383.5 mm. The region benefits from ample solar radiation and heat resources; however, it is also subject to frequent and intense wind and sand activities. The prevailing wind direction is northwest, with an annual average wind speed of approximately 3.1 m·s<sup>-1</sup> and a maximum wind speed of 21 m·s<sup>-1</sup>. The predominant soil types consist predominantly of sandy soil. The topography is primarily characterized by three distinct types of sand dunes: mobile, semi-stable, and stable sand dunes. The vegetation in the region can be classified into two categories: natural and artificial. The primary species of vegetation include *Haloxyylon ammodendron*, *Tamarix ramosissima*, *Nitraria tangutorum*, *Elaeagnus angustifolia*, *Calligonum mongolicum*, and other desert vegetation [32–34].

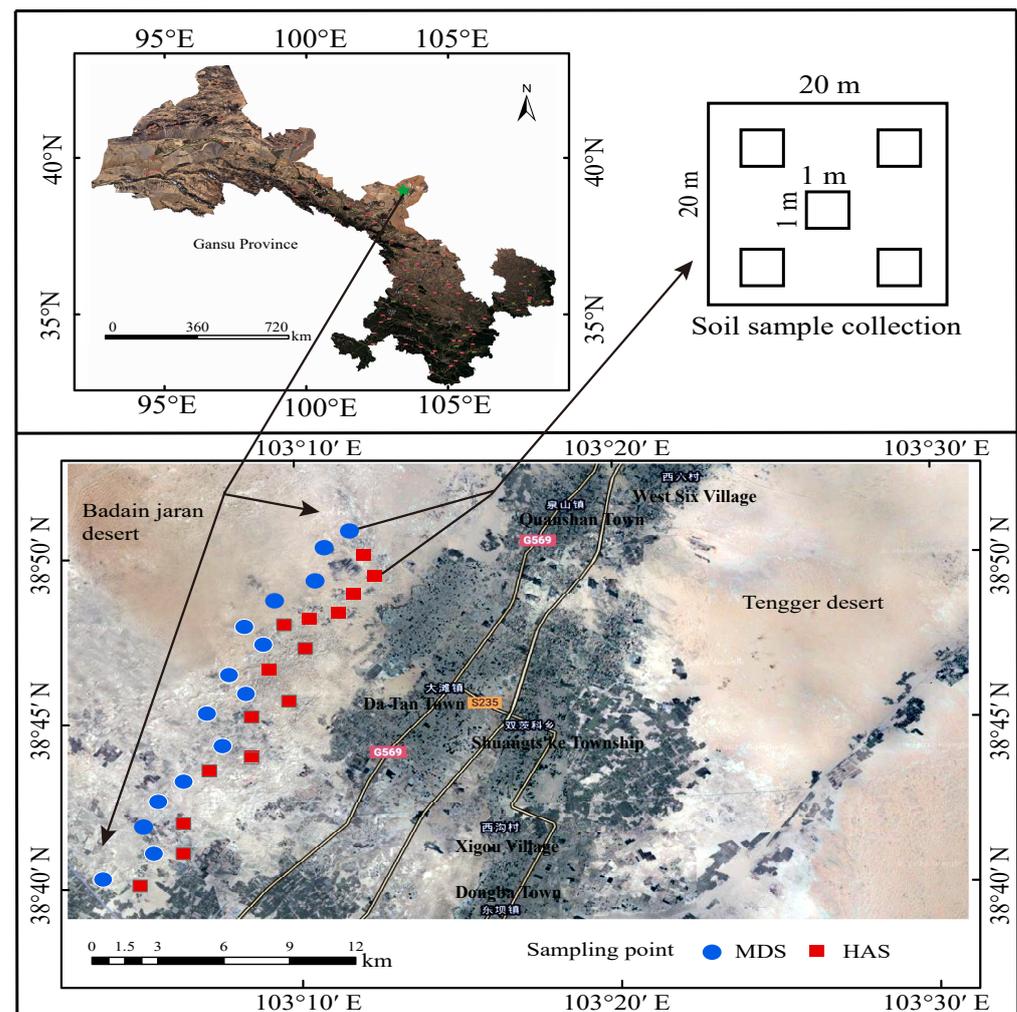
### 2.2. Experimental Design and Sample Collection

In August 2022, during the zenith of vegetative growth, field surveys were undertaken to evaluate the flora and procure soil specimens in the Laohukou Desert Control and Prevention Demonstration Area. Following a three-year effort toward artificial *H. ammodendron* afforestation, the sand pressure afforestation and beach afforestation areas had expanded to 6666.67 hm<sup>2</sup> and 3066.68 hm<sup>2</sup>, respectively, by 2008. Presently, the *H. ammodendron* forest belt, serving as a windbreak and sand stabilizer, has attained a state of rudimentary establishment. For the purpose of this study, the soil derived from an *H. ammodendron* forest (HAS) that had been cultivated for a span of 15 years was designated as the experimental group, while the soil originating from the mobile dune (MDS) in the upwind direction was selected as the control group. In the *H. ammodendron* forest, single standardized sampling plots measuring 20 m × 20 m were randomly established at intervals of 100 m along a direction perpendicular to the principal wind direction (northwestward). A cumulative 15 standardized quadrats were established in the experimental group, wherein the stature

and extent of the *H. ammodendron* forest in each plot were analyzed (Table 1). Correspondingly, a total of 15 (20 m × 20 m) control groups were instituted in the vicinity of the upwind region of the mobile dune soil area, perpendicular to the standardized quadrats of each experimental group (Figure 1). The 5-point technique was employed to demarcate five diminutive sample squares (1 m × 1 m) uniformly in each standardized sample plot. Surface weeds and litter were removed, and soil samples were procured from a depth of 0–20 cm in the confines of the five small sample squares. These five portions of soil were subsequently integrated thoroughly to yield a singular standardized soil sample. In the control group, 15 standardized soil samples were collected utilizing the same methodology, resulting in a total of 30 soil samples. Each standardized soil sample was promptly partitioned into two segments. Approximately 10 mL of soil sample was transferred into a sterile centrifuge tube and preserved in a refrigerator at −80 °C for subsequent soil microbial analysis. The remaining segment was subjected to natural desiccation and subsequently sieved using a 2 mm mesh to evaluate the physicochemical properties of the soil [24].

**Table 1.** Height and coverage characteristics of *Haloxylon ammodendron* forest.

Sampling Area	Latitude	Longitude	Altitude (m)	Dominant Tree	Height (cm)	Coverage (%)
MDS	38°45' N	103°05' E	1311.56	—	—	—
HAS	38°50' N	103°08' E	1304.95	<i>Haloxylon ammodendron</i>	163.22 ± 44.05	35.30 ± 7.25



**Figure 1.** Geographical location of study area. MDS and HAS represent mobile dune and *H. ammodendron* forest soil, respectively.

### 2.3. Soil Physicochemical Measurements

Soil water content (SWC) was identified through the utilization of the drying–weighing method. The determination of soil pH and electrical conductivity (EC) was conducted employing the potentiometric method (utilizing water-to-soil ratios of 2.5:1 and 5:1, respectively) (MP-551 pH/Conductivity Meter, Shanghai, China.) [23,24]. The quantification of soil organic matter (SOM) was accomplished utilizing the potassium dichromate sulfuric acid volumetric method [24]. The determination of soil total nitrogen (TN) was executed using the Kjeldahl method (K9840 Automatic Kjeldahl Nitrogen Analyzer, Shandong, China). Soil total phosphorus (TP) was determined employing the acid digestion–molybdenum antimony anti-colorimetric method. Soil total potassium (TK) was quantified utilizing flame spectrophotometry (Flame photometer FP6410, Shanghai, China). The determination of soil available phosphorus (AP) was carried out through the sodium hydrogen hydrochloride extraction–molybdenum antimony colorimetric method. Soil available potassium (AK) was determined using ammonium acetate extraction–flame spectrophotometry (Flame photometer FP6410, Shanghai, China) [35]. The detailed methodologies for each index determination can be found in the relevant literature [36].

