frontiers | Frontiers in Forests and Global Change

TYPE Original Research
PUBLISHED 06 March 2023
DOI 10.3389/ffgc.2023.1135692

OPEN ACCESS

EDITED BY
Ling Zhang,
Jiangxi Agricultural University, China

REVIEWED BY
Zhang Yun,
Jiangxi Agricultural University, China
Zhenfeng Xu,
Sichuan Agricultural University, China

*CORRESPONDENCE
Ming Li
✉ limingly@126.com

SPECIALTY SECTION
This article was submitted to Frontiers in Forests and Global Change Forest Soils, a section of the journal Frontiers in Forests and Global Change

RECEIVED 01 January 2023
ACCEPTED 17 February 2023
PUBLISHED 06 March 2023

CITATION
Wang L, Sun Y, Li J, Tigabu M, Xu Q, Ma X and Li M (2023) Rhizosphere soil nutrients and bacterial community diversity of four broad-leaved trees planted under Chinese fir stands with different stocking density levels. *Front. For. Glob. Change* 6:1135692. doi: 10.3389/ffgc.2023.1135692

Rhizosphere soil nutrients and bacterial community diversity of four broad-leaved trees planted under Chinese fir stands with different stocking density levels

Liyan Wang[1], Yangyang Sun[1], Jing Li[1], Mulualem Tigabu[2], Qingli Xu[3], Xiangqing Ma[1,4] and Ming Li[1,4]*

[1]College of Forestry, Fujian Agriculture and Forestry University, Fuzhou, China, [2]Southern Swedish Forest Research Center, Faculty of Forest Science, Swedish University of Agricultural Sciences, Lomma, Sweden, [3]Pusang State-owned Forestry Farm, Shunchang, Fujian, China, [4]Chinese Fir Engineering Technology Research Center of National Forestry and Grassland Administration, Fuzhou, Fujian, China

Objective: Rhizosphere soil nutrients and bacterial diversity of four broad-leaved tree species underplanted in Chinese fir plantation with different stand density levels were analyzed to reveal characteristics of the rhizosphere soil environment and selection of suitable underplanted tree species.

Methods: Chinese fir plantation with three density levels (900, 1,200, and 1,875 stems ha^{-1}, respectively) were selected and underplanted with *Michelia macclurei*, *Schima superba*, *Phoebe zhennan,* and *Tsoongiodendron odorum*. The rhizosphere soil nutrients and bacterial community of the broad-leaved tree species were determined after 4 years.

Results: Significant differences in rhizosphere nutrient content were detected among different tree density levels, where the contents of total K, available K and available P in 900 stems ha^{-1} stands were significantly higher than the other stocking density levels. There were also significant differences in the contents of total C, total N, total K, available K and available P in the rhizosphere soils of the four trees species, while there were no significant differences in pH and total P. Rhizosphere soil nutrient contents were higher under *S. superba* and *M. macclurei* than under *P. zhennan* and *T. odorum*. The rhizosphere soil nutrient contents and bacterial diversity decreased with the increase of stand density, and the bacterial diversity showed significant differences in the rhizosphere soils of *P. zhennan*, *T. odorum* and *S. superba* when underplanted in different stand densities. The bacterial diversity was positively correlated with the available P content of rhizosphere soils, suggesting that soil available P content plays an important role in shaping the structure of bacterial community.

Conclusion: The nutrient contents and bacterial diversity of rhizosphere soils of underplated broad-leaved species decreased with increasing stand density of Chinese fir plantation. Rhizosphere soils of *M. macclurei* and *S. superba* were rich in nutrient contents and bacterial diversity. Thus, low density of Chinese fir plantation (900 stems ha^{-1}) underplanted with *M. macclurei* and *S. superba* is suitable for the establishment of mixed forest, which will facilitate better tree growth and maintaining soil fertility to realize sustainable management of forests.

KEYWORDS

understory interplanting, broad-leaved trees, bacterial diversity, rhizosphere soil, soil nutrition

1. Introduction

Chinese fir (*Cunninghamia lanceolata*) is an important fast-growing coniferous timber species in southern China, with an area of 9.902 million hectares and a stock volume of 755 million m^3 (Wang et al., 2022; Wang and Shen, 2022). Traditional Chinese fir cultivation is mainly based on multi-generation continuous planting of pure monoculture. However, long-term continuous cultivation is prone to problems such as soil degradation, productivity decline, soil fertility and microbial diversity decline, which seriously affects the forest ecosystem services and the sustainable management (Guo et al., 2023). The most effective tending measures in the management of Chinese fir plantation are thinning and interplanting to solve these ecological problems. Stand density regulation with thinning is a key technical procedure, especially for the cultivation of large-diameter timber in Chinese fir plantations. Underplanting of broad-leaved trees in the low-density and medium-aged Chinese fir plantations can create mixed-species forests with multi-level vertical stands with different ecological niches, which can enhance the utilization rate of forest land, promote the improvement of understory vegetation diversity, improve the quality of forest stands and enhance the stability of forest ecosystems (Zou, 2020). *Michelia macclurei*, *Schima superba*, *Phoebe zhennan*, and *Tsoongiodendron odorum* are precious broad-leaved tree species, and are also more successful in building coniferous and broad-leaved mixed forest with Chinese fir, which can better improve the site and promote the productivity of the forest land (Liu J. et al., 2021; Ding et al., 2022; Xu et al., 2022). Thus, in recent years, broad-leaved tree species such as *M. macclurei*, *S. superba*, *P. zhennan*, and *T. odorum* have been widely planted in the understory of Chinese fir plantations. A sustainable management system for intermediate-aged Chinese fir plantation with stand density regulation and underplanting of broad-leaved trees has become an important direction for the cultivation of large-diameter Chinese fir in China (Liu et al., 2018).

In the forest ecosystem, soil bacteria are an important part of soil, participate in many ecological processes, and play an extremely important role in promoting the material cycle, energy flow and information transmission of the ecosystem (An et al., 2019). Rhizosphere soil bacteria are the main group of rhizosphere microorganisms, which concentrate in large quantities around the root system and have a strong mutual relationship with the root system, playing an important role in the secretion, transformation, recycling and nutrient supply to plant roots (Liang et al., 2021). The rhizosphere of trees, as a hub for various chemical nutrients in nature to enter the roots of trees and participate in the material cycle in the growth process of trees, carries interactions among soil, roots and rhizosphere bacteria (Ai et al., 2015). Thus, the rhizosphere of trees has good aeration conditions, water conditions and substance secretion, which is a good habitat for rhizosphere bacteria, which is generally interdependent with the bacteria with the largest number, rapid reproduction rate and various types of soil microorganisms, forming a complex soil microbial system among rhizosphere soil, forest trees and bacteria (Liu J. W. et al., 2021). Thinning and interplanting will affect the changes of bacterial community composition in the rhizosphere of forest trees and improve the bacterial diversity in the rhizosphere of forest trees. When *Armeniaca vulgaris* and *Sabina chinensis* were mixed with other tree species, the bacterial diversity in the mixed forest increased compared with the pure forest of *A. vulgaris* and *S. chinensis* (Wang et al., 2022). The rhizosphere soil bacterial communities analysis of pure Chinese fir plantation and mixed plantations of Chinese fir with different broad-leaved tree species revealed the mixed plantations had higher total absolute abundance and more unique operational taxon (OTU) than that of pure forest (Lei et al., 2023). Therefore, exploring the relationship between thinning intensity, rhizosphere soil nutrients and the bacteria diversity of underplanted broadleaved trees has paramount importance in selecting the suitable thinning density and broadleaved tree species for establishment mixed Chinese fir plantation.

Thinning of monoculture plantation followed by planting of broad-leaved trees in the understory can not only change the light, air and vegetation diversity in the upper part of the stand, but also have an important impact on nutrient availability in the underground, which in turn affects the microbial activity and community structure of the rhizosphere soil (Zhang X. et al., 2019). In recent years, several studies have been conducted on the changes of soil and bacterial diversity in Chinese fir plantations under different thinning intensities, and it has been found that too low or high density is not conducive to the vegetation growth and soil nutrient cycling, especially high-density Chinese fir plantations are exposed to greater environmental stresses (Wang M. J. et al., 2021) than low-density Chinese fir plantations (Liu et al., 2017; Wang et al., 2019; Zhang X. et al., 2019; Ding et al., 2021). A comparative study of soil nutrients and bacterial diversity of three different densities levels of 17-year-old Chinese fir plantation revealed the moderate reduction in stand density was beneficial in the growth of understory vegetation and in maintaining a reasonable bacterial community structure, which helps to maintain the soil fertility of the Chinese fir forests and to achieve sustainable management in the long run (Ding et al., 2021). The Study on five plantation densities of 5- and 35-year-old Chinese fir plantations showed that after long-term rotation, increasing planting density enrich the soil organic carbon storage and reduces soil microbial activity and enzyme activity. Therefore, moderate thinning seems to be the most beneficial to improve soil nutrients and root vitality of Chinese fir plantations.

