

Impact of *Robinia pseudoacacia* stand conversion on soil bacterial communities and soil properties

Kun Li

shandong agricultural university

Xu Han

shandong agricultural university

Ruiqiang Ni

shandong agricultural university

Ge Shi

shandong agricultural university

Sergio de-Miguel

Universitat de Lleida

Chuanrong Li (✉ chrlisd@126.com)

shandong agricultural university <https://orcid.org/0000-0003-3933-6436>

Weixing Shen

mount tai scenic spot management committee

Yikun Zhang

mount tai scenic spot management committee

Xingzhong Zhang

mount tai scenic spot management committee

Research

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Abstract

Background: *Robinia pseudoacacia* is a widely planted pioneer tree species in reforestations on barren mountains in northern China. Because of its nitrogen-fixing ability, it can play a positive role in soil and forest restoration. After clear-cutting of planted stands, *R. pseudoacacia* stands become coppice plantations. The impacts of shifting from seedling to coppice plantations on soil bacterial community and soil properties have not been well described. This study aims to quantify how soil properties and bacterial community composition vary between planted seedling versus coppice stands.

Methods: Three 20 × 20 m plots were randomly selected in each seedling and coppice stand. The bulk soil and rhizosphere soil were sampled in the nine above-mentioned sample plots in the summer of 2017. Bulk soil was sampled at 10 cm from the soil surface using a soil auger. Rhizosphere soil samples were collected by brush. The soil samples were transported to the laboratory for chemical analysis and bacterial community composition and diversity was obtained through DNA extraction, 16S rRNA gene amplification and high throughput sequencing.

Results: The results showed that, compared to seedling plantations, soil quality decreased significantly in coppice stands, but without affecting soil exchangeable Mg^{2+} and K^{2+} . Total carbon (C) and nitrogen (N) were lower in the rhizosphere than in bulk soil, whereas nutrient availability showed an opposite trend. The conversion from seedling to coppice plantations was also related to significant differences in soil bacterial community structure and to the reduction of soil bacterial α -diversity. Principal component analysis (PCA) showed that, bacterial community composition was similar in both bulk and rhizosphere soils in second generation coppice plantations. Specially, the conversion from seedling to coppice increased the relative abundance of *Proteobacteria* and *Rhizobium*, but reduced that of *Actinobacteria*, which may result in a decline of soil nutrient availability. Mantel tests revealed that C, N, Soil organic matter (SOM), nitrate nitrogen (NO_3^- -N) and available phosphorus positively correlated with bacterial community composition, while a variation partition analysis (VPA) showed that NO_3^- -N explained a relatively greater proportion of bacterial distribution (15.12%), compared with C and SOM. Surprisingly, N showed no relationship with bacterial community composition, which may be related to nitrogen transportation.

Conclusions: The conversion from seedling to coppice stands reduced soil quality and led to spatial-temporal homogenization of the soil bacterial community structure in both the rhizosphere and bulk soils. Such imbalance in microbial structure can accelerate the decline of *R. pseudoacacia*. This may affect the role of *R. pseudoacacia* coppice stands in soil and forest restoration of barren lands in mountain areas.

Background

Black locust (*Robinia pseudoacacia*) is a leguminous tree which can rapidly fix nitrogen (N) from the atmosphere via *Rhizobium* (Zhang et al. 2019) and further alter soil properties by increasing mineral N (Medina-Villar et al. 2016). *R. pseudoacacia* is able to disperse quickly and colonize a broad range of

xeric habitats, including steep rocks or toxic man-made substrata (Cierjacks et al. 2013), and has been extensively naturalized in the temperate regions of North America, Europe, and Asia (Sabo, 2000; Lee et al. 2004; Vítková et al. 2017; Yang et al. 2019). Natural reproduction of *R. pseudoacacia* plantations is primarily vegetative through root suckering and stump sprouting, allowing vigorous regeneration after coppicing and disturbance (Peng et al. 2003). However, after two or three rotations, the productivity of *R. pseudoacacia* coppice plantations tends to decline (Cierjacks et al. 2013), which may further jeopardize its ecological role in soil and forest restoration.

Plant community structure and productivity in natural environments depends, among other factors, on soil nutrient availability and soil microbial communities (Reynolds, H. L., & Haubensak, K. A. 2009; Vitkova et al. 2015; Liu et al. 2018; Chen et al. 2020). Soil nutrient availability can alter soil processes catalyzed by soil microbial communities (Yang et al. 2016). Therefore, changes in soil microbial community composition can affect the plant community (Balota et al. 2013; Ma et al. 2018) and nutrient absorption by plants (Weidner et al. 2015; Zhang et al. 2018b). In turn, plants can directly and indirectly influence microbial communities environment by effect of root exudation (Sasse et al. 2018). So soil ecological transformation may provide a simple means of identifying stable state within the ecosystem (Macdonald et al. 2019).

Rhizosphere is a critical interface supporting the exchange of resources between plants and the surrounding soil environment, which provides microhabitats and niches for diverse microorganisms and microbial species (Philippot et al. 2013; Mendes et al. 2013). Rhizosphere microorganisms play a key role in plant growth and soil properties, especially in the rhizosphere niche (Philippot et al. 2013; Zhang et al. 2018a), which influences several plant physiological processes such as growth and energy metabolism affecting overall plant health (Fonseca et al. 2018). Generally, there are significant differences between rhizosphere and bulk soil microenvironments, the most obvious of which is that the higher nutrient content and root exudates in the rhizosphere contribute to improving soil carbon and nitrogen concentrations (Yin et al. 2018). Such differences may affect the composition of the rhizosphere microbial community (Neumann et al. 2014). Soil properties and their ecological processes provide a scientific basis for understanding the interaction between root physiological activity and soil physical and biological environments. At the same time, rhizosphere micro-ecology may be a key driver for predicting tree growth mechanisms.

Previous research has reported the high capacity of *R. pseudoacacia* for nitrogen fixation (Buzhdygan et al. 2016), and higher N mineralization and nitrification rates in black locust plantations compared to surrounding soils (Williard et al. 2005). Moreover, the excess of N can accumulate in the soil (Berthold et al. 2009) by means of root exudates, contributing to increasing soil fertility (Joëlle et al. 2010). The main nitrogen form uptaken by plants is inorganic nitrogen including nitrate and ammonium. *R. pseudoacacia* benefits from nitrogen fixation associated with symbiotic rhizobia in root nodules (Cierjacks et al. 2013). The reduction of soil N availability induces nodulation and biological nitrogen fixing of *R. pseudoacacia* in order to sustain the required nitrogen amounts for plant growth (Mantovani et al. 2015). Therefore,

both bacteria and N play an important role in the growth and development of *R. pseudoacacia* plantations.

With the development of *R. pseudoacacia* coppice plantations, unexpected problems have arisen in Mount Tai (China) forest ecosystems, including the decline of landscape quality, soil erosion and plant dwarfing, in line with previous research suggesting tree growth decline and trunk shape worsening (Geng et al. 2013). However, to date, most studies have attempted to investigate the effects of conversion from natural forests to plantations on soil properties, soil microbes and their community structure (Zhang et al. 2017; Yang et al. 2018). But there is a gap in knowledge concerning the effects of the transition from seedling plantations to coppice stands. Radtke et al. (2013) showed that repeated clear cuttings every 20–30 years favored the spread of *R. pseudoacacia*. Yet, the effects of shift from seedling to coppice plantations on soil properties and soil microbes are not yet well understood, and information is scarce. The aim of this study was to (1) shed light on the effects of shifting from seedling to coppice stands in black locust plantations on soil properties and soil bacterial community composition, especially *Rhizobium*, and (2) investigate the relationships between soil properties and bacterial community composition in seedling and coppice plantations, respectively. The study was performed in first generation seedling plantation stands (F), first generation coppice plantations (S) and second generation coppice plantations (T) in Mount Tai, China. We hypothesized that (1) the changes caused by the conversion of seedling to coppice stands lead to decline of soil quality, and to alterations in soil bacterial community composition, (2) nutrient availability plays an important role in shaping the bacterial community, and (3) the relative abundance of *Rhizobium* decreases in coppice plantations.