### 2.4. Illumina Sequencing Analysis of 16S rRNA Gene Amplicons

The total DNA of soil bacteria was extracted using the Magabi soil genome 50 ng DNA purification kit (Maga Bio Soil Genomic DNA Purification Kit, Carlsbad, CA, USA). Genomic DNA served as the template for amplifying the V3-V4 variable region of the bacterial 16S rRNA gene. This amplification was carried out with barcode-specific primers and TaKaRa Premix Taq<sup>®</sup> Version 2.0 (TaKaRa Biotechnology Co, Dalian, China) [30]. The universal primers used were 338F (5'-ACTCCTACGGGGAGGCAGCA-3') and 806R (5'-GGACTACHVGGGTWTCTAAT-3') [37]. The polymerase chain reaction (PCR) amplification reaction system consisted of 25  $\mu$ L of 2 x Premix Taq, 1  $\mu$ L of Primer-F and Primer-R, 50 ng of template DNA, and nuclease-free water to a final volume of 50  $\mu$ L. The PCR procedure involved an initial denaturation step at 94 °C for 5 min, followed by 30 cycles of denaturation at 94 °C for 30 s, annealing at 52 °C for 30 s, and extension at 72 °C for 30 s. A final extension step was performed at 72 °C for 10 min [30,38]. The resulting PCR products were analyzed by 1% agarose gel electrophoresis to determine fragment length and concentration. The amplicon library was constructed using the Illumina Nova 6000 platform standard process and subjected to PE250 high-throughput sequencing.

### 2.5. Bioinformatic Analysis

The RawReads data at both ends were subjected to individual quality clipping using the Fastp software (version 0.14.4), while the primers at both ends were eliminated through the employment of the Cutadapt software (version 1.14), thereby yielding valid sequences [39]. Subsequently, the Usearch software's Uparse (version 10.0.240) algorithm was employed to cluster the sample quality sequences into OTUs, and the Silva 16S database was utilized to annotate the species, thereby obtaining taxonomic information for the OTUs. Statistical information on the taxonomic level sequences of phylum and genus in OTUs was collected and the calculation of the relative abundance of each taxon was performed. The bacterial Alpha diversity index was calculated using the QIIME2 software (version 2020.11). To elucidate the Beta diversity of soil bacteria in the artificial *H. ammodendron* forest, principal coordinate analysis (PCoA) was employed. The functional information of the samples in terms of KEGG Orthology was obtained by comparing the KEGG database information using the PICRUSt2 function prediction software (version 2.3.0-b).

### 2.6. Data Analysis

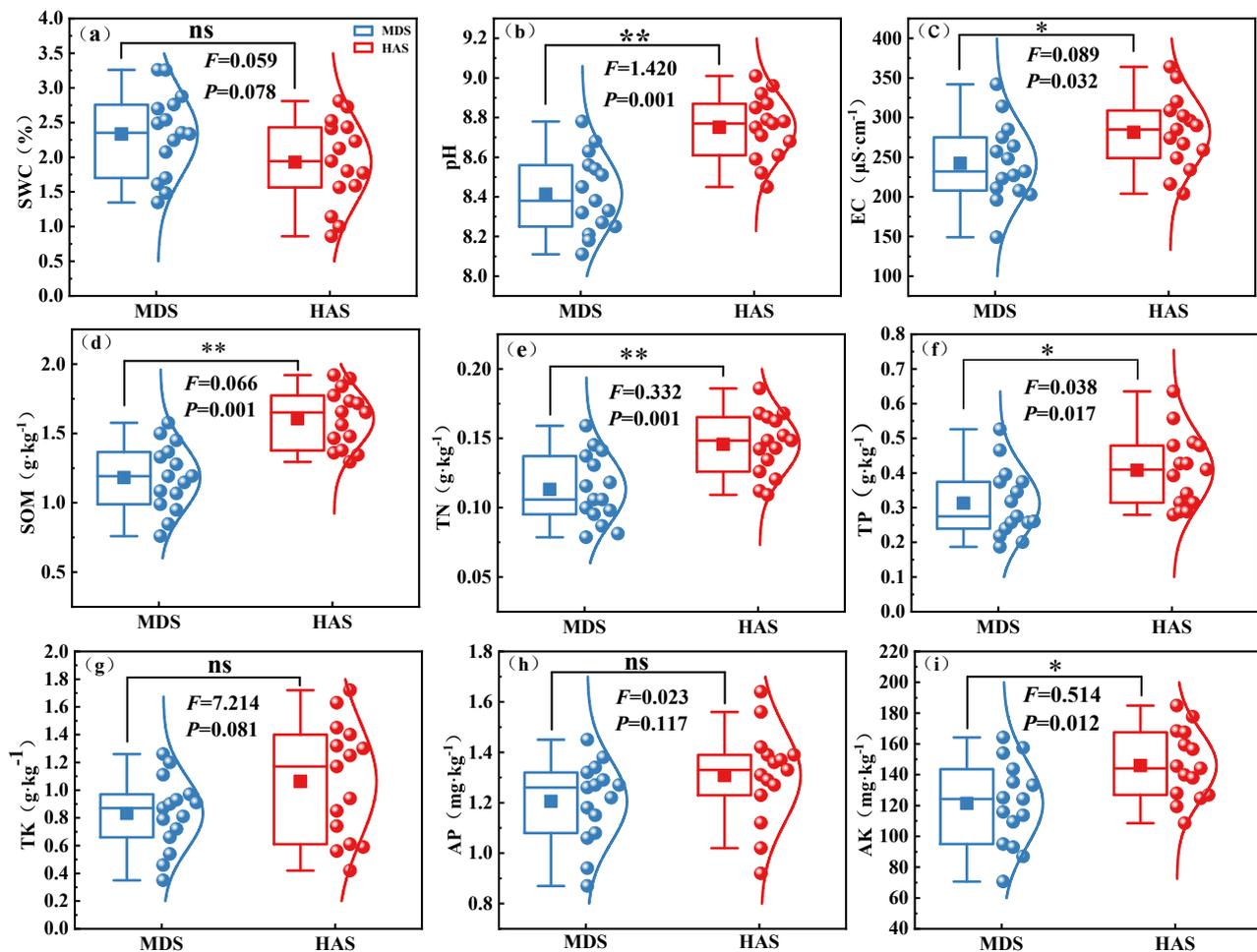
The standardized soil microbiological and physicochemical data were subjected to statistical analysis using SPSS 26.0 software (SPSS Inc., Chicago, IL, USA), and the differences in soil physicochemical properties, soil bacterial community structure, diversity, and the relative abundance of metabolic function between HAS and MDS were analyzed

by independent sample *T*-tests ( $p < 0.05$ ). In order to explore the key physicochemical drivers affecting bacterial structure, redundancy analysis (RDA) was conducted using the Canoco 5 software. The Monte Carlo replacement test with 499 test replicates was utilized in this analysis (Microcomputer Power, Ithaca, NY, USA). In addition, the environmental factors influencing bacterial function were assessed using the “ggcor” package Mantel test correlation tests in R software (version 4.2.1).