The meta-analysis of species mixing effects in Chinese fir plantations revealed a positive effects of species mixing on soil nutrient cycling and ecosystem function, which increased 13.97 and 36.34% of soil physicochemical properties and enzymatic activities (Guo et al., 2023). The interplanting or species mixing are recommend to support the sustainable and healthy development of Chinese fir plantation, however, there is a coupling between density regulation and interplanting tree species selection. Inappropriate stand density or selection of tree species for interplanting will not only lead to unfair competition for sunlight, heat and growth space in the upper layer, but also lead to serious water and nutrient competition in the root layer, resulting in negative feedback effect on forest growth (Fu and Meinzer, 2019). The impact on the yield of the mixed forests are mainly caused by the interspecific complementarity and the composition of species traits, and the yield increase shows an increasing trend with the increase of mixed species (Feng et al., 2022). The effect of interspecies mixing on increasing yield is stronger with different leaf types, different leaf life histories, different nutrient acquisition strategies and planting densities (Gurevitch, 2022). In addition, most studies have shown that the diversity and function of soil microbial communities in mixed-species forest ecosystems are significantly higher than that of single species forests (Jiang et al., 2012; Xu H. D. et al., 2021; Ding et al., 2022). Mixed forests of conifers and broadleaved trees in subtropical China can return higher stand biomass and additional litter than coniferous forests, thereby increasing soil microbial biomass and related functions (Wu et al., 2019). The mixed *Eucalyptus urophylla* with *E. grandis* significantly increased the rhizosphere soil water content, pH value, organic matter, total nitrogen and total potassium content than the pure *E. grandis* plantation (Han et al., 2020). Wu et al. (2022) found that the mixing of *Pinus massoniana*, *Pinus elliottii Engelmann* and *S. superba* significantly increased the content of ammonium nitrogen, mineral nitrogen and available phosphorus in the coniferous rhizosphere soil, but had no significant effect on nitrate nitrogen, and was conducive to the significant increase of the total microbial biomass and fungi/bacteria ratio in the coniferous rhizosphere. A mixed planting of Chinese fir and broadleaf species *Cinnamomum camphora*, *Liquidambar formosana,* and *M. macclurei* revealed broadleaf species chemically mediate the growth of Chinese fir through root exudates, *C. camphora* roots released allelochemicals to inhibited the Chinese fir and changes in main soil microbial groups, and *M. macclurei* promote the growth of Chinese fir, which indirectly regulated the soil microbial community structure (Xia et al., 2019). However, most current research on the establishment of mixed Chinese fir forests focuses on soil microbial analysis under different stand density levels with interplanting single species, or on the ecosystem changes of the same broadleaf tree under the same stand density. There is a lack of comparative studies on planting multiple broadleaf tree species under different stand density levels (Wang and Wang, 2008; Zhang et al., 2021).

Thus, this study was conducted to examine the effects of stand density and broad-leaved species mixed with Chinese fir on rhizosphere nutrient content and bacterial diversity, as well as the relationship between nutrient content and bacterial diversity. The broad-leaved species used for interplanting in Chinese fir stands were *M. macclurei*, *S. superba*, *P. zhennan* and *T. odorum*. The results will provide evidence for deciding stand density level and selection of broad-leaved species suitable for establishment of mixed Chinese fir forests and long-term productivity of forests.

2. Materials and methods

2.1. Study site

The study area is located in the Pusang state-owned forestry farm in Shunchang County, Fujian Province (117°46′E, 26°55′N), with a subtropical monsoon climate. The annual mean temperature is 18.5°C, and annual precipitation is 1,880 mm, with 230 frost-free days and relative humidity of 82%. Chinese fir was planted in 2006 on the same slope direction, at a slope of 22–31° and an elevation of 135–228 m. The initial planting density of Chinese fir is 1,500–1,980 stems ha^{-1}. The Chinese fir stand was thinned in 2017 to reduce the stocking density to 900, 1,200, and 1,875 stems ha^{-1}, and the 2 years old broad-leaved trees seedlings of *S. superba*, *P. zhennan*, *M. macclurei,* and *T. odorum* were planted with the density of 225 stems ha^{-1} per species. In each of the three thinned stand, three standard plots of 20 m × 20 m were set up (9 per species of broad-leaved trees). The total C, total N and total P in the soil of Chinese fir forest land before thinning and interplanting were 7.45–27.321, 0.595–1.945, and 13.064–34.313 mg/kg, respectively. The growth of Chinese fir and the four broad-leaved species was recorded annually.

2.2. Soil sample collection

Soil profiles were excavated in the subplots in September 2020 according to the diagonal sampling method (On the diagonal of each standard plot, and then select the upper, middle and lower diagonal, with a total of three points), and soil samples were taken from 0 to 10 cm, 10 to 20 cm, and 20 to 40 cm soil layers with a 100 cm^3 cutting rings for the determination of soil physical properties of Chinese fir forests with different thinning reserve densities; at the same time, the chemical soil of each standard plot is collected. After mixing the soil samples of the same layer in the standard plot, that is, as a test soil sample. Each standard plot has three soil samples, a total of 27 soil samples, for the determination of soil nutrients of Chinese fir forest under different thinning reserve densities. In each standard plot, each broad-leaved tree species selects three seedlings with the same growth, collects soil samples within about 50 cm of the bottom of the tree trunk, peels the soil attached to the root, and mixes the same broad-leaved tree rhizosphere soil samples as a rhizosphere soil sample. We collected 36 rhizosphere soil samples from stands with three densities with four broad-leaved trees underplanted. The soil samples were divided into three equal parts, one part was air-dried and ground for soil nutrient content determination, while the remaining part was collected and stored at 4°C for soil nutrient determination. The remaining part was collected and stored at −80°C for total soil DNA extraction.

TABLE 1 Growth of Chinese fir after different thinning and interplanting treatments.

Year	Density (stems ha^{-1})	H (m)	DBH (cm)
	900	15.12 ± 0.12a	17.29 ± 0.36a
2017	1,200	14.92 ± 0.17a	16.59 ± 0.45a
	1,875	14.49 ± 0.32a	15.51 ± 0.79a
	900	15.87 ± 0.09a	19.16 ± 0.25a
2018	1,200	15.51 ± 0.17ab	18.15 ± 0.46ab
	1,875	15.03 ± 0.30c	16.89 ± 0.79c
	900	17.17 ± 0.21a	23.01 ± 0.67a
2022	1,200	16.81 ± 0.35ab	21.97 ± 1.05ab
	1,875	16.11 ± 0.39b	19.84 ± 1.12bc

Small letters indicate significant differences between different densities in the same year ($p < 0.05$) (Mean ± SE).

2.3. Soil nutrient analysis

Soil total C and N contents were measured by elemental analyzer (Elementar, Vario MAX CN, Germany). Total P and total K with hydrofluoric acid–perchloric acid digestion and determined by ICP emission spectrometry (Optima, 7,000 DV, Germany), the available P content was measured by HCl-NH_4F leaching method, and the available K content was measured by the method of ammonium acetate leaching. The soil pH value shall be measured by pH acidimeter after being diluted and shaken by soil: water = 1:2.5 and then standing for 30 min.

2.4. Extraction and amplification of soil bacterial DNA for sequencing

Soil DNA was extracted using the CTAB method, DNA quality was detected using 1% agarose gel electrophoresis, and DNA concentration was detected using Nanodrop. The primers were designed to amplify the V3 and V4 regions of the bacterial 16S ribosomal coding sequence, and the primer sequences were (ACTCCTACGGGAGGCAGCAG) and (GGACTACHVGGGTWTCTAAT). The amplification conditions were set at 94°C pre-denaturation for 5 min, 94°C denaturation for 30 s, 55°C annealing for 30 s, 72°C extension for 60 s, 28 cycles, and 72°C extension for 7 min. The amplified PCR products were detected by 1% agarose gel electrophoresis and purified by Agencourt AMPure XP Nucleic Acid Purification Kit, and sequenced by Illumina MiSeq PE300 platform (Beijing Ovison Bioinformatics Co., Ltd., Guangzhou, China).

2.5. Bioinformatics analysis

The Pair-End double-ended Fastq format data obtained from the sequencing were processed using Trimmomatic with a sliding window strategy, with a window size set at 50 bp, an average quality value of 20, a minimum retained sequence length of 120, and sequences with N were removed using Pear software. The reads for each sample were stitched using Flash to obtain the original Tags data. The original sequencing data were deposited in the NCBI SRA database under the accession number PRJNA918639.

Chimeric sequences from the UCHIME Algorithm database were compared and removed by the uchime method, short sequences that did not fit the requirements were also removed, and the high-quality Clean Tags sequences were obtained after quality control filtering. Based on the sequence similarity, the Clean Tags sequences were clustered to produce operational taxonomic units (OTUs), and those with more than 97% sequence similarity were classified as an OUT. The UNITE taxonomic database and the RDP Classifier database were used for species annotation of OUT representative sequences and analysis of sample community composition at each taxonomic level to obtain information on bacterial species in different rhizosphere soil samples.

2.6. Data analysis

SPSS 22.0 was used to conduct statistical analyses. We used a one-way analysis of variance (ANOVA) to test for differences in soil properties, bacterial community structure, and microbial diversity. The obtained OUT clustering results and species information were analyzed using Mothur software, and the abundance index of Chao 1 and Observed species, diversity index of Simpson and Shannon were calculated, and the statistical results of species composition and relative abundance of the samples were plotted using the Origin 8.5 software package. Pearson correlation analysis was performed using SPSS 22.0

TABLE 2 Average tree height (H), diameter at breast height (DBH), and ground diameter (GD) of seedlings of broad-leaved trees planted under different stocking density of Chinese fir.