Materials And Methods

Study area

This study was conducted in Mount Tai region of Shandong Province, which is located in eastern China. The region is characterized by a typical temperature climate. The mean annual temperature is 12.8 °C, and the mean annual precipitation is 1124.6 mm. In the 1920s, *R. pseudoacacia* was introduced to Mount Tai because of its potential for soil and forest restoration. Afforestation was mainly conducted between 1956 and 1958 by seedling direct planting. However, with increasing timber demand for use in construction, seedling plantations were gradually harvested leading to naturally-regenerated coppice plantations. Nowadays, most *R. pseudoacacia* stands are coppice plantations, mainly distributed along an elevational gradient from 500 to 1000 meters above sea level, and southern aspects.

We selected three stands representing different *R. pseudoacacia* plantation types (Figure S1), namely, first generation seedling plantations (F, 36°16'45"N, 117°3'26"E), first generation coppice plantations (S, 36°16'40"N, 117°3' 21"E) and second generation coppice plantations (T, 36°16'40"N, 117°3' 22"E). The three forest stands were close to each other as shown in Figure S1, and therefore represented homogeneous conditions in terms of topography (i.e., slope 25° and southwestern aspect), previous land use (i.e., stands developed from barren land) and initial soil properties.

Sampling

Three 20 × 20 m plots were randomly selected in each seedling and coppice stand (i.e., a total of nine plots). The bulk soil and rhizosphere soil were sampled in the nine above-mentioned sample plots in the summer of 2017. Bulk soil was sampled at 10 cm from the soil surface by using a soil auger (length 50 cm, diameter 5 cm, volume 100 cm³). Rhizosphere soil samples were collected by brush (5 samples per plot). The soil samples were transported on ice to the laboratory, where they were sieved (mesh size 2 mm) and divided into two parts, one was air-dried and stored at room temperature prior to chemical analysis and the other was stored at -80°C for further analysis. Hereafter in this manuscript, FR, SR and TR refer to the rhizosphere of F, S and T, respectively; and FNR, SNR and TNR refer to bulk soil of F, S and T, respectively.

Analysis of soil physicochemical properties

Total soil carbon (C) and nitrogen (N) contents were measured by dry combustion in an Elemental Analyzer (Costech ECS4010, Italy). The soil nitrate (NO₃⁻-N) and ammonium (NH₄⁺-N) were extracted by shaking 20 g of fresh soil in 100 ml of 2M KCl solution for 1 h and were analyzed with continuous flow analytical system (AA3, German). Available N (A.N) was a sum of NO₃⁻-N and NH₄⁺-N. The available P in the soil was measured using the colorimetric method with 0.5M NaHCO₃ extraction, the total soil phosphorus (P) and available P (A.P) were measured with a continuous flow analytical system (AA3, German), and the soil organic matter (SOM) was measured using the K₂Cr₂O₇ method. The exchangeable cations (Ca²⁺, Mg²⁺ and K⁺) were measured using titration and atomic absorption spectroscopy (AAS, TAS-990MFG, China). Soil moisture was determined using the soil core method, and obtained by calculating the ratio of soil mass to total volume (g·cm⁻³) after oven-drying to a constant weight at 105 °C (Zhang et al. 2019). To better describe changes in soil properties, soil quality index (*SQI*) (Guo, 2019) was calculated.

DNA extraction, 16S rRNA gene amplification, and high throughput sequencing

Total genomic DNA from samples was extracted using CTAB method. 16S rRNA genes of distinct regions (16SV4-V5) were amplified using a specific primer with the barcode. All PCR reactions were carried out with Phusion® High-Fidelity PCR Master Mix (New England Biolabs). The 16S rRNA genes were analyzed to evaluate bacterial diversity using IlluminaHiSeq (Novogene Bioinformatics Technology Co., Ltd., Beijing, China).

Sequences were analyzed using QIIME software package (Quantitative Insights Into Microbial Ecology), and in-house Perl scripts were used to analyze alpha- (within samples) and beta- (among samples) diversities. We picked a representative sequence for each OTU and used the RDP classifier to annotate taxonomic information for each representative sequence (Wang et al. 2007).

Statistical analysis

Duncan's one-way ANOVA was conducted to examine differences in soil characteristics, *SQI* and relative abundance of *Rhizobioum* between bulk and rhizosphere soils. A T-test was conducted to examine differences in Shannon and Simpson indices between bulk and rhizosphere soils. These analyses were performed using SPSS 24.0 (IBM, USA). Principal component analysis (PCA) was conducted to test for differences in the OUT-based community composition using Bray-Curtis distance. The relationships between soil properties and dominant bacterial community composition (TOP 10) were determined using Spearman correlation analysis. Mantel-tests and variation partition analysis (VPA) were used to determine the relative importance of the measured soil properties in shaping soil bacterial community, which were calculated using the Bray-Curtis distance. These analysis were carried out using the "vegan" package of R software (Version 2.15.3). The graphics were drawn using Origin 2019.

Results

Impact of the conversion to coppice stands on soil quality

Soil nutrient contents diminished mostly from seedling to coppice plantations (Table 1). Soil characteristics varied considerably in both rhizosphere and bulk soil from F stands to T stands. Total C, N and NO_3^- -N concentration and SOM content in both the rhizosphere and bulk soil was significantly higher in seedling stands compared to first and second generation coppice stands. There were significant differences in P concentration in the rhizosphere and bulk soil. There were no statistically significant difference in available phosphorous (A.P) concentrations between FNR and SNR, but A.P concentration was significantly greater in FNR and SNR compared to TNR. No differences were found regarding exchangeable ions in bulk soil between seedling and coppice plantation, while significantly higher concentrations appeared in the rhizosphere of coppice plantations compared to seedling stands. The *SQI* of both bulk soil and rhizosphere was higher in seedling plantations than in coppice stands, i.e., the highest *SQI* value (29.14) was found in the rhizosphere of seedling stands whereas the lowest *SQI* (24.33) was found in the bulk soil of second generation coppice stands.

Table 1

Bulk soil and rhizosphere soil properties (mean \pm standard error) of the three types of *Robinia pseudoacacia* plantations following forest conversion from seedling to coppice stands.

	Rhizosphere			Bulk soil		
	FR	SR	TR	FNR	SNR	TNR
N/%	0.38 \pm 0.03a	0.32 \pm 0.01b	0.33 \pm 0.01b	0.43 \pm 0.02a	0.32 \pm 0.01c	0.36 \pm 0.02b
C/%	3.80 \pm 0.27a	3.31 \pm 0.14b	3.50 \pm 0.15b	4.56 \pm 0.16a	3.33 \pm 0.16c	3.77 \pm 0.30b
P/%	1.58 \pm 0.13b	1.88 \pm 0.05a	1.63 \pm 0.08b	1.66 \pm 0.05a	0.93 \pm 0.03b	0.85 \pm 0.02c
C/N	10.14 \pm 0.18b	10.22 \pm 0.31b	10.57 \pm 0.22a	10.52 \pm 0.26a	10.35 \pm 0.47a	10.51 \pm 0.17a
C/P	2.31 \pm 0.30a	1.76 \pm 0.11c	2.15 \pm 0.18b	2.75 \pm 0.10c	3.59 \pm 0.24b	4.43 \pm 0.28a
N/P	0.24 \pm 0.03a	0.17 \pm 0.01c	0.20 \pm 0.01b	0.26 \pm 0.01c	0.35 \pm 0.03b	0.42 \pm 0.02a
NO ₃ ⁻ -N (mg/kg)	69.06 \pm 1.53a	63.29 \pm 1.63b	59.50 \pm 1.84c	67.20 \pm 2.99a	60.52 \pm 1.39b	60.71 \pm 2.14b
NH ₄ ⁺ -N (mg/kg)	58.60 \pm 1.24a	58.81 \pm 1.62a	55.20 \pm 2.42b	45.99 \pm 4.02b	54.25 \pm 0.43a	39.41 \pm 1.48c
AN (mg/kg)	127.66 \pm 2.27a	122.10 \pm 2.95a	114.70 \pm 4.10b	113.19 \pm 4.19a	114.77 \pm 1.36b	100.12 \pm 2.87c
AP (mg/kg)	16.93 \pm 1.26a	11.18 \pm 0.9b	8.35 \pm 0.98c	14.41 \pm 0.91a	14.24 \pm 1.08a	9.60 \pm 1.27b
SOM (g/kg)	64.91 \pm 0.92a	62.84 \pm 1.29b	50.73 \pm 1.05c	61.93 \pm 1.78a	51.69 \pm 0.58b	46.70 \pm 1.47c
Exchangeable Ca (cmol/kg)	48.74 \pm 9.48b	44.63 \pm 11.21b	65.83 \pm 12.46a	61.78 \pm 13.15a	51.01 \pm 7.96a	65.26 \pm 11.27a
Exchangeable Mg (cmol/kg)	12.09 \pm 1.60b	12.01 \pm 1.17ab	13.17 \pm 0.75a	11.68 \pm 0.93a	12.66 \pm 0.78a	13.07 \pm 0.74a
Exchangeable K (cmol/kg)	0.71 \pm 0.05ab	0.70 \pm 0.03b	0.76 \pm 0.05a	0.72 \pm 0.05a	0.86 \pm 0.28a	0.72 \pm 0.07a