### 3. Results

#### 3.1. Soil Physical and Chemical Properties

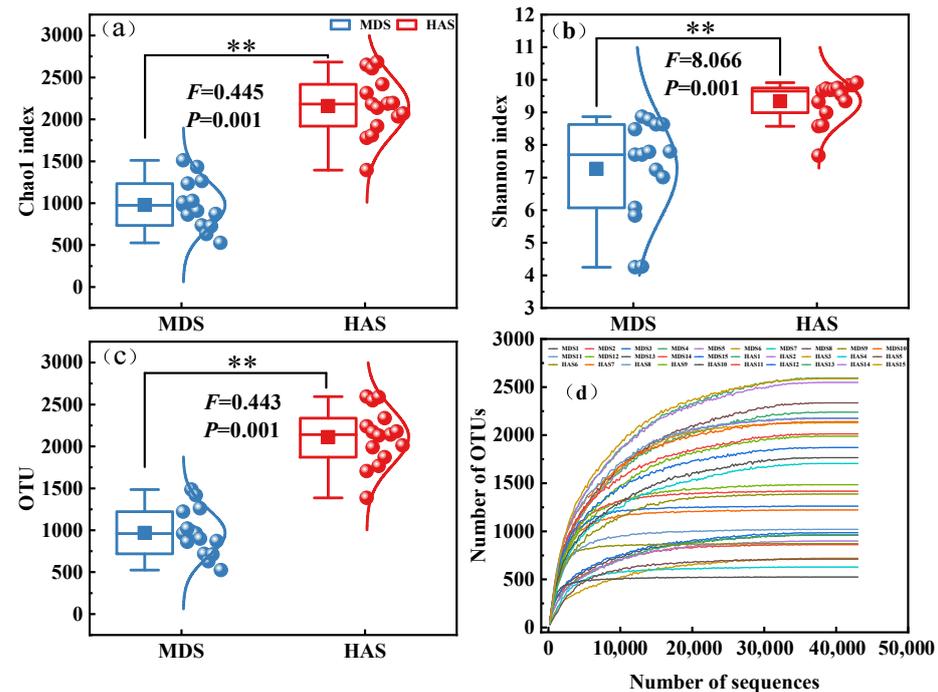
The variation in soil factors subsequent to the establishment of *H. ammodendron* forests is illustrated in Figure 2. Planting *H. ammodendron* forests consumed the surface SWC, which decreased by 17.17% in HAS compared to MDS. However, it resulted in significant improvements in various soil nutrient factors. The pH of the study area ranged between 8.11 and 9.01, and EC ranged between 149 and 364  $\mu\text{S}\cdot\text{cm}^{-1}$ , and both pH and EC in HAS exhibited significant differences compared to MDS. The contents of SOM, TN, TP, and AK in HAS soil increased ( $p < 0.05$ ). SOM increased by 35.59%, TN by 36.36%, TP by 32.26%, and AK by 20.18% compared to MDS. However, there were no major differences in TK and AP content.



**Figure 2.** Soil physicochemical properties of *H. ammodendron* forest and mobile dune. Note: MDS and HAS represent mobile dune and *H. ammodendron* forest soil, respectively. (a): SWC, soil water content; (b): pH, soil pH; (c): EC, soil electrical conductivity; (d): SOM, soil organic matter; (e): TN, total nitrogen; (f): TP, total phosphorus; (g): TK, total potassium; (h): AP, available phosphorus; (i): AK, available potassium. “\*\*\*”, “\*” and “ns” indicate  $p < 0.01$ ,  $p < 0.05$  and  $p > 0.05$ , respectively. The same as below.

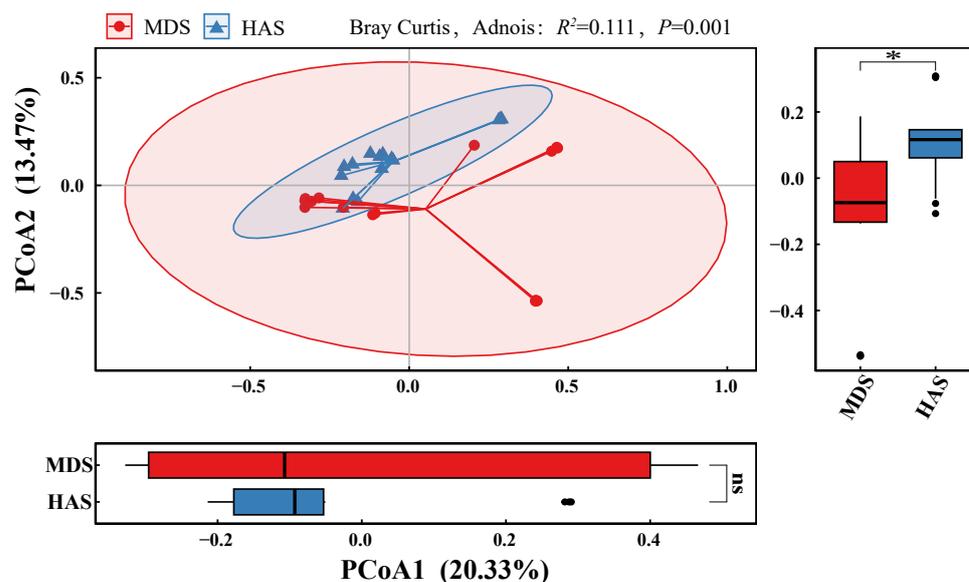
### 3.2. Soil Bacterial Diversity

The total number of original sequences obtained from all samples of MDS and HAS was 1,714,258 and 1,796,338, respectively. The effective sequences obtained after undergoing quality control filtration and chimera removal were 1,690,381 and 1,771,937, respectively. Subsequently, the effective sequences were subjected to random sampling in order to derive representative bacterial dilution curves (Figure 3d). These curves were constructed by plotting the extracted sequences alongside the corresponding number of OTUs they represented. As the number of sequences progressively increased, the dilution curve gradually reached a plateau, thereby indicating that the inclusion of additional sequences yielded reducing returns in terms of the discovery of novel OTUs. This observation strongly suggests that the OTU coverage of the sample approached saturation, and thus, the sequencing results effectively encapsulated the entirety of pertinent microbiological information. The standardization process involved utilizing the minimum number of sample sequences, which were uniformly drawn and subsequently clustered based on a similarity threshold of greater than 97%. This procedure yielded a total of 46,187 OTUs across all samples. Notably, there was a significant difference between the mean number of OTUs observed in the HAS group (2110) and the MDS group (969) ( $p < 0.01$ ). Moreover, the mean Chao1 and Shannon index values for the HAS group were 2158 and 9.34, respectively, while the corresponding values for the MDS group were 979 and 7.27, respectively. These differences were also found to be statistically significant between the two groups.



**Figure 3.** Soil bacterial  $\alpha$  diversity characteristics of artificial *H. ammodendron* forest. MDS and HAS represent mobile dune and *H. ammodendron* forest soil, respectively. (a–c) Soil bacterial Chao1 index, Shannon index, and OTU numbers, respectively; (d) soil bacterial dilution curve, MDS 1–15 and HAS 1–15 represent mobile dune and *H. ammodendron* forest soil samples. “\*\*” indicate  $p < 0.01$ .

Principal coordinate analysis (PCoA) was employed to assess the  $\beta$  diversity of soil bacterial communities at the OTU level. The results of the analysis revealed distinct spatial distributions between the HAS and MDS groups, it indicates that the structure of soil bacterial community structures changed significantly after the planting of *H. ammodendron* forest ( $p < 0.01$ ) (Figure 4).