Year	Density (stems ha^{-1})	*S. superba*		*T. odorum*		*M. macclurei*		*P. zhennan*	
		H (m)	GD (cm)	H (m)	GD (cm)	H (m)	GD (cm)	H (m)	GD (cm)
	900	0.57 ± 0.06b	0.41 ± 0.04a	0.23 ± 0.04c	0.37 ± 0.03a	0.50 ± 0.03a	0.41 ± 0.05a	0.43 ± 0.03ab	0.32 ± 0.01a
2018	1,200	0.53 ± 0.03a	0.39 ± 0.02b	0.20 ± 0.02b	0.32 ± 0.01b	0.55 ± 0.04a	0.45 ± 0.03a	0.55 ± 0.04a	0.33 ± 0.04ab
	1,875	0.42 ± 0.03a	0.37 ± 0.02b	0.19 ± 0.02b	0.35 ± 0.04ab	0.47 ± 0.04a	0.44 ± 0.03ab	0.45 ± 0.02a	0.31 ± 0.02a
	900	2.09 ± 0.18a	2.32 ± 0.19a	1.68 ± 0.46a	1.84 ± 0.53ab	1.90 ± 0.21a	1.84 ± 0.14ab	1.87 ± 0.90a	1.10 ± 0.03b
2022	1,200	1.50 ± 0.06ab	1.70 ± 0.23a	1.30 ± 0.31ab	1.76 ± 0.36a	1.71 ± 0.09a	1.79 ± 0.00a	0.83 ± 0.39b	1.12 ± 0.07a
	1,875	1.43 ± 0.43a	1.00 ± 0.06a	0.93 ± 0.13a	1.29 ± 0.22a	1.06 ± 0.07a	1.19 ± 0.14a	1.24 ± 0.23a	0.92 ± 0.04a

Lower case letters indicate significant differences among stocking in the same year ($p < 0.05$).

to analyze the correlation between soil nutrient contents and the structure of dominant bacterial community and bacterial diversity in rhizosphere soil. Canoco5 software was used to analyze the relationship between soil nutrients and dominant bacterial community structure and bacterial diversity in rhizosphere soil by RDA constrained sequencing method.

3. Results

3.1. Growth of trees in different stand density

There was no significant difference in the DBH in different stand densities in 2017 (p < 0.05), but the DBH decreased significantly with the increasing of stand densities after thinning (Table 1). The H and GD of *S. superba* and *T. odorum* decreased with the increasing of stand density, that is, they grow better under low density, which indicates the biological characteristics of *S. superba* and *T. odorum* that like light. In the 900 and 1,200 stems ha^{-1} treatments, the H and GD of *S. superba* and *M. macclurei* are higher than those of the other two species, indicating they are more suitable for planting under the Chinese fir plantation at the low and middle stocking density (Table 2).

3.2. Soil physical and chemical properties of plantation

There were significant differences in the contents of total K, available P and available K in the soil of Chinese fir plantation with different thinning reserve densities (Table 3). The contents of total K, available K and available P were higher in the density of 900 stems ha^{-1}, while the total nitrogen content of 0–10 cm increased with the increasing of stand density. Under the same stocking density, the total K, total N, total C, available K, available P, pH and water content in the soil decreased significantly with increasing of soil layer. Across all stocking density levels, the contents of total K and available P in the 0–10 cm soil layer were significantly higher than those in the 20–40 cm soil layer. In the 900 and 1,200 stems ha^{-1} treatments, while the contents of total N, total C and available K in the 0–10 cm soil layer were significantly higher than those in the 20–40 cm soil layer.

3.3. Chemical properties of rhizosphere soil of broad-leaved trees

There were significant differences in the contents of total C, total N, total K, available K and available P in the rhizosphere soils of the four broad-leaved tree species in the same stocking density, while there were no significant differences in the pH and total P (Table 4). The rhizosphere soil contents of available P, total N, total C and total K increased with the decreasing of stocking density. At low stocking density (900 stems ha^{-1}), the rhizosphere soil contents of total C, total N, total K and available K increased in the following order:

TABLE 3 Physical and chemical properties of bulk soils in Chinese fir plantations with different stocking densities.

Thinning reserve density/(stems ha^{-1})	Soil thickness/cm	Total K/g·kg^{-1}	Total N/g·kg^{-1}	Total C/g·kg^{-1}	Total P/g·kg^{-1}	Available K/g·kg^{-1}	Available P/mg·kg^{-1}	pH	Moisture content/%
	0–10	4.14 ± 0.53Aa	1.11 ± 0.08Aa	23.22 ± 2.20Aa	0.13 ± 0.00Aa	6.37 ± 0.14Aa	79.97 ± 1.12Aa	4.84 ± 0.17Aa	29.00 ± 0.02Aa
900	10–20	3.32 ± 0.20Aab	0.91 ± 0.08Aa	18.30 ± 2.40Aab	0.13 ± 0.00Aa	4.38 ± 0.15Ab	74.13 ± 0.41Ab	4.72 ± 0.01Aa	27.00 ± 0.02Aa
	20–40	2.78 ± 0.09Ab	0.62 ± 0.04Ab	11.42 ± 1.28Ab	0.13 ± 0.00Aa	3.53 ± 0.36Ac	72.31 ± 0.35Ab	4.58 ± 0.08Aa	24.00 ± 0.01Aa
	0–10	2.87 ± 0.04Ba	1.33 ± 0.11Aa	29.16 ± 3.93Aa	0.13 ± 0.00Aa	2.44 ± 0.22Ba	70.41 ± 0.10Ba	4.90 ± 0.06Aa	28.00 ± 0.02Aa
1,200	10–20	2.75 ± 0.08ABab	0.84 ± 0.09Ab	18.69 ± 4.36Aab	0.13 ± 0.00Aa	1.62 ± 0.16Bb	67.94 ± 0.50Bb	4.77 ± 0.10Aa	27.00 ± 0.02Aa
	20–40	2.51 ± 0.14ABb	0.52 ± 0.03Ac	10.11 ± 1.19Ab	0.13 ± 0.00Aa	1.29 ± 0.02Bb	66.56 ± 0.16Bc	4.68 ± 0.07Aa	26.00 ± 0.04Aa
	0–10	2.80 ± 0.08Ba	1.44 ± 0.35Aa	27.16 ± 6.72Aa	0.13 ± 0.00Aa	1.09 ± 0.42Ca	63.05 ± 1.25Ca	4.73 ± 0.03Aa	35.00 ± 0.06Aa
1,875	10–20	2.28 ± 0.22Bab	0.80 ± 0.17Aa	18.50 ± 6.79Aa	0.13 ± 0.00Aa	0.77 ± 0.24Ca	57.55 ± 0.33Ca	4.63 ± 0.03Aa	29.00 ± 0.02Aa
	20–40	1.89 ± 0.31Bb	0.72 ± 0.12Aa	15.39 ± 3.86Aa	0.13 ± 0.00Aa	0.66 ± 0.26Ba	48.12 ± 3.98Bb	4.61 ± 0.04Aa	24.00 ± 0.00Aa

Capital letters indicate significant differences in the same soil layer under different thinning retention densities, while lowercase letters indicate significant differences in different soil layers under the same thinning retention densities (p < 0.05) (Mean ± SE).

S. superba > *M. macclurei* > *T. odorum* > *P. zhennan*. At medium (1,200 stems ha^{-1}) and high (1,875 stems ha^{-1}) stocking density, the rhizosphere soil contents of total C, total N, total K, and available K were significantly higher in *M. macclurei* than in other species, while the available P content was significantly higher than in *T. odorum* and *P. zhennan*. In general, Chinese fir plantations underplanted with *S. superba* and *M. macclurei* had higher rhizosphere soil nutrient contents than *T. odorum* and *P. zhennan*.

3.4. Bacterial diversity of rhizosphere soil of broad-leaved trees

The rhizosphere soil bacterial diversity of *S. superba*, *P. zhennan* and *T. odorum* were significantly different at different densities, but there was no significant difference in *M. macclurei* (**Table 5**). The highest rhizosphere soil bacterial diversity of *S. superba* appeared under the density of 1,200 stems ha^{-1}. The Chao 1, the number of observed species and the PD whole_tree and Shannon indices of *P. zhennan* increased with the increasing of stocking density, revealing the rhizosphere bacterial diversity of *P. zhennan* was richer under high-density Chinese fir plantation. The Chao 1 and the Shannon indices of rhizosphere soils of *T. odorum* decreased with the increasing of stocking density indicating that *T. odorum* may be more suitable for high-light environment, and *T. odorum* planted under the low-density Chinese fir forest has higher rhizosphere bacterial diversity.