Mean values \pm SE (n = 5) are shown. FR, SR and TR represent the rhizosphere of seedling plantations, first generation coppice plantations and second generation coppice plantations, respectively; FNR, SNR and TNR represent bulk soil of seedling plantations, first generation coppice plantations and second generation coppice plantations, respectively. Different lowercase letters indicate significant differences in soil properties among the bulk soil or rhizosphere in different *R. pseudoacacia* plantations ($p < 0.05$).

	Rhizosphere			Bulk soil		
Soil moisture %				7.66 ± 0.61b	13.28 ± 0.52a	13.95 ± 0.60a
Soil quality index	29.14 ± 0.36a	27.42 ± 0.33b	26.72 ± 0.64b	27.59 ± 0.29a	26.14 ± 0.29b	24.33 ± 0.97b

Mean values ± SE (n = 5) are shown. FR, SR and TR represent the rhizosphere of seedling plantations, first generation coppice plantations and second generation coppice plantations, respectively; FNR, SNR and TNR represent bulk soil of seedling plantations, first generation coppice plantations and second generation coppice plantations, respectively. Different lowercase letters indicate significant differences in soil properties among the bulk soil or rhizosphere in different *R. pseudoacacia* plantations (p < 0.05).

Differences in soil bacterial abundance and diversity

In total, we obtained 2,562,381 sequences and 2,358,270 combined sequences were obtained. The read lengths ranged from 211 to 407 bp, with an average of 373 bp. When grouped at the 97% similarity level, there were 42 different phylotypes in all soils. The dominant groups (TOP 10) across all soil samples (Fig. 1A) were *Proteobacteria* (30.54%), *Actinobacteria* (25.30%), *Acidobacteria* (13.94%), *Firmicutes* (7.19%), *Verrucomicrobia* (6.86%), *Planctomycetes* (5.22%), *Chloroflexi* (3.87%), *Gemmatimonadetes* (2.37%), *Bacteroidetes* (1.14%), and *Cyanobacteria* (0.40%), and these groups accounted for more than 96.43% of the bacterial sequences. Moreover, the Shannon and Simpson indices for alpha bacterial diversity declined from seedling to coppice plantations and from first-rotation to second-rotation coppice plantations by 2% and 0.2%, respectively (Table 2).

Table 2

Differences in bacterial α-diversity in the rhizosphere and bulk soil between seedling and coppice R. pseudoacacia plantations.

	FR	SR	TR	FNR	SNR	TNR
Shannon	9.2205 ± 0.0473a	9.1055 ± 0.0119bc	9.1803 ± 0.0155ab	9.2186 ± 0.0482a	9.0159 ± 0.0329c	9.0336 ± 0.0339c
Simpson	0.9954 ± 0.0001a	0.9949 ± 0.0001ab	0.9945 ± 0.0002b	0.9954 ± 0.0003a	0.9945 ± 0.0002b	0.9934 ± 0.0004c

At the genus level (Fig. 1B), the six most abundant bacteria (≥ 1%) were *Bacillus* (4.22%), *Bradyrhizobium* (2.82%), *Acidothermus* (1.88%), *Bryobacter* (1.44%), *Burkholderia-Paraburkholderia* (2.00%) and *Streptomyces* (1.41%). The relative abundance of *Bacillus* and *Burkholderia-Paraburkholderia* in the rhizosphere were lower than that of bulk soil in seedling plantations, but the opposite trend was found in coppice plantations. In addition, the relative abundance of other bacteria in the rhizosphere was higher than that of bulk soil in seedling and coppice plantations.

Relative abundance of Rhizobium in seedling and coppice plantations

The relative abundance of *Rhizobium* in both bulk soil and rhizosphere in second generation coppice stands was significantly higher than in seedling and first generation coppice stands. The relative abundance of *Rhizobium* was the highest in the rhizosphere of T stands (0.32%), while the lowest was found in the bulk soil of seedling stands (0.11%). Moreover, the difference in *Rhizobium* abundance between rhizosphere soil and bulk soil was significant in seedling plantations ($p = 0.002$), while there was no difference in coppice plantations (Fig. 2).

Bacterial community composition in seedling and coppice plantations

The results showed five replicates usually clustered closely (Fig. 3). The first and second PCA axes revealed that the rhizosphere- and bulk soil-associated bacterial microbiota were inhomogeneous at phylum (12.77% and 8.23%, respectively, Fig. 3A) and genus (17.21% and 13.16%, respectively, Fig. 3B) levels. The soil layer and plantation type rendered a significant effect on bacterial community composition. The similarities in bacterial community composition within rhizosphere and bulk soil were lower in seedling plantations than in coppice plantations (Fig. 3).

We found that C, N, SOM, NO_3^- -N and A.P were positively correlated with bacterial community composition by Mantel tests at both the phylum and genus levels (Table 3). Spearman correlation analysis of the relationships between soil properties and bacterial community at the phylum (Fig. 4A) and genus levels (Fig. 4B) also confirmed the positive correlation between bacterial communities and nutrient concentrations. At the phylum level, SOM, NO_3^- -N, and A.P were significantly and negatively correlated with *Proteobacteria* ($r = -0.66$, $p = 0.000$; $r = -0.62$, $p = 0.000$ and $r = -0.73$, $p = 0.000$, respectively), and were significantly and positively correlated with *Actinobacteria* ($r = 0.71$, $p = 0.000$; $r = 0.64$, $p = 0.000$ and $r = 0.59$, $p = 0.001$, respectively), but there was no significant correlation with *Acidobacteria*. At the genus level, *Acidotherrmus*, *Bryobacter* and *Mizugakiibacter* were significantly and positively correlated with SOM, NO_3^- -N, and A.P ($r = 0.65$, 0.62 and 0.68 ; $p = 0.000$, $p = 0.000$ and $p = 0.000$, respectively). Bacterial taxa were also more correlated with soil nutrient concentrations at the genus level than at the phylum level.

Table 3
Mantel-test between bacteria phylum and genus and soil properties.