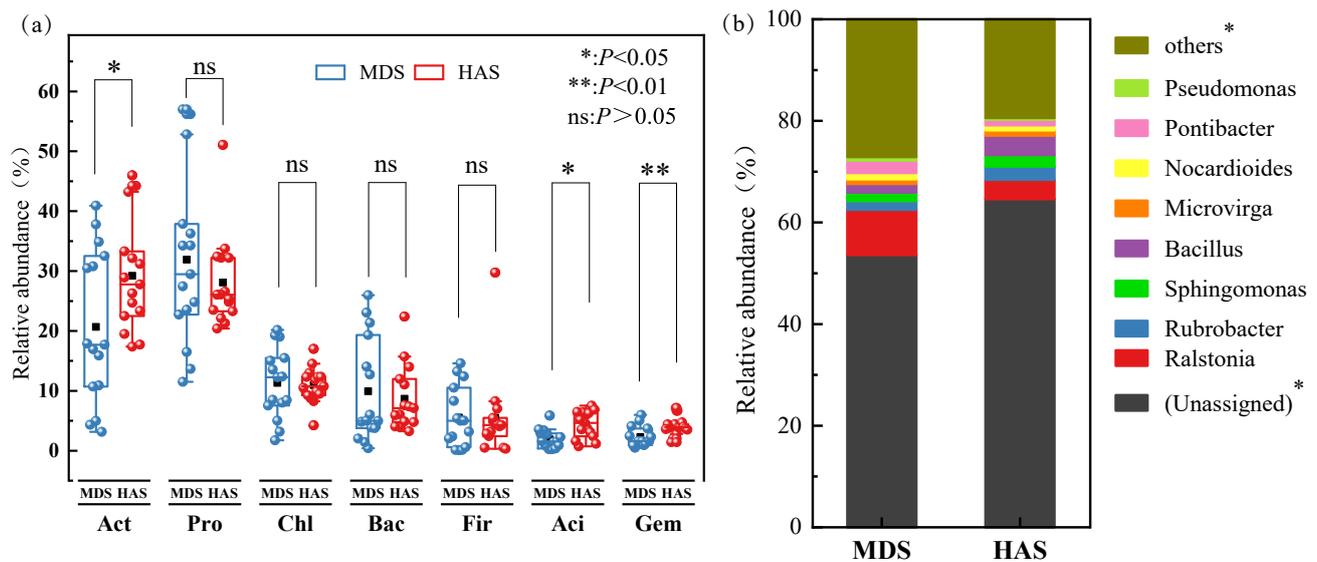
**Figure 4.** Principal coordinate analysis (PCoA) of soil bacterial structure in artificial *H. ammodendron* forest. MDS and HAS represent mobile dune and *H. ammodendron* forest soil, respectively. “\*” and “ns”: indicate  $p < 0.05$  and  $p > 0.05$ .

### 3.3. Soil Bacterial Community Structure and Differences

All 16S rRNA sequences were subjected to comprehensive annotation, resulting in the identification of a total of 27 bacterial phyla. Among these, there were seven bacterial phyla exhibiting a relative abundance of  $>1\%$  (Figure 5a). The bacterial community structure observed in the MDS and HAS plots exhibited similarities, albeit with notable differences in relative abundance. Notably, Actinobacteria, Proteobacteria, and Chloroflexi emerged as the top three bacterial phyla in terms of their relative abundance in the soil of the study area. Their respective average abundances were  $24.94\% \pm 11.85\%$ ,  $29.99\% \pm 11.56\%$ , and  $11.14\% \pm 4.55\%$ . Additionally, the cumulative abundance of Bacteroidetes, Firmicutes, Acidobacteria, and Gemmatimonadetes reached 21.12%, thereby establishing their prominence as major bacterial phyla in the soil of the *H. ammodendron* forest. Notably, the abundances of Actinobacteria, Acidobacteria, and Gemmatimonadetes exhibited a significant increase in the HAS plot ( $p < 0.05$ ). Conversely, the abundances of Proteobacteria and Bacteroidetes experienced respective decreases of 11.95% and 12.69%. At the genus level, a significant proportion of bacterial genera, amounting to 82.37%, eluded classification and exhibited a relative abundance of less than 1%, thereby presenting certain impediments to the comprehensive analysis of bacterial ecological functions. Moreover, a total of eight distinct categories of bacterial genera were identified (Figure 5b). The relative abundance of these aforementioned genera displayed an evident pattern across the two groups of plots. Specifically, in comparison to the MDS group, the relative abundance of *Rubrobacter*, *Sphingomonas*, *Bacillus*, and *Microvirga* in the HAS group experienced a significant increase of 53.53%, 34.52%, 124.7%, and 13.19%, respectively. Conversely, the relative abundance of *Ralstonia*, *Nocardioides*, *Pontibacter*, and *Pseudomonas* witnessed a decline of 57.29%, 19.35%, 55.47%, and 51.47%, respectively, in the HAS group when compared to the MDS group.

### 3.4. Characteristics of the Metabolic Function of Soil Bacteria

The functional prediction conducted by PICRUSt2 revealed the acquisition of six distinct classes of primary biometabolic pathways across all samples, namely Metabolism, Genetic Information Processing, Cellular Processes, Environmental Information Processing, Organismal Systems, and Human Diseases. Notably, the functional abundance of Genetic Information Processing and Human Diseases exhibited a higher prevalence in the HAS group, whereas the functional abundance of Metabolism demonstrated a greater predominance in the MDS group ( $p < 0.05$ ) (Table 2).



**Figure 5.** Relative abundance and difference in soil bacterial community at phylum (a) and genus (b) levels. (a), Act: Actinobacteria; Pro: Proteobacteria; Chl: Chloroflexi; Bac: Bacteroidetes; Fir: Firmicutes; Aci: Acidobacteria; Gem: Gemmatimonadetes. MDS and HAS represent mobile dune and *H. ammodendron* forest soil, respectively. (b): “\*”,  $p < 0.05$ .