3.5. Structure of bacterial community of the rhizosphere soil

At the phylum level, 11 most abundant bacteria shared by the rhizosphere soil of four tree species (**Figure 1**). Acidobacterium, Proteobacterium, and Chloroflexi had relative abundances greater than 12% and Actinomycetes and Verrucomicrobia had relative abundances greater than 2%, making them the dominant groups among the rhizosphere soil bacteria. The bacterial community composition structure of different broad-leaved trees under the same stocking density is different, but there is no obvious rule. The bacterial community composition structure of the same broad-leaved tree species under different stocking densities is also different, with the relative abundance of Acidiobacter in the rhizosphere soil of *T. odorum* decreased with increasing of stocking density, while the opposite trend was observed for the Acidiobacter in *P. zhennan*. The relative abundance of the phylum Acidiobacter and Chloroflexi in the rhizosphere soil of *M. macclurei* increased as the stocking density increased. The relative abundance of the phylum Metaphyllobacteria in the rhizosphere soils of *M. macclurei* decreased with the increasing of stocking density. The genus Acidobacteria had the highest abundance in the four broad-leaved tree species (**Figure 2**), and Acidiobacter showed an increasing trend in *M. macclurei* and *P. zhennan* with the increasing of stocking density, while it decreased in *T. odorum* and *S. superb* with increasing of stocking density.

TABLE 4 Chemical properties of rhizosphere soil of four broad-leaved trees planted under different stocking densities.

Thinning reserve density/(stems ha^{-1})	Tree species	Total K/g·kg^{-1}	Total N/g·kg^{-1}	Total C/g·kg^{-1}	Total P/g·kg^{-1}	Available K/g·kg^{-1}	Available P/mg·kg^{-1}	pH
	M. macclurei	224.21 ± 3.32Ab	2.32 ± 0.04Ab	39.48 ± 0.46Ab	1.56 ± 0.9Aa	5.57 ± 0.02Ab	176.81 ± 11.17Aa	4.870 ± 0.15Aa
900	*S. superba*	271.72 ± 11.03Ba	2.55 ± 0.07Aa	43.50 ± 0.37Aa	0.62 ± 0.34Aa	5.89 ± 0.05Aa	202.05 ± 11.53Aab	4.790 ± 0.03Aa
	P. zhennan	154.04 ± 4.52Ad	1.860 ± 0.05Ad	37.05 ± 0.62Ad	1.30 ± 0.530Aa	4.56 ± 0.05Bd	107.75 ± 7.40Ac	4.720 ± 0.16Aa
	T. odorum	192.17 ± 2.10Ac	2.08 ± 0.03Ac	38.25 ± 0.58Ac	0.91 ± 0.370Aa	4.86 ± 0.05Ac	158.07 ± 12.87Ab	4.850 ± 0.13Aa
	M. macclurei	176.20 ± 6.67Ba	1.73 ± 0.02Ba	35.71 ± 0.64Ba	2.58 ± 1.280Aa	5.39 ± 0.10Aa	129.84 ± 6.19ABa	4.820 ± 0.10Aa
1,200	*S. superba*	124.19 ± 1.81Ab	1.23 ± 0.02Bd	24.52 ± 0.52Bb	1.23 ± 0.550Aa	3.74 ± 0.11Bd	169.28 ± 17.82Bb	4.890 ± 0.20Aa
	P. zhennan	136.16 ± 4.74Bb	1.56 ± 0.03Bb	31.64 ± 1.17Bb	1.89 ± 1.130Aa	5.01 ± 0.06Ab	97.73 ± 4.17Ab	4.640 ± 0.06Aa
	T. odorum	135.00 ± 2.79Bb	1.37 ± 0.01Bc	29.85 ± 0.41Bb	1.56 ± 0.84Aa	4.48 ± 0.05Bc	112.65 ± 6.30Bb	4.860 ± 0.20Aa
	M. macclurei	125.92 ± 5.48Ca	1.21 ± 0.01Ca	20.32 ± 0.61Ca	1.05 ± 0.24Aa	4.68 ± 0.06Ba	117.79 ± 3.42Ba	5.010 ± 0.21Aa
1,875	*S. superba*	111.16 ± 0.32Abc	1.11 ± 0.03Bb	15.27 ± 0.61Cbc	0.96 ± 0.89Aa	3.53 ± 0.10Bc	135.25 ± 4.90Bb	4.790 ± 0.16Aa
	P. zhennan	120.76 ± 3.51Cab	1.18 ± 0.01Ca	18.37 ± 0.63Cab	2.65 ± 1.41Aa	4.18 ± 0.04Cb	98.26 ± 2.16Ac	4.890 ± 0.23Aa
	T. odorum	104.73 ± 2.68Cc	1.02 ± 0.01Cc	10.98 ± 0.31Cc	0.81 ± 0.18Aa	2.67 ± 0.05Cd	103.24 ± 4.81Bc	4.840 ± 0.120Aa

Lowercase letters represent significant differences in rhizosphere soil physicochemical properties of four broad-leaved trees under the same stocking density, and capital letters represent significant differences in rhizosphere soil physicochemical properties of the same broad-leaved tree species under different stocking densities ($p < 0.05$) (Mean ± SE).

TABLE 5 Bacterial diversity in the rhizosphere soil of four broad-leaved trees planted under different stocking densities.

Stocking density (stems ha^{-1})	Tree species	Diversity indices			
		Chao1 index	Observed species number	PD_whole_tree index	Shannon index
	M. macclurei	3052.20 ± 196.00Aa	2249.00 ± 163.10Aa	162.30 ± 10.78Aa	8.90 ± 0.10Aa
900	*S. superba*	3158.40 ± 5.00Ba	2315.400 ± 40.10Aa	165.25 ± 2.75Aa	9.00 ± 0.10Ba
	P. zhennan	2633.10 ± 75.00Bb	1865.10 ± 65.40Bb	136.62 ± 5.47Ba	8.20 ± 0.30Ab
	T. odorum	3110.30 ± 77.90Aa	2336.40 ± 118.00Aa	168.18 ± 7.15Aa	9.00 ± 0.10Aa
	M. macclurei	3178.00 ± 173.20Aab	2274.20 ± 158.00Aa	160.80 ± 9.80Aa	8.70 ± 0.20Aa
1,200	*S. superba*	3705.40 ± 20.20Aa	2457.50 ± 209.50Aa	173.60 ± 11.00Aa	8.90 ± 0.40ABa
	P. zhennan	2829.30 ± 127.10ABb	1965.90 ± 50.90ABa	148.00 ± 2.90ABa	8.40 ± 0.00Aa
	T. odorum	2918.70 ± 259.70ABb	2116.80 ± 197.70Aa	155.40 ± 12.50Aa	8.70 ± 0.30ABa
	M. macclurei	2679.30 ± 47.60Ab	1915.40 ± 40.70Aab	145.00 ± 4.33Aab	8.40 ± 0.30Aa
1,875	*S. superba*	2203.60 ± 92.30Cc	1567.80 ± 65.30Bc	125.10 ± 3.30Bb	7.90 ± 0.20Ba
	P. zhennan	3082.50 ± 103.80Aa	2175.80 ± 73.10Aa	159.10 ± 4.20Aa	8.60 ± 0.10Aa
	T. odorum	2373.30 ± 197.30Bab	1733.30 ± 169.90Aab	131.20 ± 10.00Ab	7.70 ± 0.40Ba

Lowercase letters represent significant differences in the rhizosphere soil bacterial diversity of four broad-leaved trees planted under the same stocking density and capital letters represent significant differences in the rhizosphere soil bacterial diversity of the same broad-leaved tree species planted under different stocking densities ($p < 0.05$) (Mean ± SE).

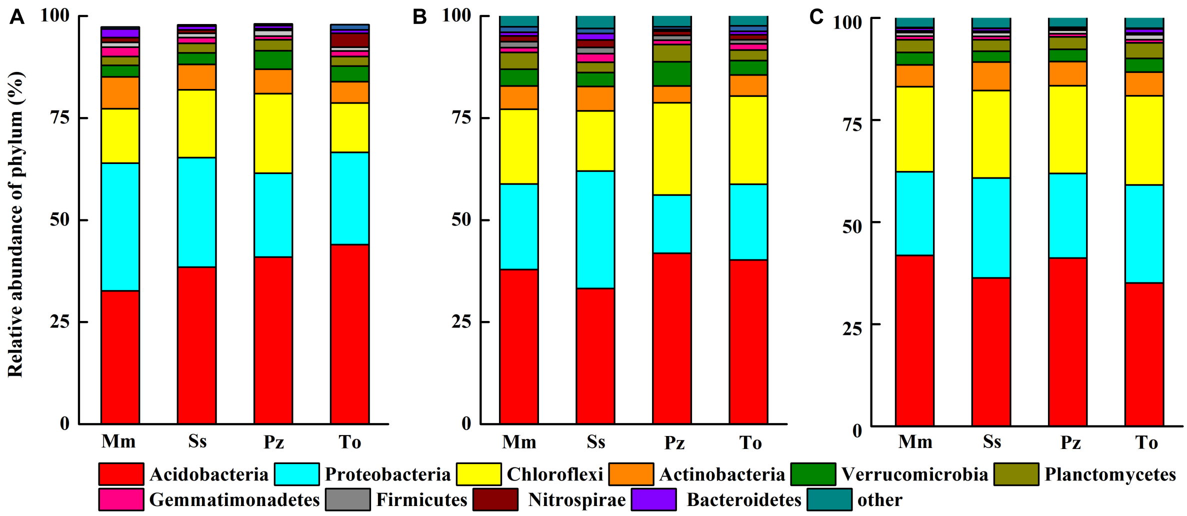

FIGURE 1
The relative abundance of dominant bacterial phyla in the rhizosphere soils of four broad-leaved tree species under 900 stems ha^{-1} **(A)**, 1,200 stems ha^{-1} **(B)** and 1,875 stems ha^{-1} **(C)** of stocking density. The Mm, SS, Pz and To stand for *Michelia macclurei, Schima superba, Phoebe zhennan*, and *Tsoongiodendron odorum*, respectively.