Soil properties	Phylum		Genus	
	r	p	r	p
N	0.495	0.001	0.505	0.001
C	0.4433	0.001	0.4419	0.001
P	0.08502	0.07	0.04408	0.236
C/N	0.008762	0.499	0.04093	0.665
C/P	0.1329	0.046	0.09815	0.106
N/P	0.1254	0.044	0.09049	0.13
SOM	0.4002	0.001	0.3239	0.001
NO ₃ ⁻ -N	0.5758	0.001	0.5383	0.001
NH ₄ ⁺ -N	0.2009	0.016	0.1892	0.017
A.N	0.2144	0.007	0.2028	0.015
A.P	0.4528	0.001	0.4239	0.001
Exchangeable Ca	0.03213	0.308	0.04071	0.285
Exchangeable Mg	0.1988	0.017	0.187	0.033
Exchangeable K	0.06525	0.767	0.07211	0.764

N, SOM and NO₃⁻-N, the most relevant factors based on mantel tests results ($p < 0.001$, at the phylum and genus levels), were selected for variance partitioning canonical correspondence analysis (VPA), to quantify the relative contributions of soil properties to bacterial structure. The soil properties explained 75.46% of the observed variation, leaving 24.54% of the variation unexplained. Among them, C, N, SOM and NO₃⁻-N explained 9.28%, 0.00%, 3.52% and 15.12%, respectively. Thus, NO₃⁻-N, but not N, was the most important factor in shaping the bacterial community structure.

Discussion

Conversion from seedling to coppice plantations reduced soil quality

Forest conversion has a great impact on plant and soil characteristics, altering soil bacterial community structure, soil nutrients and plant diversity and composition (Zhao et al. 2019). Previous research has

shown that *R. pseudoacacia* may induce significant changes on several physical and chemical properties of the soil (Khan et al. 2010). In *R. pseudoacacia* coppice plantations, intra-specific competition increases because of the high stem density, which may result in differences in microclimatic and ecological conditions as compared to seedling stands. In this regard, our results provide incremental knowledge to previous research by further showing that the conversion from seedling to coppice stands reduced soil quality (Table 1), consistently with the findings of Johnson (2001) and Luo (2006). Therefore, it supports hypothesis 1. that *R. pseudoacacia* is a N-fixing species with a strong nitrogen fixation ability. However, our results showed that soil N (N, NO_3^- -N and A.N) concentrations declined in coppice plantations. It possibly indicates that the nitrogen fixation ability of *R. pseudoacacia* coppice decreased to a certain extent, and the N mineralization rate was significantly lower than seedling plantation (Unpublished data). The main reason may be that the conversion decreased the net primary production and aboveground biomass and productivity (Liao et al. 2012). Specially, the coppice plantation had a lower stand productivity than seedling plantation (Figure S2), and which could modify soil structure and lead to less inputs and more losses of soil nutrients (Zheng et al. 2005), then finally affect the absorption of N by trees (Zhang et al. 2018b). Additionally, we found that the greater moisture content occurred in coppice plantations (13.95%), which might reduce root and microbial activity (Banerjee et al. 2016), then reduce the soil total N concentration, N storage, N cycling and availability (Wang et al. 2010).

Due to root exudations, microbiota activity, and plant absorption, which may lead to the accumulation of nutrients in the rhizosphere, the microenvironments between the rhizosphere and bulk soil may differ markedly (Philippot et al. 2013). Our results showed that N and C contents in bulk soil were higher than those in the rhizosphere, but the concentrations of other nutrients (eg. SOM, NO_3^- -N and A.P) were lower in the bulk soil than in the rhizosphere (Table 1). These results are consistent with previous research (Chaudhary et al. 2015). One main possible reason is that plant roots directly take up lower available nutrients and reduce carbon loss in the rhizosphere (Jones et al. 2009), and they could also adapt to the change of soil nutrient availability through the elastic distribution of underground roots (Bardgett et al. 2014). The consumption of N for growth, the strong physiological metabolism function of root system and the activity of rhizosphere microorganisms drive the transformation of N to A.N, and this may be the reason why we found that rhizosphere soil had lower N content and higher A.N content (Table 1).

Conversion from seedling to coppice plantations altered the structure of bacterial communities

Changes in forest community types can affect soil microbial structure (Cardenas et al. 2015) and α -diversity (Vitali et al. 2016). Our results showed that Shannon and Simpson indices declined from seedling to coppice plantations (Table 2). These shifts can be accompanied by changes in bacterial functional activity (Kaiser et al. 2014), contributing to one of reported changes of soil nutrients (Zhao et al. 2018). Previous research (Shi et al. 2016) found that rhizosphere microbes displayed higher levels of interactions than bulk soil microbes. However, we found that the bacterial community structures of bulk soil and rhizosphere were not significantly different in coppice plantations (Fig. 3), which supports the hypothesis that the bacterial community structures of rhizosphere soil and bulk soil tend to be consistent.

At the phylum level, the three most abundant bacteria in both rhizosphere and bulk soil samples were *Proteobacteria*, *Actinobacteria* and *Acidobacteria*, consistent with the findings of Fonseca (2018). The relative abundance of *Actinobacteria* and *Verrucomicrobia* decreased from F to T, while *Proteobacteria* showed an opposite trend (Figure. 1A). A possible explanation for this result is that the *Proteobacteria* is generally a fast-growing r-strategist with the ability to use a wide range of root-derived carbon substrates (Philippot et al. 2013). Furthermore, the decline in soil quality will drive *Proteobacteria* to acquire more abundant carbon sources to sustain growth, but the underlying mechanisms need to be further explored. The main function of *Actinobacteria* is to absorb nutrients and excrete metabolic products, which results in the decline of soil quality (Wang et al. 2017a). At the genus level, the relative abundance of *Bacillus* and *Bradyrhizobium* increased from F to T, while *Acidothymus* and *Bryobacter* showed the opposite trend (Figure. 1B). Therefore, the proportion of dominant species changed, which resulted in bacterial community composition homogeneity of bulk soil and rhizosphere in coppice plantations.

Conversion from seedling to coppice plantations increased the relative abundance of Rhizobium

R. pseudoacacia can increase the availability of soil inorganic N, presumably because of *Robinia's* ability to fix N_2 by association with *Rhizobium* (Zhang et al. 2019), which is the main source of nitrogen in *Robinia* stands (Papaioannou et al. 2016). Our results showed that the relative abundance of *Rhizobium* increased from seedling to coppice plantations, which was against hypothesis 3. The reason may be that most of the *Rhizobium* bacteria are free-living individuals in the soil, resulting in the decrease of the symbiotic fixation of atmospheric N within the root nodules of legume hosts (Joëlle et al. 2010; Wang et al. 2018b). Another plausible reason may be that the biological nitrogen fixation requires an expenditure of more C and P (Tye and Drake, 2011; Liu and Deng, 1991). Deficit of C and P in *R. pseudoacacia* stands would decrease and, finally, inhibit symbiotic fixation of atmospheric nitrogen. In the meantime, some study has showed that soil nitrogen-fixing bacterial communities can increase the level of soil available N via biological N-fixation (Wang et al. 2018a), but our results showed an opposite trend. This may be related to the decline of soil C and N or to the little amount of litter biomass (Cao et al. 2018).

Relationships between bacterial community and soil properties

Soil bacterial communities are strongly influenced by abiotic controls (Thoms and Gleixner, 2013), such as total organic carbon (TOC), total nitrogen (TN) (Zhou et al. 2012; Lazzaro et al. 2017). And, vice versa, shifts in microbial communities can affect multiple environmental factors (Fonseca et al. 2018), including potential negative impacts on soil health and plant nutrient acquisition. Therefore, environmental conditions mainly affect the diversity of bacterial communities by changing the physical and chemical properties of the soil (Zhang et al. 2018b). In this study, we found that bacterial communities in both the rhizosphere and bulk soil were strongly influenced by soil C, N, SOM, A.P and NO_3^- -N (Table 2, Figs. 4 and 5), which supports hypothesis 2, i.e., that nutrient availability plays an important role in shaping the bacterial community. C and N contents exhibited a strong significantly

positive correlation with *Bacteroidetes*, and a negative correlation with *Proteobacteria* and *Firmicutes*, but no correlation with *Actinobacteria* and *Acidobacteria* (Fig. 4), which was consistent with the results of Fierer (2007) and Zhao (2018). *Proteobacteria* are considered to be rhizospheric- plant-promoting bacteria that can influence C accumulation (Ren et al. 2016), and have a significantly positive effect on C fractions. But our results showed an opposite trend. The reason may be that *Bacteroidetes* can influence the rate of C mineralization and fix atmospheric nitrogen in symbiosis (Fierer et al. 2007).