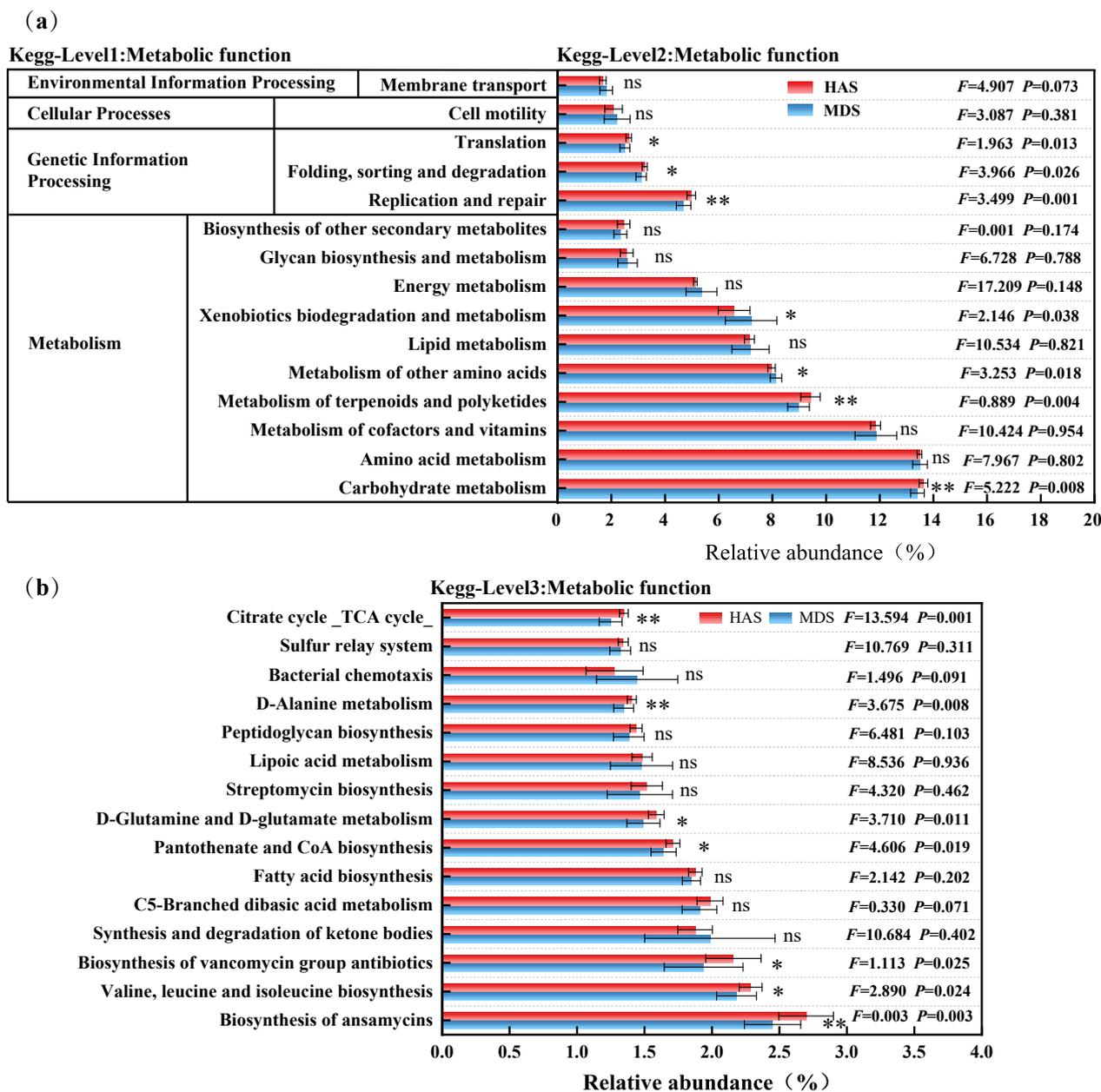
**Table 2.** Relative abundance and difference in the primary function of soil bacteria.

Primary Function of Bacteria	Relative Abundance (%)				T-Test	
	MDS	HAS	F	P		
Metabolism	82.10 ± 0.23	81.79 ± 0.44	5.397	0.023		<0.05
Genetic Information Processing	11.11 ± 0.65	11.70 ± 0.36	3.267	0.005		<0.01
Cellular Processes	4.03 ± 0.44	3.90 ± 0.34	2.633	0.368		>0.05
Environmental Information Processing	2.28 ± 0.33	2.09 ± 0.17	4.998	0.059		>0.05
Organismal Systems	0.27 ± 0.04	0.27 ± 0.10	0.641	0.915		>0.05
Human Diseases	0.19 ± 0.05	0.23 ± 0.06	3.616	0.041		<0.05

A total of 15 secondary functions, exhibiting an abundance exceeding 1%, were identified in the bacterial communities dispersed across six metabolic pathways. The principal secondary metabolic functions of soil bacteria in the study area comprised carbohydrate metabolism (13.52% ± 0.24%), amino acid metabolism (13.49% ± 0.20%), and the metabolism of cofactors and vitamins (11.85% ± 0.56%) (Figure 6a). In comparison to MDS, the relative abundance of carbohydrate metabolism, the metabolism of terpenoids and polyketides, replication and repair, folding, sorting, and degradation, and translation exhibited a significant increase in HAS ( $p < 0.05$ ). Conversely, the relative abundance of the metabolism of other amino acids and xenobiotics biodegradation and metabolism experienced a significant decrease ( $p < 0.05$ ). However, the relative abundance of the remaining eight secondary functions displayed no significant differences.

To appraise the impact of *H. ammodendron* plantation on soil functional traits, an analysis was conducted on the tertiary metabolic functional pathways of soil bacteria. A total of 15 categories exhibited a relative abundance exceeding 1% (Figure 6b). While most tertiary metabolic pathways demonstrated similarity, the relative abundance of each pathway varied. Notably, crucial functions pertaining to energy metabolism, nucleotide metabolism, antibiotics, and enzymes, such as the biosynthesis of ansamycins and valine, were observed. The primary functional characteristics of soil bacteria included leucine and isoleucine biosynthesis, the biosynthesis of vancomycin group antibiotics, the synthesis and degradation of ketone bodies, C5-branched dibasic acid metabolism, and fatty acid biosynthesis. In summary, the relative abundances of metabolic pathways, including the

biosynthesis of ansamycins, valine, leucine, and isoleucine, the biosynthesis of vancomycin group antibiotics, D-Alanine metabolism, and citrate cycle\_TCA cycle\_, exhibited a significant increase in HAS ( $p < 0.05$ ) compared to MDS. This suggests that the plantation of *H. ammodendron* forest contributes to the enhancement of ecological functions, such as soil bacterial metabolism.



**Figure 6.** Prediction of the metabolic functions of soil bacteria. Metabolic functional pathways in HAS and MDS soil bacteria; (a,b) denote secondary and tertiary metabolic pathways. “\*\*\*”, “\*\*” and “ns” indicate  $p < 0.01$  and  $p < 0.05$  and  $p > 0.05$ , respectively.

### 3.5. The Main Physicochemical Factors Affecting the Structure and Function of Soil Bacterial Communities

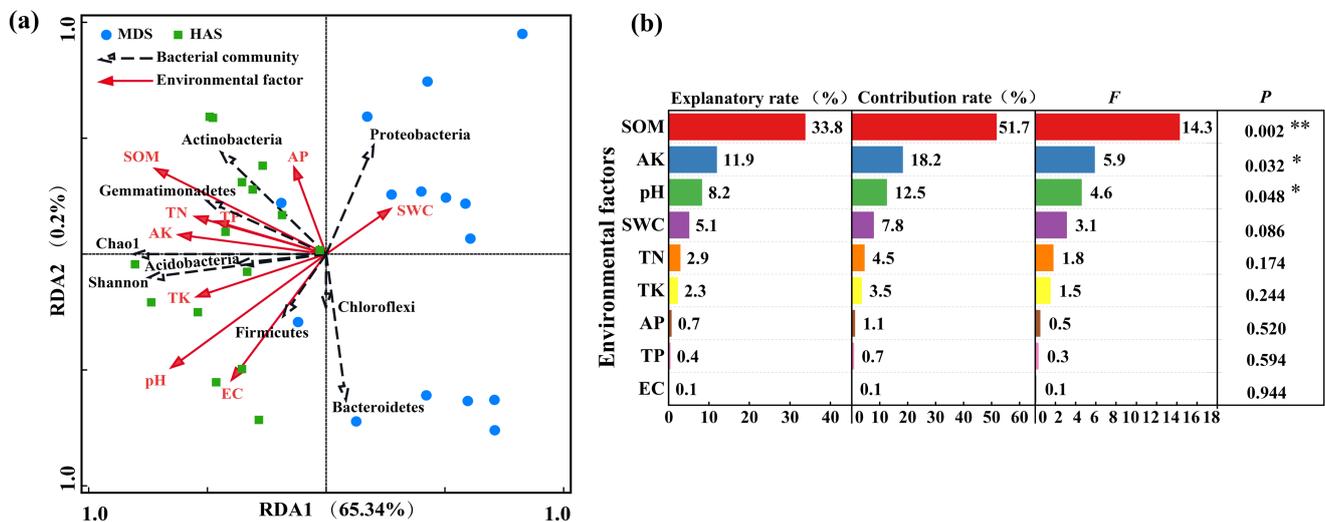
Redundancy analysis (RDA) refers to a linear model ranking variables by combining correspondence analysis and multiple regression analysis. It provides an intuitive measure of the influence of environmental factors on the impact of soil bacteria. The cumulative interpretation rate of the first and second axes in RDA was found to be 65.36%. The correlation coefficient between soil bacterial properties and physicochemical attributes

on the first axis was 0.8086, explaining 99.96% of the cumulative variance. This suggests that the first axis plays a decisive role in determining the relationship between these variables (Table 3).