3.6. Effects of soil chemical properties on bacterial community

The correlation analysis between the stand soil nutrient contents and rhizosphere bacterial community structure showed that soil effective P, total N and total K contents were negatively correlated with Chloroflexi, the available P content was highly positively correlated with Proteobacteria, the available P content was positively correlated with Gemmatimonadetes, and the soil pH was negatively correlated with Verrucomicrobia (Table 6). Redundancy analysis (RDA) revealed that the structure of rhizosphere bacterial community was related to soil nutrients, and the bacterial community structure is mainly affected by available P, pH and available K (Figure 3). The total interpretation rate of the seven soil physical and chemical indicators reached 74.94%. The interpretation rate and contribution rate of the soil available P content were the highest (37.8 and 47.8%, respectively), indicating that the soil available P content had a great impact on the bacterial community, followed by the soil available K content (17.6 and 22.7%, respectively). There was a significant positive correlation between soil available P and Nitrospirae and Bacteroides, a significant negative correlation between total P and Actinobacia, and a significant negative correlation between soil total N and total K content and Chloroflex. The contents of total N and total K were significantly positively correlated with Gemmatimonadetes.

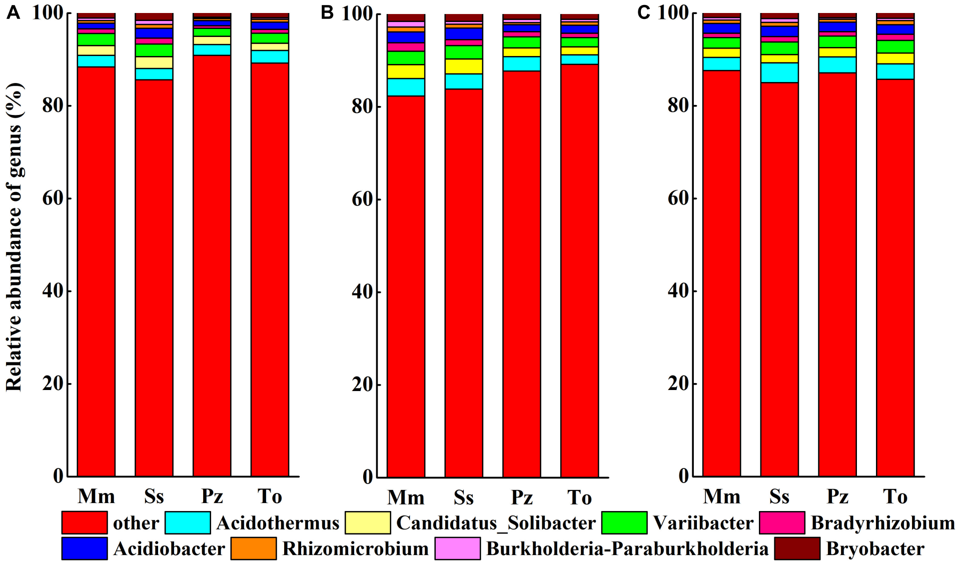

FIGURE 2
Bacterial communities at the genus level in the rhizosphere soil of four broad-leaved trees species under 900 stems ha^{-1} **(A)**, 1,200 stems ha^{-1} **(B)** and 1,875 stems ha^{-1} **(C)** of stocking density. The Mm, SS, Pz and To stand for *Michelia macclurei*, *Schima superba*, *Phoebe zhennan,* and *Tsoongiodendron odorum*, respectively.

TABLE 6 Correlation between bacterial community structure and soil chemical properties.

Bacteria	Available K	Available P	Total N	Total C	Total P	Total K	pH
Acidobacteria	0.23	−0.42	−0.05	0.04	0.25	−0.08	0.24
Proteobacteria	−0.05	0.77**	0.32	0.12	−0.41	0.39	0.14
Chloroflexi	−0.44	−0.71*	−0.60*	−0.55	0.10	−0.60*	−0.37
Actinobacteria	−0.07	0.51	0.21	0.03	−0.32	0.24	−0.04
Verrucomicrobia	0.21	−0.47	0.05	0.28	0.39	−0.12	−0.59*
Planctomycetes	−0.20	−0.61*	−0.36	−0.27	0.50	−0.38	−0.46
Gemmatimonadetes	0.34	0.70*	0.46	0.49	−0.07	0.47	0.10
Firmicutes	0.04	0.16	0.19	0.32	0.10	0.13	−0.36
Nitrospirae	0.26	0.41	0.37	0.47	−0.11	0.32	0.03
Bacteroidetes	0.11	0.62*	0.33	0.24	−0.18	0.35	0.27
Latescibacteria	0.26	0.18	0.17	0.44	0.19	0.14	0.03

*Indicate significant influence at $p < 0.05$ and **indicate significant influence at $p < 0.01$.

3.7. Effects of soil chemical properties on bacterial diversity

The correlation analysis between rhizosphere soil nutrient contents and bacterial diversity of the rhizosphere soil showed that the Shannon diversity index was positively correlated with available K, total P and total K content (Table 7), with total N content being highly significant and positively correlated with the Shannon index. Available P content is positively correlated with species number, PD_whole_tree index and Shannon index. Total N and available K content were positively correlated with observed species number. In contrast, total C content and pH were not significantly correlated with bacterial diversity. The bacterial diversity in the rhizosphere soil of broad-leaved trees is mainly affected by the available P, total P, and pH (Figure 4). The total interpretation rate of the seven soil nutrients reached 79.7%, and the interpretation rate and contribution rate of soil available P content were the highest (28.3 and 35.5%, respectively), indicating that the soil available P content had a great impact on bacterial diversity. The bacterial diversity index was positively correlated with soil nutrients, and PD_whole_tree, shannon and observed spries number index were significantly positively correlated with the available P and pH.

4. Discussion

4.1. Effects of thinning and interplanting on soil physicochemical properties

Thinning and interplanting change the species composition of understory vegetation, which then leads to differences in soil physicochemical properties (Pretzsch et al., 2021). Low stocking density decreases the competition between trees, leading to increase in soil nutrients and microbial diversity, which is conducive to

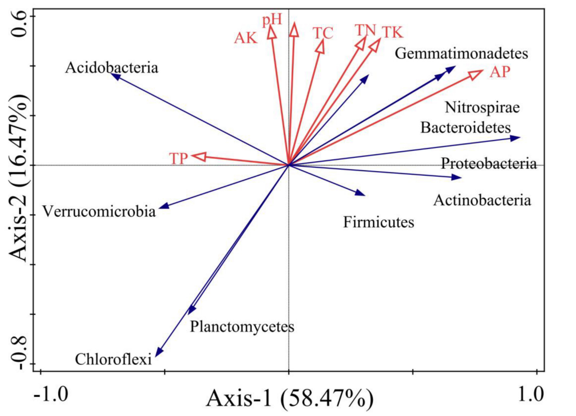

FIGURE 3
Redundancy analysis of bacterial community structure and soil chemical properties. The TP, TC, TN, TK, AK, and AP stand for total P, total C, total N, total K, available K and available P, respectively.

the growth of trees and heterophyllous forests (Shu et al., 2021). In this study, the soil physicochemical properties and the growth of Chinese fir were the best under lower thinning reserve density. A short-term of thinning study after 3 years revealed the soil total N increased with the increase of thinning reserve density in Chinese fir plantation (Wang Y. L. et al., 2021). This should be attributed to the effect of thinning on soil nutrition of fast-growing conifer species, which may be more favorable for nutrient accumulation in low-density stands. The soil nutrient content decreased with the increase of forest density, and that the low soil physicochemical properties and medium density of forest were better than those of high density of forest stands (Ding et al., 2021). The pH, total P and physical properties of the surface soil were not significantly affected by thinning intensity after 3 years of thinning on Chinese fir plantation, which may be caused by short-term thinning effect, which is consistent with the results of this study (Xu et al., 2019).

Stand density not only affects the growth of trees, but also significantly affects the growth of underplanted species. With the growth of four broad-leaved trees gradually decreasing as the density of the thinning reserve increased, and the best growth being at 900 stems ha^{-1}. The growth rates of *M. macclureiand* and *S. superba* were significantly higher than those of *P. zhennan* and *T. odorum* when the thinning reserve density was 900 and 1,200 stems ha^{-1}. However, the different underplanted tree species can also affect soil physicochemical properties through their litter input and root exudates (Mayer et al., 2020). Thinning and interplanting not only have an effect on the physicochemical properties of plantations, but also have a significant effect on the rhizosphere soil physicochemical properties of broad-leaved trees underplanted in plantation (Huang et al., 2021). Huang et al. (2021) demonstrated that interplanting of three broad-leaved tree species, *Castanopsis hystrix*, *Mytilaria laosensis,* and *M. macclureiand* under different thinning intensity treatments of eucalyptus plantation improve the nutrient content of eucalyptus continuous cropping forest soil to a certain extent, and the modified forest stands with low stand density have high contents of organic matter, total P, total N, available P, available N and available K. In this study, the rhizosphere soil nutrients of the four broad-leaved trees were the highest under low stand density level (900 stems ha^{-1}). The available P, total N, total C and total K content of the four broad-leaved trees decreased with the increase of thinning reserve density. The rhizosphere soil nutrients of *T. odorum* decrease with increasing thinning reserve density, and it grows better at low thinning reserve density, consistent with its biological preference for better light and warmer climates. We believe that the differences in rhizosphere physical and chemical properties among different underplanted broad-leaved tree species could be due to the interspecific differences in root respiration and nutrient uptake among different tree species, resulting in the quantities and quality of litter and root exudates differences. This, in turn, results in changes of bacterial community structure and microbial diversity in rhizosphere soil (Xu M. P. et al., 2021). Thus, thinning and interplanting significantly affected the nutrients of the rhizosphere soil of broad-leaved trees, indicating that these two tending measures had a significant impact on improving the physicochemical properties of rhizosphere soil in Chinese fir plantation.