Soil bacterial community can increase soil NO_3^- -N content (Zhang et al. 2015; Lazzaro et al. 2017). The conversion from seedling to coppice stands altered the structure of the soil bacterial community and decreased soil resource availability (Zhang et al. 2017), which also partly supports the hypothesis that nutrient availability plays an important role in shaping the bacterial community. In this study, we found that bacterial communities in both the rhizosphere and bulk soil were strongly influenced by soil NO_3^- -N (Fig. 5). Nitrogen in soil can be decomposed by bacteria to promote N absorption by trees. All N transformation and uptake processes are correlated with soil carbon resources and regulated by soil microbes (Geisseler et al. 2010). Our results showed that C and NO_3^- -N contents in the coppice plantations were lower than those in the seedling stands, leading to inhibition of microbial activity.

Conclusions

This research revealed three important findings for assessing the impacts of converting seedling to coppice plantations on soil habitat. First, we found that this conversion can negatively affect soil properties. Second, the conversion from seedling to coppice stands could alter soil bacterial community composition, resulting in higher homogeneity of the bacterial community composition in bulk soil and rhizosphere in coppice plantations. Furthermore, this can lead to the imbalance of soil microenvironment structure and the decline of soil functions. Additionally, stand conversion increased the relative abundance of *Rhizobium*, but the soil N and available N decreased, implying that the activity of *Rhizobium* was limited. Eventually, we found that NO_3^- -N is the most important factor in shaping soil bacterial structure in this ecosystem.

Although the impacts of the conversion from seedling to coppice plantations on soil properties and soil bacterial community were studied, we can not state that the contribution rate of N to bacterial community was zero (Fig. 5). Further research with N cycling and understory coverages conversion from seedling to coppice plantations would help to better assess this phenomenon, including mineralization, nitrification, anammox, denitrification and nitrogen fixation.

Declarations

Availability of data and materials

The datasets used and/or analysed during the current study are available from the corresponding author on reasonable request.

Ethics approval and consent to participate

Not applicable.

Consent for publication

Not applicable.

Competing interests

The authors declare that they have no competing interests.

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Authors' Contributions

Conceived and designed the study: Kun Li, Xu Han, Chuanrong Li. Collected data and samples in the field: Kun Li, Ge Shi, Weixing Shen, Yikun Zhang, Xingzhong Zhang. Processed samples in the lab: Kun Li, Ge Shi. Analyzed the data: Kun Li and Xu Han. Wrote the paper: Kun Li, Ruiqiang Ni and Sergio de-Miguel. All authors read and approved the final manuscript.

References

1. Balota EL, Yada IF, Amaral H, Nakatani AS, Dick RP, Coyne MS (2013) Long-term land use influences soil microbial biomass P and S, phosphatase and arylsulfatase activities, and S mineralization in a Brazilian oxisol. *Land Degradation Development* 25(4):397–406. <https://doi.org/10.1002/ldr.2242>
2. Bardgett RD, Mommer L, De Vries FT (2014) Going underground: root traits as drivers of ecosystem processes. *Trends in Ecology Evolution* 29(12):692–699. <https://doi.org/10.1016/j.tree.2014.10.006>
3. Banerjee S, Helgason B, Wang L, Winsley T, Ferrari BC, Siciliano SD (2016) Legacy effects of soil moisture on microbial community structure and N₂O emissions. *Soil Biology and Biochemistry* 95:40–50. <https://doi.org/10.1016/j.soilbio.2015.12.004>
4. Berthold D, Vor T, Beese F (2009) Effects of cultivating black locust (*Robinia pseudoacacia* L.) on soil chemical properties in Hungary. *Forstarchiv* 80(6):307–313. <http://media.repro-mayr.de/77/548177.pdf>
5. Buzhdygan OY, Rudenko SS, Kazanci C, Patten BC (2016) Effect of invasive black locust (*Robinia pseudoacacia* L.) on nitrogen cycle in floodplain ecosystem. *Ecol Model* 319:170–177. <https://doi.org/10.1016/j.ecolmodel.2015.07.025>
6. Cao Y, Zhang P, Chen Y (2018) Soil C:N:P stoichiometry in plantations of N-fixing black locust and indigenous pine, and secondary oak forests in northwest China. *Journal of Soil Sediments* 18(4):1478–1489. <https://doi.org/10.1007/s11368-017-1884-0>
7. Cardenas E, Kranabetter JM, Hope G, Maas KR, Hallam S, Mohn WW (2015) Forest harvesting reduces the soil metagenomic potential for biomass decomposition. *ISME J* 9:2465–2476. <https://doi.org/10.1038/ismej.2015.57>
8. Chaudhary DR, Gautam RK, Yousuf B, Mishra A, Jha B (2015) Nutrients, microbial community structure and functional gene abundance of rhizosphere and bulk soils of halophytes. *Applied Soil Ecology* 91:16–26. <https://doi.org/10.1016/j.apsoil.2015.02.003>
9. Chen C, Fang X, Xiang W, Lei P, Ouyang S, Kuzyakov Y (2020) Soil-plant co-stimulation during forest vegetation restoration in a subtropical area of southern China. *Forest Ecosystems* 7:1–17. <https://doi.org/10.1186/s40663-020-00242-3>
10. Cierjacks A, Kowarik I, Joshi J, Hempel S, Ristow M, Von LM, Weber E (2013) Biological Flora of the British Isles: *Robinia pseudoacacia*. *J Ecol* 101:1623–1640. <https://doi.org/10.1111/1365-2745.12162>
11. Fierer N, Bradford MA, Jackson RB (2007) Toward an ecological classification of soil bacteria. *Ecology* 88:1354–1364. <https://doi.org/10.1016/j.jglr.2009.01.002>
12. Fonseca JP, Hoffmann L, Cabral BCA, Dias VHG, Miranda MR, Azevedo MAC, Boschiero C, Bastos WR, Silva R (2018) Contrasting the microbiomes from forest rhizosphere and deeper bulk soil from an Amazon rainforest reserve. *Gene* 642:389–397. <https://doi.org/10.1016/j.gene.2017.11.039>
13. Geisseler D, Horwath WR, Joergensen RG, Ludwig B (2010) Pathways of nitrogen utilization by soil microorganisms—A review. *Soil Biol Biochem* 42:2058–2067. <https://doi.org/10.1016/j.soilbio.2010.08.021>