**Table 3.** Soil bacterial community structure RDA ordination characteristic value and interpretation.

Item	Axis 1	Axis 2	Axis 3	Axis 4
Characteristic values of soil bacterial community structure	0.6534	0.0002	0.0001	0.0000
Correlation between soil bacterial community structure and environmental factors	0.8086	0.7469	0.4797	0.3822
Cumulative interpretation of soil bacterial community structure	65.34	65.36	65.37	65.37
Cumulative interpretation of soil bacterial community and environmental factors	99.96	99.99	100.00	100.00
Canonical eigenvalue		0.6537		
Total eigenvalue		1.0000		

The RDA ordination model diagram reveals that amongst the three dominant phyla, Actinobacteria and the SOM, TN, TP, AK, and AP are situated in the second quadrant. This positioning suggests a positive correlation between Actinobacteria and these physicochemical factors. On the other hand, Proteobacteria exhibit a positive correlation with SWC and AP, while displaying a negative correlation with soil pH, EC, and TK. Conversely, Chloroflexi demonstrate a positive correlation with pH, EC, and TK, but exhibit a negative correlation with SOM, AP, and SWC. The Chao1 and Shannon indices were significantly positively correlated with SOM, pH, AK, and EC (Figure 7a). Monte Carlo tests (Figure 7b) demonstrate that SOM exerts the greatest influence on the soil bacterial community, accounting for 51.7% of the variation, and this effect is highly significant ( $p = 0.002$ ). Additionally, AK ( $p = 0.032$ ) and pH ( $p = 0.048$ ) are also found to significantly impact the community composition.

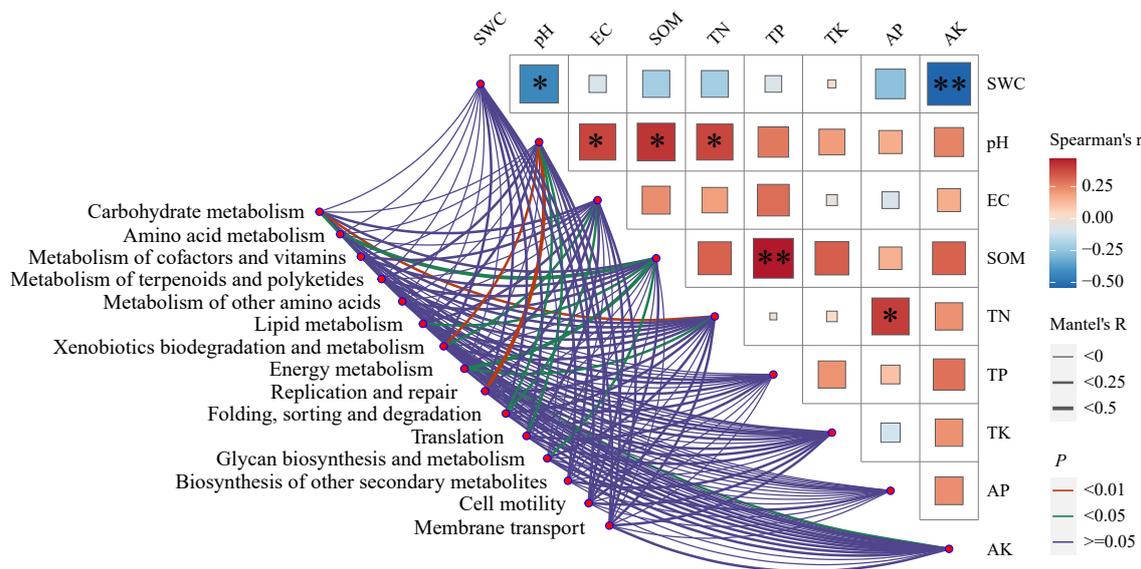


**Figure 7.** (a) RDA analysis of the effect of soil physicochemical factors on soil bacterial community structure; (b) explanation and significance test of soil physicochemical factors. \*\*  $p < 0.01$ , \*  $p < 0.05$ .

The Bray–Curtis distance matrix of secondary metabolic function abundance and the Euclidean distance matrix of soil physicochemical parameters were utilized for the Mantel test correlation analysis. The findings revealed significant correlations between SOM, TN, AK, pH, and EC with the secondary metabolic functions of specific soil bacteria (Figure 8).

Notably, SOM exhibited significant positive correlations with amino acid metabolism, lipid metabolism, energy metabolism, and glycan biosynthesis and metabolism ( $p < 0.05$ ). TN demonstrated significant positive associations with carbohydrate metabolism ( $p < 0.01$ ) and energy metabolism ( $p < 0.05$ ). AK displayed a positive correlation with carbohydrate metabolism ( $p < 0.05$ ). pH exhibited a significant positive relationship with xenobiotics

biodegradation and metabolism, as well as replication and repair ( $p < 0.01$ ), and significant positive associations with folding, sorting, and degradation and translation ( $p < 0.05$ ). Finally, EC exhibited significant positive correlations with xenobiotics biodegradation and metabolism, as well as folding, sorting, and degradation ( $p < 0.05$ ) (Table 4). The results verify the significant role played by the aforementioned soil physicochemical factors in both the stability of the soil bacterial community structure and its function.



**Figure 8.** Mantel test of the effect of soil physicochemical factors on soil bacterial functions. \*\*  $p < 0.01$ , \*  $p < 0.05$ .

**Table 4.** The significance of bacterial metabolic function and main physicochemical factors in the Mantel test.

The Second-Level Function of Bacteria	Physicochemical Factors									
	pH		EC		SOM		TN		AK	
	<i>r</i>	<i>p</i>	<i>r</i>	<i>p</i>	<i>r</i>	<i>p</i>	<i>r</i>	<i>p</i>	<i>r</i>	<i>p</i>
Carbohydrate metabolism							0.209	**	0.173	*
Amino acid metabolism					0.290	*				
Lipid metabolism					0.192	*				
Xenobiotics biodegradation and metabolism	0.225	**	0.202	*						
Energy metabolism					0.275	*	0.194	*		
Replication and repair	0.259	**								
Folding, sorting, and degradation	0.207	*	0.240	*						
Translation	0.199	*								
Glycan biosynthesis and metabolism					0.171	*				

“\*\*\*” and “\*\*” indicate  $p < 0.01$  and  $p < 0.05$ , respectively. Abbreviations for soil physicochemical factors are shown in Figure 2.