The amount and nutrient composition of litter and root exudates produced by different broad-leaved tree species are different, so also the litter decomposition and nutrient release rates, which has a selective stimulating effect on soil microbial growth, thereby affecting the microbial community structure and diversity (Zhang et al., 2021). In this study, there were six main types of bacteria in the rhizosphere soil of the four broad-leaved trees, and the abundance of Acidobacteria, Proteobacteria and Chloroflexi were significantly higher across different thinning reserve densities than the other bacterial phyla, which could be related to the larger width of the ecological niche and the low impact on the environment (Xu et al., 2020). Moreover, Acidobacteria has a strong ability to adapt to the environment, and most of them are acidophils (Kalam et al., 2020). As a fast-growing conifer species with continuous planted in the acidic red soil area of south China, the abundance of the Acidobacteria in soil is reasonable. The relative abundance of Acidobacteria in the rhizosphere soil of *P. zhennan* was significantly higher than that of other broad-leaved trees under different thinning reserve densities, which may be due to the secretion of more acidic substances such as organic acids and protons into the rhizosphere soil. The relative abundance of Acidobacteria decreased with the increase of thinning reserve density in the rhizosphere of *T. odorum*, while the relative abundance of Acidobacteria showed the opposite trend, indicating that the Acidobacteria in the rhizosphere of *T. odorum* and *M. macclureiand* were more sensitive to thinning response.

4.2. Relationship between soil chemical properties and bacterial community

Rhizosphere soil bacterial community structure and diversity are influenced by environmental factors, which focus on the rhizosphere nutrition, pH and carbon source (Gao et al., 2019). In this study, there was a clear correlation between the soil bacterial community diversity and structure and the chemical properties of the rhizosphere soils of the four broad-leaved trees. The soil bacterial diversity of the rhizosphere soils was significantly positively correlated with available K and total N content. Studies

TABLE 7 Correlations between rhizosphere soil chemical properties of four broad-leaved trees planted under different stocking densities and soil bacterial diversity.

Index	Chao1 index	Observed species number	PD_whole_tree index	Shannon index	Available K	Available P	Total N	Total C	Total P	Total K	pH
Chao1 index	1										
Observed species number	0.97**	1									
PD_whole_tree index	0.96**	0.99**	1								
Shannon index	0.87**	0.94**	0.95**	1							
Available K	0.42	0.54	0.54	0.70*	1						
Available P	0.51	0.58*	0.580*	0.64*	0.46	1					
Total P	0.35	0.51	0.48	0.63*	0.83**	0.79**	1				
Total N	0.47	0.59*	0.56	0.72**	0.88**	0.91**	0.929**	1			
Total C	0.28	0.23	0.23	0.16	0.20	0.03	−0.15	0.02	1		
Total K	0.39	0.56	0.53	0.65*	0.82**	0.67*	0.97**	0.86**	−0.18	1	
pH	0.20	0.23	0.26	0.19	−0.14	−0.23	−0.26	−0.32	−0.07	−0.12	1

*Indicate significant influence at $p < 0.05$ and **indicate significant influence at $p < 0.01$.

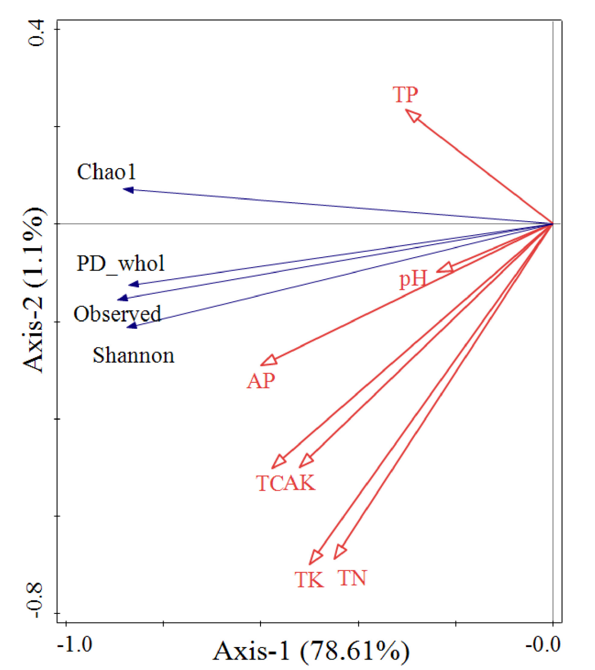

FIGURE 4
Redundancy analysis of bacterial diversity and soil chemical properties. The TP, TC, TN, TK, AK, and AP stand for total P, total C, total N, total K, available K and available P, respectively.

on the environmental adaptability of bacterial communities in rice rhizosphere soil showed that available K played a decisive role in regulating bacterial community assemblage (Tian et al., 2022). The study on *Camellia sinensis* rhizosphere soil from Qinling Mountains revealed N content had the greatest effect on the bacterial diversity at genus level, and C, K and pH were positively correlated with Pedobacter and Mucilaginibacter genera (Wang M. J. et al., 2021). However, our results revealed the relative abundance of Acidobacteria and Proteobacteria positively correlated with total N while the relative abundance of Chloroflexi showed a significant negative correlation with total N. Studies on the soil bacterial diversity of four pinus species forests revealed that Acidobacteria was correlated with pH, and the Chloroflexi was correlated with total N (Deng et al., 2019). Fei et al. (2020) also found that the relative abundance of Proteobacteria was positively correlated with the soil total N content. In this study, the total N content was the highest at lower thinning reserve density, and the relative abundance of Proteobacteria was also the highest. The soil in stands with intermediate (1,200 stems ha^{-1}) and high (1,875 stems ha^{-1}) density is poorer, and the relative abundance of the Chloroflexi was higher. In general, the soil available K and total N content has an important effect on rhizosphere bacterial community composition.

The available P content of the rhizosphere soil of the four broad-leaved trees significantly positively correlated with bacteria diversity indices, mainly the number of species, the PD_whole_tree index and the Shannon index. The results of redundancy analysis also showed that the rhizosphere bacterial diversity of four broad-leaved trees was mainly affected by soil available P. It is consistent with previous study that demonstrated a significant positive correlation between available P in subtropical Chinese fir soil and various microbial communities (Guo et al., 2022). The Chinese fir is continuous planted in the subtropical red soil area, where the soil is strongly aluminized and strongly acidic with the pH 4.0–5.5. Most of the available P is fixed by Fe, Al, etc., forming Fe-P, Al-P that are difficult to use by the plant, thus it is the main limiting factor for Chinese fir plantation productivity (Wu et al., 2011). In this study, the available P was revealed as the main environmental factor affecting the community structure of four broad-leaved tree rhizosphere bacteria. In forest ecosystems, the availability of P in soil depends on the mineralization, desorption and release, and the content of availability of P in different soil types and vegetation types varies greatly (Wang et al., 2020). The available P content had a significant effect on bacterial diversity in Chinese fir soil, and bacterial diversity in soil was positively correlated with AP content (Fei et al., 2020). Ding et al. (2018) found that the available P content in the rhizosphere soil of four different tree species in the Yellow River Delta was different, and the flavonoids, phenolic compounds citric acid, malic acid, oxalic acid and ferulic acid in the root exudates of different tree species were considerably different, which then led to differences in bacterial diversity and structure of rhizosphere soil. The symbiosis of different broad-leaved tree species with mycorrhiza (Lu et al., 2022), litter decomposition (Zhang H. et al., 2019) and root exudates (Xia et al., 2019) can also affect the availability of soil P in the rhizosphere (Hu et al., 2006). The carbon and nitrogen nutrients secreted by plant rhizosphere and pH of rhizosphere effectively change the composition of rhizosphere bacteria, but the P solution of rhizosphere soil bacteria can also provide an important source of available P for plant rhizosphere, and this interactive symbiotic relationship affects the composition of plant rhizosphere bacterial community (Ding et al., 2017; Bu et al., 2020; Bulgarelli et al., 2022). Therefore, soil available P content could have an important impact on the bacterial diversity in the rhizosphere of broad-leaved trees, and is the main environmental factor affecting the bacterial community structure in the rhizosphere of these four broad-leaved trees planted under different densities of Chinese fir plantation.