14. Geng B, Wang HT, Wang YP, Xue BJ, Li WQ (2013) Comparative study of coppice and seeding forest of *Robinia pseudoacacia* L. Science of soil water conservation 11(2):59–64. <https://doi.org/10.16843/j.sswc.2013.02.010>
15. Guo SJ, Xu YD, He C, Wu SJ, Ren CJ, Han XH, Feng YZ, Ren GX, Yang GH (2019) Differential responses of soil quality in revegetation types to precipitation gradients on the Loess Plateau. Agric For Meteorol 276:107622. <https://doi.org/10.1016/j.agrformet.2019.107622>
16. Joëlle F, Lesuffleur F, Stéphanie M, Cliquet JB (2010) Nitrogen rhizodeposition of legumes. A review. Agron Sustain Dev 30(1):57–66. <https://doi.org/10.1051/agro/2009003>
17. Johnson DW, Curtis PS (2001) Effects of forest management on soil C and N storage: meta-analysis. For Ecol Manage 140:227–238. [https://doi.org/10.1016/S0378-1127\(00\)00282-6](https://doi.org/10.1016/S0378-1127(00)00282-6)
18. Jones DL, Nguyen C, Finlay RD (2009) Carbon flow in the rhizosphere: carbon trading at the soil-root interface. Plant Soil 321(1/2):5–33. <https://doi.org/10.1007/s11104-009-9925-0>
19. Kaiser C, Franklin O, Dieckmann U, Richter A (2014) Microbial community dynamics alleviate stoichiometric constraints during litter decay. Ecol Lett 17:680–690. <https://doi.org/10.1111/ele.12269>
20. Khan B, Ablimit A, Mahmood R, Qasim M (2010) *Robinia pseudoacacia* leaves improve soil physical and chemical properties. Journal of Arid Land 4:266–271. <http://jal.xjegi.com/CN/10.3724/SP.J.1227.2010.00266>
21. Lazzaro L, Mazza G, d'Errico G, Fabiani A, Giuliani C, Inghilesi AF, Lagomarsino A, Landi S, Lastrucci L, Pastorelli R, Roversi PF, Torrini G, Tricarico E, Foggi B (2017) How ecosystems change following invasion by *Robinia pseudoacacia*: Insights from soil chemical properties and soil microbial, nematode, microarthropod and plant communities. Sci Total Environ 622–623:1509–1518. <https://doi.org/10.1016/j.scitotenv.2017.10.017>
22. Lee CS, Cho HJ, Yi H (2004) Stand dynamics of introduced black locust (*Robinia pseudoacacia* L.) plantation under different disturbance regimes in Korea. For Ecol Manage 189(1–3):281–293. <https://doi.org/10.1016/j.foreco.2003.08.012>
23. Liao C, Luo Y, Fang C, Chen J, Li B (2012) The effects of plantation practice on soil properties based on the comparison between natural and planted forests: a meta-analysis. 21(3):318–327. <https://doi.org/10.1111/j.1466-8238.2011.00690.x>
24. Liu D, Huang Y, Sun H, An S (2018) The restoration age of *Robinia pseudoacacia* plantation impacts soil microbial biomass and microbial community structure in the Loess Plateau. Catena 165:192–200. <https://doi.org/10.1016/j.catena.2018.02.001>
25. Liu GF, Deng TX (1991) Mathematical model of the relationship between nitrogen-fixation by black locust and soil conditions. Soil Biol Biochem 23(1):1–7
26. [https://doi.org/10.1016/0038-0717\(91\)90155-D](https://doi.org/10.1016/0038-0717(91)90155-D)
27. Luo YQ, Hui DF, Zhang DQ (2006) Elevated CO₂ stimulates net accumulations of carbon and nitrogen in land ecosystems: a meta-analysis. Ecology 87:53–63. <https://doi.org/10.1890/04-1724>

28. Ma S, Verheyen K, Props R, Wasof S, Vanhellefont M, Boeckx P, Boon N, Frenne PD (2018) Plant and soil microbe responses to light, warming and nitrogen addition in a temperate forest. *Funct Ecol* 32(5):1293–1303. <https://doi.org/10.1111/1365-2435.13061>
29. Macdonald S, Bailey T, Hunt M, Davidson N, Jordan G (2019) Stable states in soil chemistry persist in eucalypt woodland restorations. *Applied vegetation science* 22(1):105–114. <https://doi.org/10.1111/avsc.12404>
30. Mantovani D, Veste M, Boldt-Burisch K, Fritsch S, Koning LA, Freese D (2015) Carbon allocation, nodulation, and biological nitrogen fixation of black locust (*Robinia pseudoacacia* L.) under soil water limitation. *Annals Forest Research* 58:1. <https://doi.org/10.15287/afr.2015.420>
31. Medina-Villar S, Rodríguez-Echeverría S, Lorenzo P, Alonso A, Pérez-Corona E, Castro-Díez P (2016) Impacts of the alien trees *Ailanthus altissima* (Mill.) Swingle and *Robinia pseudoacacia* L. on soil nutrients and microbial communities. *Soil Biol Biochem* 96:65–73. <https://doi.org/10.1016/j.soilbio.2016.01.015>
32. Mendes R, Garbeva P, Raaijmakers JM (2013) The rhizosphere microbiome: significance of plant beneficial, plant pathogenic, and human pathogenic microorganisms. *Fems Microbiology Reviews* 37(5):634–663. <https://doi.org/10.1111/1574-6976.12028>
33. Neumann D, Heuer A, Hemkemeyer M, Martens R, Tebbe CC (2014) Response of microbial communities to long-term fertilization depends on their microhabitat. *Fems Microbiology Ecology* 86(1):71–84. <https://doi.org/10.1111/1574-6941.12092>
34. Papaioannou A, Chatzistathis T, Papaioannou E, Papadopoulos G (2016) *Robinia pseudoacacia* as a valuable invasive species for the restoration of degraded croplands. *Catena* 137:310–317. <https://doi.org/10.1016/j.catena.2015.09.019>
35. Peng H, Chen XR, Yu ZD (2003) Know-how on silviculture of black locust plantation. *Journal of soil water conservation* 17(5):11–15. <https://doi.org/10.3321/j.issn:1009-2242.2003.05.004>
36. Philippot L, Raaijmakers JM, Lemanceau P, Van PWH (2013) Going back to the roots: the microbial ecology of the rhizosphere. *Nat Rev Microbiol* 11:789–799. <https://doi.org/10.1038/nrmicro3109>
37. Radtke A, Ambraß S, Zerbe S, Tonon G, Fontana V, Ammer C (2013) Traditional coppice forest management drives the invasion of *Ailanthus altissima* and *Robinia pseudoacacia* into deciduous forests. *For Ecol Manage* 291:308–317. <https://doi.org/10.1016/j.foreco.2012.11.022>
38. Reynolds HL, Haubensak KA (2009) Soil fertility, heterogeneity, and microbes: towards an integrated understanding of grassland structure and dynamics. *Appl Veg Sci* 12(1):33–44. <https://doi.org/10.1111/j.1654-109X.2009.01020.x>
39. Sabo AE (2000) *Robinia pseudoacacia* invasions and control in North America and Europe
40. Sasse J, Martinoia E, Northen T (2018) Feed Your Friends: Do Plant Exudates Shape the Root Microbiome? *Trends Plant Sci* 23:25–41. <https://doi.org/10.1016/j.tplants.2017.09.003>
41. Shi S, Nuccio EE, Shi ZJ, He Z, Zhou J, Firestone MK (2016) The interconnected rhizosphere: high network complexity dominates rhizosphere assemblages. *Ecol Lett* 19:926–936. <https://doi.org/10.1111/ele.12630>