#### 4. Discussion

##### 4.1. Effects of Vegetation Reconstruction on Soil Physicochemical Properties

Afforestation is widely recognized as a potent strategy for mitigating desertification in arid regions across the globe [9,40]. The restoration of vegetation assumes a pivotal role in the broader context of ecological restoration, as it leads to a reciprocal relationship between the soil and plants. This symbiotic interaction between vegetation and soil results in a complex system that facilitates the circulation of ecosystem materials and the flow of energy [41]. The study observed a decrease of 17.17% in the surface soil water content in the *H. ammodendron* forest. This observed change can be ascribed to the utilization of surface soil

water during the growth phase of the vegetation. The enhancement of evapotranspiration, which arises from the expansion and maturation of the root, stem, and leaf structures in the *H. ammodendron* forest, significantly contributes to this phenomenon [42,43]. However, it is noteworthy that the soil pH and EC exhibited a significant increase, predominantly attributable to the cumulative impact of *H. ammodendron* on salt ions under conditions devoid of irrigation. The accumulation of salts in the soil resulted in a reduction in tissue osmotic potential and water potential, while concurrently enhancing the capacity for water uptake and strengthening drought resistance through salt accumulation [44–46]. Prior studies have explained that *H. ammodendron* predominantly absorbs soil  $\text{NO}_3^-$  and subsequently releases one  $\text{OH}^-$  for each absorbed  $\text{NO}_3^-$  ion, thereby exerting an influence on soil pH [40]. The presence of vegetation drives changes in soil factors through ecological mechanisms, including the secretion of root exudates, the decomposition of deceased foliage, and the “fertile island effect” [16,47,48]. Measures such as the stabilization of sand through the implementation of artificial vegetation can yield significant enhancements in the physicochemical properties of soils, as well as other habitat qualities [40]. This is substantiated by the observed increments in the soil quality index, as well as the significant amplification of soil organic carbon, nitrogen, phosphorus, and other nutrient contents [49].

The SOM, TN, TP, and AK contents of the *H. ammodendron* forests exhibited a consistent and notable pattern of significant increases in the scope of this study. The primary rationale behind this phenomenon can be attributed to the establishment of *H. ammodendron*, whereby the towering flora effectively intercepted and amassed the minute particulate matter, as well as branch and leaf detritus, carried by the wind–sand flow [50,51]. Therefore, this interception mechanism served to mitigate wind–sand erosion while concurrently enriching the topsoil’s fertility. It is worth noting that, in arid and semi-arid sandy regions, the soil parent material contributes only a negligible proportion of the diverse array of nutrients, with soil organic matter and total nitrogen constituting the principal constituents [52]. Instead, the metabolic processes responsible for nutrient accumulation are predominantly derived from particle deposition and the inherent vegetation dynamics [53].

#### 4.2. Soil Bacterial Communities and Diversity in *H. ammodendron* Forests

The mechanism underlying plant community construction is primarily attributed to habitat heterogeneity under the context of environmental filtering [54]. Soil factors, being pivotal constituents that exert a profound influence on the growth and development of vegetation, also exert a strong impact on the differentiation of ecological niches. Simultaneously, the decomposition function of soil microorganisms exerts a significant influence on the transformation of soil nutrients and the growth of aboveground vegetation [55,56]. Research findings suggest that a higher soil bacterial diversity index corresponds to greater resistance to environmental stress, thereby fostering a more stable micro-ecological function in the soil [57]. The introduction of sand-fixing vegetation not only expedites soil formation but also offers essential nutrients for the growth and development of surface soil microorganisms through the decomposition of its organic matter and root exudates [16–18,23–25,40,47,48]. Therefore, this process significantly modifies the structure and diversity of the soil microbial community. This study has demonstrated a significant improvement in both the Chao1 and Shannon indices of soil bacteria in *H. ammodendron* forests. In addition, significant differences in the composition of soil bacterial communities were also observed (Figure 3). These findings serve to indicate that the growth process and root exudation of *H. ammodendron* forests lead to a propitious habitat for the growth of soil bacteria [30].

The subtle shifts occurring in the soil habitat possess the capacity to directly or indirectly exert a profound influence on the configuration of soil bacteria [16,45,46]. The assemblage of soil bacterial structure in arid and desert regions exhibits a striking resemblance, primarily comprising approximately ten groups, including *Actinobacteria*, *Proteobacteria*, *Chloroflexi*, *Bacteroidetes*, *Acidobacteria*, and *Cyanobacteria* [23–25,30,46,58–60]. This consensus, which has been established by scholars, was derived from an extensive analysis of diverse

representative artificial vegetation sand-fixing areas. The overall characteristics of bacterial communities in the soil of both the *H. ammodendron* forest and mobile dunes were found to be congruous. However, notable variations were observed in their respective relative abundances. Specifically, *Actinobacteria*, *Proteobacteria*, and *Chloroflexi* were identified as the preeminent phyla, a finding that aligns with the results reported by Bi et al. [24] and Sun et al. [60]. The exacerbation of soil salinization in the transitional zone of the Minqin desert oasis can be attributed to the adverse climatic factors of drought and intense radiation, which have contributed to the debilitation of elemental cycling processes, particularly those pertaining to soil carbon and nitrogen [61,62]. *Actinobacteria*, a member of the Gram-positive bacterial group, exhibits remarkable competitiveness in harsh saline-alkali and arid environments owing to its diverse physiological traits. These include spore reproduction, multiple mechanisms for repairing UV-induced damage, heat and drought resistance, and active involvement in the intricate processes of organic matter decomposition [59,63]. In addition, the growth of *H. ammodendron*, a notable carbon sink, creates favorable conditions for the growth and reproduction of actinomycetes [27]. This phenomenon may account for the greater abundance of soil actinomycetes in the *H. ammodendron* forest. *Proteobacteria*, on the other hand, are widely distributed and comprise a vast number of species. They possess significant morphological and physiological characteristics, endowing them with a competitive advantage in various ecological niches [64]. These bacteria demonstrate a robust capacity to adapt to their surroundings, making them highly adaptable organisms. In desert soil, the primary pathways governing the carbon and nitrogen cycles involve dissimilatory nitrate reduction, nitrification, and denitrification. *Actinobacteria* and *Proteobacteria* assume a pivotal role in the aforementioned cycles as they serve as the primary contributors [15,18,65]. Moreover, *Chloroflexi*, a light-energy-trophic microorganism, exerts dominance in CO<sub>2</sub> fixation and microbial photosynthesis through the reductive tricarboxylic acid cycle and the C<sub>4</sub>-dicarboxylic acid cycle [66]. This study was conducted in an arid desert region that exhibits abundant light resources, thereby providing optimal conditions for the growth and maturation of these bacteria. A staggering 82.37% of the bacterial genera at the taxonomic level pose impediments to the analysis of ecological functions, while a mere 17.63% of the known bacterial genus structure may selectively shape the soil bacterial type suitable for the habitat due to distinct site conditions and root exudates [67]. Therefore, this difference may lead to alienation characteristics between the *H. ammodendron* forest and the mobile dune soil. As the biomass of *H. ammodendron* gradually increases, certain nutrients accumulate in the soil, primarily from the decomposition of apoplastic material and root secretions [17,28–30]. This accumulation significantly contributes to the decomposition of organic matter by the bacterial community, as well as to their own growth and development. The influence of carbon and nitrogen sources, derived from residual vegetation roots and litter decomposition, on soil bacteria was explained by Urbanova et al. [68]. The prevalence of microorganisms engaged in carbon fixation and nitrogen fixation sustains the capacity for carbon and nitrogen cycling within desert ecosystems, thereby enhancing material transformation and energy flow in the soil. Moreover, this process facilitates an amplified provision of chemical elements essential for vegetation growth, thus enhancing the ecological carrying capacity and stability of the soil [65]. The observed changes in soil bacteria and the greater diversity in the *H. ammodendron* forest, as documented in this study, signify an improvement in the desert soil environment and the nutritional status of the plants.