5. Conclusion

The results in the present study demonstrated that the height and ground diameter of *S. superba* and *T. odorum* decreased with the increase of density. Planting broad-leaved trees under different stand densities. Rhizosphere soil nutrient content and bacterial community vary among the stocking density of the original forest plantation and species underplanted, the contents of total K, available K and available P in 900 stems ha^{-1} stand of Chinese fir plantation were significantly higher than 1,200 stems ha^{-1} and 1,875 stems ha^{-1}. The rhizosphere soils of the four broad-leaved trees showed significant differences in the contents of total C, total N, total K, available K and available P, while the highest content was found under 900 stems ha^{-1}. Compared with *T. odorum* and *P. zhennan*, Chinese fir plantations planted with *S. superba* and *M. macclurei* had higher rhizosphere soil nutrient content. The rhizosphere soil bacterial diversity indices of *S. superba*, *P. zhennan* and *T. odorum* were significantly different at different densities, but there was no significant difference in *M. macclurei.* The rhizosphere soil bacterial diversity of *P. zhennan* increased with the increase of thinning retention density, but that in *T. odorum* showed the opposite trend. Acidobacterium, Proteobacterium, and Chloroflexi were the dominant bacterial phyla with relative abundances greater than 12%. The soil available P content is an important factor influencing the structure of bacterial communities, and the bacterial diversity index is positively correlated with the available P content of rhizosphere soils. Overall, low stocking density (900 stems ha^{-1}) is more suitable for cultivating large diameter woods of Chinese fir, and planting of *M. macclurei* and *S. superba* under Chinese fir plantation will be helpful for tree growth and maintaining soil fertility and bacterial diversity to realize sustainable management of Chinese fir plantation.

Data availability statement

The datasets presented in this study can be found in online repositories. The names of the repository/repositories and accession number(s) can be found below: https://www.ncbi.nlm.nih.gov/- PRJNA918639.

Author contributions

XM and ML: conceptualization. LW and ML: formal analysis and visualization. ML: funding acquisition and supervision. LW, YS, and QX: investigation. LW, YS, JL, and ML: methodology. LW, YS, and JL: validation. LW: writing—original draft. ML and MT: writing—review and editing. All authors contributed to the article and approved the submitted version.

Funding

This work was financially supported by the National Key Research and Development Program of China (2021YFD2201304).

Acknowledgments

We are grateful for Jing Liu and Mingzhen Zhao for valuable discussion and their assistance during the field work.

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.

References

Ai, C., Sun, J. W., Wang, X. B., Liang, G. Q., He, P., and Zhou, W. (2015). Research progress on the relationship between plant inter-root sedimentation and soil microorganisms. *J. Plant Nutr. Fert.* 21, 1343–1351. doi: 10.11674/zwyf.2015.0530

An, R., Ma, F. Y., Cui, H. R., Qin, G. H., Huang, Y. L., and Tian, Q. (2019). Analysis of bacterial community structure and diversity characteristics of mixed forest of *Robinia pseudoacacia* and *Ailanthus altissima* and there pure forest in the Yellow river Delta. *Acta Ecol. Sin.* 39, 7960–7967. doi: 10.5846/stxb201809041886

Bu, W. S., Gu, H. J., Zhang, C. C., and Chen, F. S. (2020). Mixed broadleaved tree species increases soil phosphorus availability but decreases the coniferous tree nutrient concentration in subtropical China. *Forests* 11:461. doi: 10.3390/f11040461

Bulgarelli, R. G., Leite, M. F. A., De Hollander, M., Mazzafera, P., Andrade, S. A. L., and Kuramae, E. E. (2022). Eucalypt species drive rhizosphere bacterial and fungal community assembly but soil phosphorus availability rearranges the microbiome. *Sci. Total Environ.* 836:155667. doi: 10.1016/j.scitotenv.2022.155667

Deng, J. J., Zhou, Y. B., Yin, Y., Wei, Y. W., Qin, S. J., and Zhu, W. X. (2019). Characterization of soil bacterial community diversity in a typical planted coniferous forest in the mountainous region of Liaodong. *Acta Ecol. Sin.* 39, 997–1008. doi: 10.5846/stxb201803090471

Ding, K., Zhang, Y., Liu, H. Y., Yang, X., Zhang, J., and Tong, Z. K. (2022). Soil bacterial community structure and functions but not assembly processes are affected by the conversion from monospecific *Cunninghamia lanceolata* plantations to mixed plantations. *Appl. Soil Ecol.* 185:104775. doi: 10.1016/J.APSOIL.2022.104775

Ding, K., Zhang, Y. T., Zhang, J. H., Chai, X., Zhou, S. S., and Tong, Z. K. (2021). Effects of different densities of fir forests on understory vegetation and soil microbial community structure. *Chin. J. Plant Ecol.* 45, 62–73. doi: 10.17521/cjpe.2020.0158

Ding, X. J., Huang, Y. L., Jing, R. Y., Ma, F. Y., An, R., Tian, Q., et al. (2018). Structure and diversity of soil bacteria in four plantation forests in the Yellow River Delta based on high-throughput sequencing. *Acta Ecol. Sin.* 38, 5857–5864. doi: 10.5846/stxb201703260522

Ding, X. J., Jing, R. Y., Huang, Y. L., Chen, B. J., and Ma, F. Y. (2017). Structure and diversity of inter- and non-inter-rhizosphere bacteria of *Acacia japonica* in the Yellow River Delta. *J. Soil Sci.* 54, 1293–1302. doi: 10.11766/trxb201703230510

Fei, Y. C., Wu, Q. Z., Lu, J., Ji, C. S., Zheng, H., Cao, S. J., et al. (2020). Effects of undergrowth vegetation management measures on the soil bacterial community structure of large diameter timber plantation of *Cunninghamia lanceolata*. *J. Appl. Ecol.* 31, 407–416. doi: 10.13287/j.1001-9332.202002.035

Feng, Y. H., Schmid, B., Loreau, M., Forrester, D. I., Fei, S. L., Zhu, J. X., et al. (2022). Multispecies forest plantations outyield monocultures across a broad range of conditions. *Science* 376, 865–868. doi: 10.1126/SCIENCE.ABM6363

Fu, X. L., and Meinzer, F. C. (2019). Metrics and proxies for stringency of regulation of plant water status (iso/anisohydry): A global data set reveals coordination and trade-offs among water transport traits. *Tree Physiol.* 39, 122–134. doi: 10.1093/treephys/tpy087

Gao, Z. L., Ida, K., Stefan, G., George, K., and Alexandre, J. (2019). Protists: Puppet masters of the rhizosphere microbiome. *Trends Plant Sci.* 24, 165–176. doi: 10.1016/j.tplants.2018.10.011

Guo, J. H., Feng, H. L., Pierce, M., Liu, Q. Y., Xu, X., Pan, C., et al. (2023). Species mixing improves soil properties and enzymatic activities in Chinese fir plantations: A meta-analysis. *Catena* 220:106723. doi: 10.1016/j.catena.2022.106723

Guo, W., Gao, L. W., Peng, Z. W., Wei, M. Q., Wang, Y. Z., Hu, Y. L., et al. (2022). Characteristics of microbial community in rhizosphere and non-rhizosphere Soil of *Cunninghamia lanceolata* plantation with different stand ages. *Soil Water Conserv. Res.* 29, 260–267. doi: 10.13869/j.cnki.rswc.2022.06.002

Gurevitch, J. (2022). Managing forests for competing goals. *Science* 376, 792–793. doi: 10.1126/SCIENCE.ABP8463

Han, X. M., Huang, Z. Y., Cheng, F., and Yang, M. (2020). Physical and chemical properties and microbial community characteristics of the rhizosphere soil of the Wangtianshu plantation. *J. Appl. Ecol.* 31, 3365–3375. doi: 10.13287/j.1001-9332.202010.019

Hu, Y. L., Wang, S. L., and Zeng, D. H. (2006). Effects of single Chinese fir and mixed leaf litters on soil chemical, microbial properties and soil enzyme activities. *Plant and Soil* 282, 379–386. doi: 10.1007/s11104-006-0004-5

Huang, M. Y., Liang, Y. F., Su, F. C., Zhu, Y. L., Li, Z. H., Liu, L. L., et al. (2021). Effects of interplanting native tree species on stand growth and soil physical and chemical properties under different thinning intensities of Eucalyptus. *J. Cent. South Univ. For. Technol.* 41, 81–90. doi: 10.14067/j.cnki.1673-923x.2021.06.009

Jiang, Y. M., Chen, C. R., Xu, Z. H., and Liu, Y. Q. (2012). Effects of single and mixed species forest ecosystems on diversity and function of soil microbial community in subtropical China. *J. Soils Sediments* 12, 228–240. doi: 10.1007/s11368-011-0442-4

Kalam, S., Basu, A., Ahmad, I., Sayyed, R. Z., ElEnshasy, H. A., Dailin, D. J., et al. (2020). Recent understanding of soil acidobacteria and their ecological significance: A critical review. *Front. Microbiol.* 11:580024. doi: 10.3389/fmicb.2020.580024

Lei, J., Wu, H. B., Li, X. Y., Guo, W. F., Duan, A. G., and Zhang, J. G. (2023). Response of rhizosphere bacterial communities to near-natural forest management and tree species within Chinese fir plantations. *Microbiol. Spectr.* 23:e0232822. doi: 10.1128/spectrum.02328-22

Liang, Y., Ming, A., He, Y., Luo, Y., Tan, L., and Qin, L. (2021). Structure and function of soil bacterial communities in a mixed Sargassum-Redbud forest and its pure stands in tropical South Asia. *J. Appl. Ecol.* 32, 878–886. doi: 10.13287/j.1001-9332.202103.37