42. Thoms C, Gleixner G (2013) Seasonal differences in tree species' influence on soil microbial communities. *Soil Biol Biochem* 66:239–248. <https://doi.org/10.1016/j.soilbio.2013.05.018>
43. Tye DRC, Drake DC (2011) An exotic Australian *Acacia* fixes more N than a coexisting indigenous *Acacia* in a South African riparian zone. *Plant Ecol* 213:251–257. <https://doi.org/10.1007/s11258-011-9971-6>
44. Vitali F, Mastromei G, Senatore G, Caroppo C, Casalone E (2016) Long lasting effects of the conversion from natural forest to poplar plantation on soil microbial communities. *Microbiol Res* 182:89–98. <https://doi.org/10.1016/j.micres.2015.10.002>
45. Vítková M, Müllerová J, Sádlo J, Pergl J, Pyšek P (2017) Black locust (*Robinia pseudoacacia*) beloved and despised: A story of an invasive tree in Central Europe. *For Ecol Manage* 384:287–302. <https://doi.org/10.1016/j.foreco.2016.10.057>
46. Vitkova M, Tonika J, Mullerova J (2015) Black locust—successful invader of a wide range of soil conditions. *Sci Total Environ* 505:315–328. <https://doi.org/10.1016/j.scitotenv.2014.09.104>
47. Wang C, Jiang K, Zhou J, Wu B (2018a) *Solidago canadensis* invasion affects soil N-fixing bacterial communities in heterogeneous landscapes in urban ecosystems in East China. *Sci Total Environ* 631–632:702–713. <https://doi.org/10.1016/j.scitotenv.2018.03.061>
48. Wang F, Zhian LI, Xia H, Zou B, Ningyu LI, Liu J, Zhu WX (2010) Effects of nitrogen-fixing and non-nitrogen-fixing tree species on soil properties and nitrogen transformation during forest restoration in Southern China. *Soil Science Plant Nutrition* 56(2):297–306. <https://doi.org/10.1111/j.1747-0765.2010.00454.x>
49. Wang Q, Garrity GM, Tiedje JM, Cole JR (2007) Naive Bayesian classifier for rapid assignment of rRNA sequences into the new bacterial taxonomy. *Appl Environ Microbiol* 73(16):5261–5267. <https://doi.org/10.1128/AEM.00062-07>
50. Wang Q, Wang S, Yu X (2011) Decline of soil fertility during forest conversion of secondary forest to Chinese fir plantations in subtropical China. *Land Degradation Development* 22:444–452. <https://doi.org/10.1002/ldr.1030>
51. Wang XL, Cui WJ, Feng XY, Zhong ZM, Li Y, Chen WX, Chen WF, Shao XM, Tian CF (2018b) Rhizobia inhabiting nodules and rhizosphere soils of alfalfa: A strong selection of facultative microsymbionts. *Soil Biol Biochem* 116:340–350. <https://doi.org/10.1016/j.soilbio.2017.10.033>
52. Weidner S, Koller R, Latz E, Kowalchuk G, Bonkowski M, Scheu S, Jousset A (2015) Bacterial diversity amplifies nutrient-based plant-soil feedbacks. *Funct Ecol* 29:1341–1349. <https://doi.org/10.1111/1365-2435.12445>
53. Williard KWJ, Dewalle DR, Edwards PJ (2005) Influence of bedrock geology and tree species composition on stream nitrate concentrations in mid-appalachian forested watersheds. *Water Air Soil Pollution* 160(1–4):55–76. <https://doi.org/10.1007/s11270-005-3649-4>
54. Yang B, Peng C, Zhu Q, Zhou X, Liu W, Duan M, Wang H, Liu ZH, Guo XY, Wang M (2019) The effects of persistent drought and waterlogging on the dynamics of nonstructural carbohydrates of *Robinia*

- pseudoacacia* L. seedlings in Northwest China. *Forest Ecosystems* 6(1):23.
<https://doi.org/10.1186/s40663-019-0181-3>
55. Yang H, Koide RT, Zhang Q (2016) Short-term waterlogging increases arbuscular mycorrhizal fungal species richness and shifts community composition. *Plant Soil* 404(1–2):373–384.
<https://doi.org/10.1007/s11104-016-2850-0>
56. Yang K, Zhu JJ, Xu S, Zheng X (2018) Conversion from temperate secondary forests into plantations (*Larix* spp.): Impact on belowground carbon and nutrient pools in northeastern China. *Land Degradation Development* 29:4129–4139. <https://doi.org/10.1002/ldr.3169>
57. Yin L, Dijkstra FA, Wang P, Zhu B, Cheng W (2018) Rhizosphere priming effects on soil carbon and nitrogen dynamics among tree species with and without intraspecific competition. *New Phytol* 218:1036–1048. <https://doi.org/10.1111/nph.15074>
58. Zhang B, Zhang J, Liu Y, Shi P, Wei G (2018a) Co-occurrence patterns of soybean rhizosphere microbiome at a continental scale. *Soil Biol Biochem* 118:178–186.
<https://doi.org/10.1016/j.soilbio.2017.12.011>
59. Zhang D, Wang C, Li X, Yang X, Zhao L, Liu L, Zhu C, Li RH (2018b) Linking plant ecological stoichiometry with soil nutrient and bacterial communities in apple orchards. *Appl Soil Ecol* 126:1–10. <https://doi.org/10.1016/j.apsoil.2017.12.017>
60. Zhang L, Wang J, Bai Z, Lv C (2015) Effects of vegetation on runoff and soil erosion on reclaimed land in an opencast coal-mine dump in a loess area. *Catena* 128:44–53.
<https://doi.org/10.1016/j.catena.2015.01.016>
61. Zhang W, Liu W, Xu M, Deng J, Han X, Yang G, Feng Y, Ren G (2019) Response of forest growth to C: N: P stoichiometry in plants and soils during *Robinia pseudoacacia* afforestation on the Loess Plateau, China. *Geoderma* 337:280–289. <https://doi.org/10.1016/j.geoderma.2018.09.042>
62. Zhang W, Lu Z, Yang K, Zhu J (2017) Impacts of conversion from secondary forests to larch plantations on the structure and function of microbial communities. *Appl Soil Ecol* 111:73–83.
<https://doi.org/10.1016/j.apsoil.2016.11.019>
63. Zhao FZ, Ren CJ, Zhang L, Han XH, Yang GH, Wang J (2018) Changes in soil microbial community are linked to soil carbon fractions after afforestation. *Eur J Soil Sci* 69:370–379.
<https://doi.org/10.1111/ejss.12525>
64. Zhao FZ, Bai L, Wang JY, Deng J, Ren CJ, Han XH, Yang GH, Wang J (2019) Change in soil bacterial community during secondary succession depend on plant and soil characteristics. *Catena* 173:246–252. <https://doi.org/10.1016/j.catena.2018.10.024>
65. Zheng H, Ouyang ZY, Wang XK, Fang ZG, Zhao TQ, Miao H (2005) Effects of regenerating forest cover on soil microbial communities: a case study in hilly red soil region, southern China. *For Ecol Manage* 217:244–254. <https://doi.org/10.1016/j.foreco.2005.06.005>
66. Zhou J, Xue K, Xie J, Deng Y, Wu L, Cheng X (2012) Microbial mediation of carbon-cycle feedbacks to climate warming. *Nature Climate Change* 2:106–110. <https://doi.org/10.1038/nclimate1331>

Figures

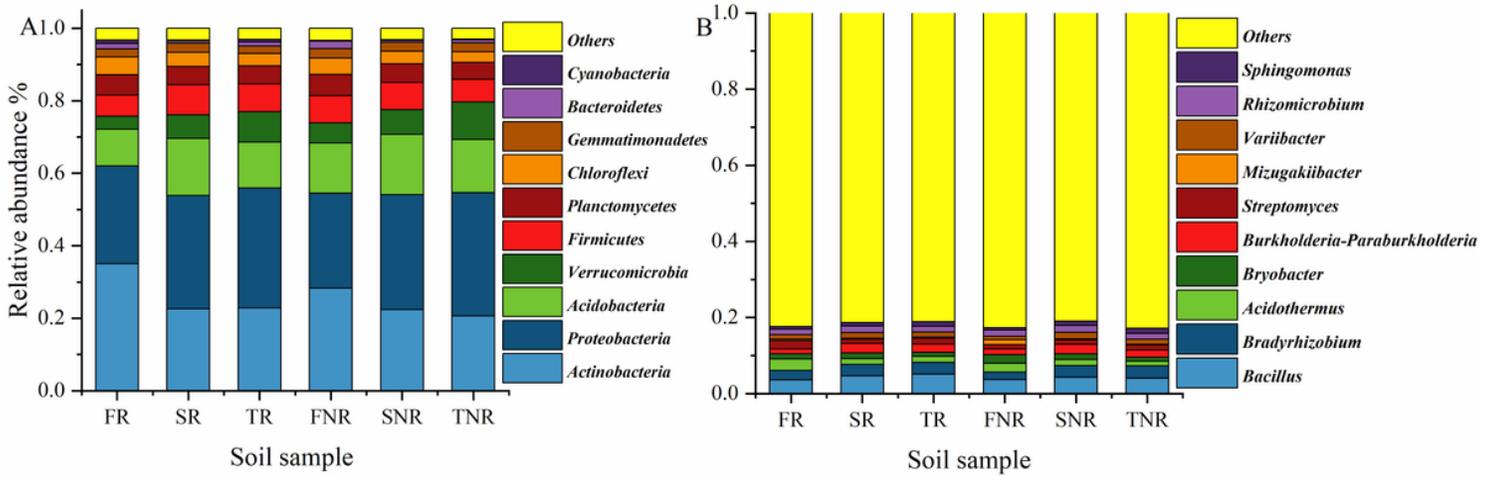


Figure 1

Relative abundance of the dominant bacteria phylum and genus among the soil bacterial phyla via sequencing of 16S rRNA gene amplicons in bulk soil and rhizosphere of different plantations.