#### 4.3. Functional Characteristics of Soil Bacteria in *H. ammodendron* Forest

The establishment of artificial sand-fixing vegetation has elicited profound shifts in the bacterial community in desert soil, thus exerting an impact on the functional attributes of soil bacteria [30,58]. Soil bacteria, through their metabolic activities, actively participate in nearly all physiological and biochemical reactions, comprising the decomposition of organic matter and the transformation of nutrients [58,69]. Our findings have unequivocally demonstrated that metabolic function constitutes the primary role of soil bacteria,

with carbohydrate metabolism, amino acid metabolism, and the metabolism of cofactors and vitamins emerging as the principal metabolic functions in the study area. Studies conducted in the Horqin and Tengger deserts have consistently underscored the paramount importance of amino acid and carbohydrate metabolism as the predominant metabolic pathways [30,58,59]. Similarly, investigations exploring the functional response of two salt-tolerant plants to soil bacteria in saline regions have revealed a greater abundance of amino acid metabolism and carbohydrate metabolism [46]. Remarkably, even in *Picea asperata* forest soil, which exhibits significant differences in physicochemical properties when compared to desert soil, carbohydrate metabolism and other metabolic functions have been identified as the primary metabolic functions of soil bacteria [70]. Recent studies have brought to light the existence of partial incongruity in the gene sequences pertaining to specific metabolic pathways among microbial populations that share similar overall metabolic functions. This divergence can be ascribed to variations in the microbial constituents responsible for these specific metabolic functions, which arise due to differences in environmental conditions. Therefore, such diversity in microbial composition plays a pivotal role in the effective regulation and preservation of ecosystem function stability [71]. Notably, the soil carbohydrate metabolism function in the *H. ammodendron* forest exhibited a substantial relative abundance in this study. These findings highlight a robust correlation between carbohydrate metabolism and nitrogen fixation, as well as phosphorus solubilization, thereby facilitating the assimilation of nitrogen and phosphorus by the roots of *H. ammodendron* [72]. In addition, amino acid metabolism, as the second most prominent metabolic function, contributes to the nitrogen cycle through processes such as deamination and transamination, thereby providing indispensable nutritional conditions for bacterial survival and reproduction [73]. The third tier of metabolism exhibited a greater relative abundance of significant functions associated with enzymes, nucleotide metabolism, energy metabolism, and antibiotics. These metabolic pathways represent a crucial aspect of the metabolic function exhibited by soil bacteria and the survival strategy adopted by bacterial communities in nutrient-depleted desert soil environments [30,58–60,63,74]. Notably, the biosynthesis of ansamycins, valine, leucine, and isoleucine and the biosynthesis of vancomycin-group antibiotics exhibited a significant upregulation in the *H. ammodendron* forest soil in comparison to the mobile dune soil. These metabolic functions actively facilitated plant growth and development through the production of antibiotics, growth-promoting hormones, and antibacterial proteins, thereby resulting in an enhanced relative abundance of these metabolic functions [75]. The findings of this study unequivocally demonstrate that the cultivation of *H. ammodendron* can expedite bacterial metabolic activity and enhance the efficiency of carbon, nitrogen, and other elemental circulation in the soil.

#### 4.4. Effects of Soil Physicochemical Factors on the Structure and Metabolic Function of Bacterial Communities

The functional structure of microbial communities is intricately linked to the environmental factors present in their respective habitats [56,60,69]. Particularly, the physicochemical properties of soil exert a profound influence on the composition and diversity of microbial communities, particularly in the face of the rapid and far-reaching effects of global climate change. These effects, in turn, have the potential to significantly impact delicate and vulnerable desert ecosystems [76,77]. Through the RDA analysis, it was determined that soil physicochemical properties accounted for a significant 65.36% of the observed variations in bacterial community structure. Notably, non-biological factors such as SOM, AK, and pH emerged as significant contributors to the overall explanatory changes. These findings align with the results reported by Bi et al. [23] in their research on rhizosphere soil bacteria associated with *Pinus sylvestris* var. *mongolica* in the Mu Us Desert, as well as the research conducted by Xu et al. [57] on soil bacteria inhabiting artificial *Robinia pseudoacacia* ecosystems. Simultaneously, the SOM, TN, AK, pH, and EC exhibited significant impacts on the primary metabolic functions of soil bacteria. This phenomenon can be readily explained. Firstly, in desert ecosystems characterized by sparse vegetation and limited soil nutrient

availability, essential nutrients such as carbon and nitrogen, which serve as pivotal energy sources shaping soil bacterial communities, assume the role of key limiting environmental factors [78,79]. Secondly, Gemmatimonadetes, known for its remarkable capacity to solubilize potassium, phosphorus, and other elements, facilitates the uptake of available nutrients by plants from the soil. The growth of Gemmatimonadetes in *H. ammodendron* forests enhances the absorption and utilization of available soil nutrients by *H. ammodendron*, thereby potentially accounting for the significant influence of available potassium content on the soil bacterial community structure in *H. ammodendron* forests [56,77]. Moreover, the study of global geographical patterns necessitates the consideration of soil pH as a pivotal determinant, as it exerts a profound influence on the characteristics of bacterial communities. This influence is primarily reflected through its direct impact on cell membrane permeability and stability [76,80]. It is widely acknowledged that EC exerts a detrimental effect on bacterial growth. This is attributable to the strong association between EC and soil salinity, which can disrupt cell permeability, induce nutrient imbalances, reduce enzyme activity, and even elicit toxic effects on microorganisms [81]. The varying degrees of salt tolerance and sensitivity exhibited by diverse microorganisms contribute to the divergence observed in soil microbial communities. Remarkably, the findings of this study reveal a significant and positive correlation between EC content and the majority of bacterial species, thereby providing further evidence that bacteria inhabiting desert soils have adeptly adapted to high-salt environments. The findings of this study explain that the impact of SOM, TN, AK, pH, and EC on bacterial community composition surpasses that of other nutrients. Nevertheless, it is important to note that this does not negate the influence of other nutrient characteristics on bacterial communities [14,19]. The complex relationship between soil physicochemical factors and bacterial communities is not unidimensional, as there may exist inherent correlations among the environmental factors themselves, which in turn affect the structure of microbial communities through interconnected effects [56,76,77]. Therefore, future research should focus on employing a combination of macrogenome sequencing and functional gene chip technology to delve into the specific mechanisms by which individual environmental factors, such as nitrogen, phosphorus, and other elements, exert their influence on the structure and functional potential of soil bacterial communities in *H. ammodendron* forests.

## 5. Conclusions

This study assessed the impact of an *H. ammodendron* plantation on the structural composition and functional dynamics of soil bacterial communities in the sand blocking and fixing belts situated at the periphery of oases. The prevailing bacterial taxa identified in the *H. ammodendron* forest soil were Actinobacteria, Proteobacteria, and Chloroflexi. Notably, Actinobacteria exhibited a significantly greater relative abundance in comparison to the mobile dune soil, thereby contributing to an overall enhancement in bacterial diversity. Moreover, the metabolic activities of the bacterial communities were primarily characterized by carbohydrate metabolism, amino acid metabolism, and cofactor and vitamin metabolism. These findings highlight the pivotal role played by the *H. ammodendron* plantation in shaping the structure and function of soil bacterial communities in sandy land ecosystems. The introduction of *H. ammodendron* cultivation resulted in a significant improvement in soil nutrient levels, comprising SOM, TN, and TP. The structure and function of the soil bacterial community were found to be significantly influenced by physicochemical factors such as soil SOM, TN, AK, pH, and EC. However, it is important to acknowledge that this intervention also involves specific adverse consequences, primarily characterized by the reduction in surface soil moisture and the accumulation of salt content. This study contributes to a deeper understanding of the ecological transformations experienced by soil microorganisms and their intricate complexity with physical and chemical factors in sandy land environments through the implementation of artificial vegetation-based sand-fixing measures.

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