Liu, J., Zhao, M. Z., Wang, L. Y., Chen, C. Y., Lin, K. M., and Li, M. (2021). Effects of logging retention density and seed set on timber species structure of fir middle-aged forests. *J. Forest Environ.* 41, 593–600. doi: 10.13324/j.cnki.jfcf.2021.06.005

Liu, J. W., Li, X. Z., and Yao, M. J. (2021). Research progress on assembly of plant rhizosphere microbial community. *Acta Microbiol. Sin.* 61, 231–248. doi: 10.13343/j.cnki.wsxb.20200154

Liu, S., Liu, X. S., Zhu, X. C., Sheng, K. Y., Guo, X. M., and Zhang, W. Y. (2017). Rhizosphere effect and fertility evaluation of soil nutrients and enzyme activities of Redwood Chenshan. *J. Plant Nutr. Fert.* 23, 492–501. doi: 10.11674/zwyf.16195

Liu, S. R., Yang, Y. J., and Wang, F. (2018). Development strategy and management countermeasures of planted forests in China: Transforming from timber-centered single objective management towards multi-purpose management for enhancing quality and benefits of ecosystem services. *Acta Ecol. Sin.* 38, 1–10. doi: 10.5846/stxb201712072201

Lu, N. N., Zhang, P., Wang, P., Wang, X. J., Ji, B. M., and Mu, J. P. (2022). Environmental factors affect the arbuscular mycorrhizal fungal community through the status of host plants in three patterns of Chinese fir in southern China. *Glob. Ecol. Conserv.* 36:e02121. doi: 10.1016/J.GECCO.2022.E02121

Mayer, M., Prescott, C. E., Abaker, W. E. A., Augusto, L., Cecillon, L., Ferreira, G. W. D., et al. (2020). Tamm Review: Influence of forest management activities on soil organic carbon stocks: A knowledge synthesis. *For. Ecol. Manag.* 466:118127. doi: 10.1016/j.foreco.2020.118127

Pretzsch, H., Poschenrieder, W., Uhl, E., Brazaitis, G., Makrickiene, E., and Calama, R. (2021). Silvicultural prescriptions for mixed-species forest stands. A European review and perspective. *Eur. J. For. Res.* 140, 1267–1294. doi: 10.1007/s10342-021-01388-7

Shu, W. W., Lu, L. H., Li, H., Nong, Y., He, R. M., Chen, H., et al. (2021). Effect of stand density on understory vegetation and soil properties in fir plantation forests. *Acta Ecol. Sin.* 41, 4521–4530. doi: 10.5846/stxb201909231988

Tian, G. L., Qiu, H. S., Li, D. W., Wang, Y. T., Zhen, B., Li, H. Z., et al. (2022). Little environmental adaptation and high stability of bacterial communities in rhizosphere rather than bulk soils in rice fields. *Appl. Soil Ecol.* 169:104183. doi: 10.1016/J.APSOIL.2021.104183

Wang, C. Q., Xue, L., Dong, Y. H., Hou, L. Y., Wei, Y. H., and Jiao, R. Z. (2019). Responses of soil microbial community structure to stand densities of Chinese fir plantations. *J. For. Res.* 24, 1–6. doi: 10.1080/13416979.2019.1601652

Wang, D., and Shen, W. X. (2022). Carbon storage calculation and carbon sequestration potential analysis of main tree species in China. *J. Nanjing For. Univ.* 46, 11–19. doi: 10.12302/j.issn.1000-2006.202109014

Wang, K. F., Qiu, Z. L., Zhang, M., Li, X. Y., Fang, X., Zhao, M. Y., et al. (2022). Effect of afforestation mode on rhizosphere soil physicochemical properties and bacterial community structure of two major tree species in Xiong'an New Area. *For. Ecol. Manag.* 520:120361. doi: 10.1016/j.foreco.2022.120361

Wang, M. J., Sun, H. Y., Xu, L. O., and Xu, Z. M. (2021). Bacterial diversity in tea plant (*Camellia sinensis*) rhizosphere soil from Qinling Mountains and its relationship with environmental elements. *Plant Soil* 460, 403–415. doi: 10.1007/S11104-020-04822-8

Wang, Q. K., and Wang, S. L. (2008). Soil microbial properties and nutrients in pure and mixed Chinese fir plantations. *J. For. Res.* 19, 131–135. doi: 10.1007/s11676-008-0022-7

Wang, T., Wan, X. H., Wang, L., Zou, B. Z., Wang, S. R., and Huang, Z. Q. (2020). Effects of broadleaf tree creation on different levels of soil phosphorus fraction and effectiveness in fir harvesting sites. *J. Appl. Ecol.* 31, 1088–1096. doi: 10.13287/j.1001-9332.202004.006

Wang, Y. L., Song, C. S., Peng, L. H., Cui, C. W., Zheng, M. M., Lin, K. M., et al. (2021). Effects of thinning on soil carbon and nitrogen fractions in a *Cunninghamia lanceolata* plantation. *J. Soil Water Conserv.* 35, 204–212. doi: 10.13870/j.cnki.stbcxb.2021.05.028

Wu, P. F., Ma, X. Q., Mulualem, T. M., Chen, W. C., Wang, A. Q., Liu, L. A., et al. (2011). Root morphological plasticity and biomass production of two Chinese fir clones with high phosphorus efficiency under low phosphorus stress. *Can. J. For. Res.* 41, 228–234. doi: 10.1139/X10-198

Wu, W. X., Zhou, X. G., Wen, Y. G., and Li, X. Q. (2019). Coniferous-broadleaf mixture increases soil microbial biomass and functions accompanied by improved stand biomass and litter production in subtropical China. *Forests* 10:879. doi: 10.3390/f10100879

Wu, Z. J., Duan, X. Q., Li, W. Q., Chen, F. S., Liu, Y. Q., and Fang, X. M. (2022). Effects of mixing on nitrogen mineralization and microbial characteristics of subtropical coniferous rhizosphere soil. *Acta Ecol. Sin.* 42, 8414–8424. doi: 10.5846/stxb202110072766

Xia, Z. C., Yu, L., He, Y., Korpelainen, H., and Li, C. Y. (2019). Broadleaf trees mediate chemically the growth of Chinese fir through root exudates. *Biol. Fert. Soils* 55, 737–749. doi: 10.1007/s00374-019-01389-0

Xu, H. D., Yu, M. K., and Cheng, X. R. (2021). Abundant fungal and rare bacterial taxa jointly reveal soil nutrient cycling and multifunctionality in uneven-aged mixed plantations. *Ecol. Indic.* 129:107932. doi: 10.1016/J.ECOLIND.2021.107932

Xu, M. P., Jian, J. N., Wang, J. Y., Zhang, Z. J., Yang, G. H., Han, X. H., et al. (2021). Response of root nutrient resorption strategies to rhizosphere soil microbial nutrient utilization along *Robinia pseudoacacia* plantation chronosequence. *For. Ecol. Manag.* 489:119053. doi: 10.1016/j.foreco.2021.119053

Xu, R., Wang, L., Zhang, J., Zhou, J., Cheng, S. D., Tigabu, M. L., et al. (2022). Growth rate and leaf functional traits of four broad-leaved species underplanted in Chinese fir plantations with different tree density levels. *Forests* 13, 308–308.

Xu, X. L., Sun, Y. J., Zhou, H., Zhang, P., Hu, Y., and Wang, X. J. (2019). Effects of thinning intensity on understory growth and soil properties in Chinese fir plantation. *Sci. Silvae Sin.* 55, 1–12. doi: 10.11707/j.1001-7488.20190301

Xu, Y. X., Du, A. P., Wang, Z. C., and Wu, L. C. (2020). Effects of different rotation periods of Eucalyptus plantations on soil physiochemical properties, enzyme activities, microbial biomass and microbial community structure and diversity. *For. Ecol. Manag.* 456:117683. doi: 10.1016/j.foreco.2019.117683

Zhang, H., Zhou, G. M., Wang, Y. X., Bai, S. B., Sun, Z. B., Berninger, F., et al. (2019). Thinning and species mixing in Chinese fir monocultures improve carbon sequestration in subtropical China. *Eur. J. For. Res.* 138, 433–443. doi: 10.1007/s10342-019-01181-7

Zhang, X., Gao, G., Wu, Z., Wen, X., Zhong, H., Zhong, Z., et al. (2019). Agroforestry alters the rhizosphere soil bacterial and fungal communities of moso bamboo plantations in subtropical China. *Appl. Soil Ecol.* 143, 192–200. doi: 10.1016/j.apsoil.2019.07.019

Zhang, Y. T., Ding, K., Yrjälä, K., Liu, H. Y., Tong, Z. K., and Zhang, J. H. (2021). Introduction of broadleaf species into monospecific *Cunninghamia lanceolata* plantations changed the soil Acidobacteria subgroups composition and nitrogen-cycling gene abundances. *Plant Soil* 467, 1–18. doi: 10.1007/S11104-021-05014-8

Zou, B. Z. (2020). Effects of thinning and interplanting on physical and chemical properties of soil and microorganisms in Chinese fir plantation. *J. Subtrop. Resour. Environ.* 15, 40–46. doi: 10.19687/j.cnki.1673-7105.2020.04.005