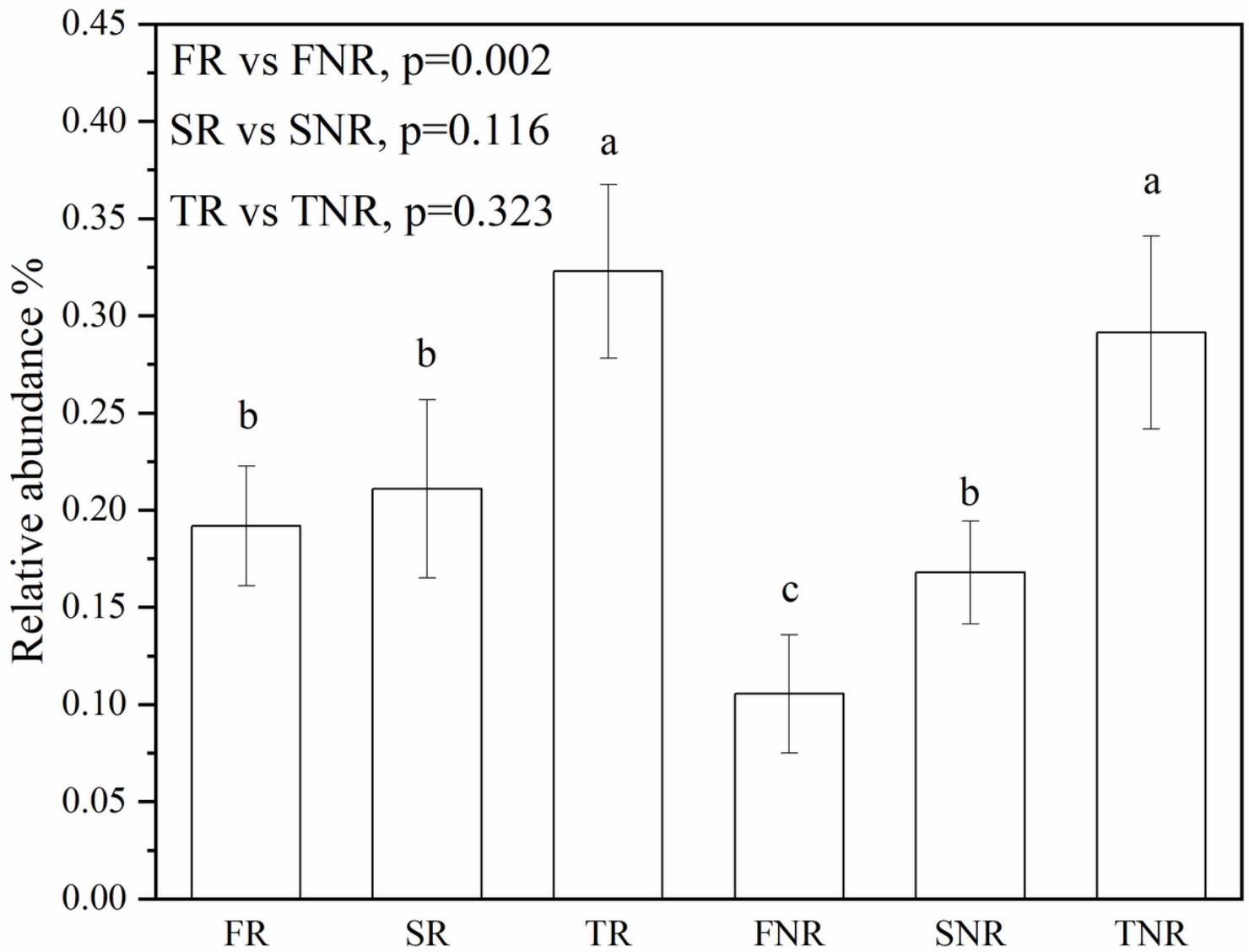


Figure 2

Differences in the relative abundance of Rhizobium between the rhizosphere and bulk soil seedling and coppice plantations. $\alpha=0.05$.

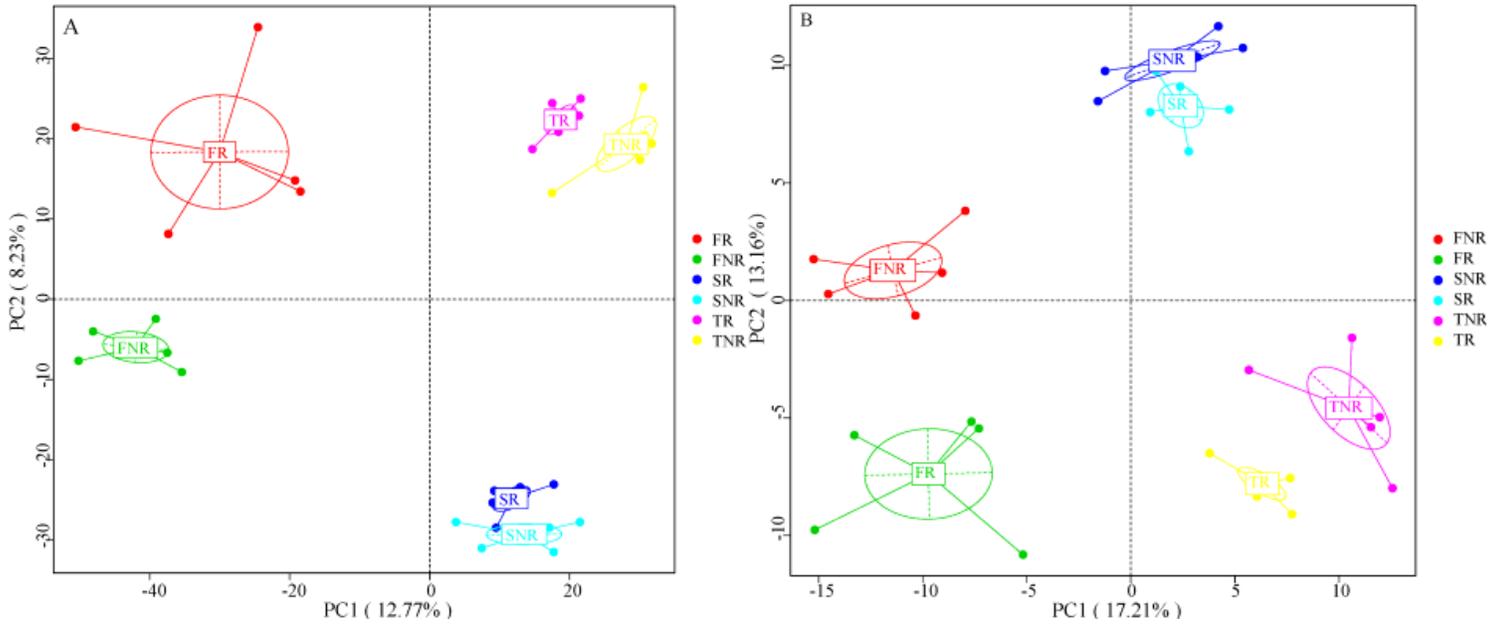


Figure 3

Principal Component Analysis (PCA) (Bray-Curtis distance) among bulk soil and rhizosphere bacterial communities at phylum (A) and genus (B) level. Red and green represent the bacterial community of bulk soil and rhizosphere in seedling plantations (F); blue and cyan represent the bacterial community of bulk soil and rhizosphere in first generation coppice plantations (S); pink and yellow represent the bacterial community of bulk soil and rhizosphere in second generation coppice plantations (T).

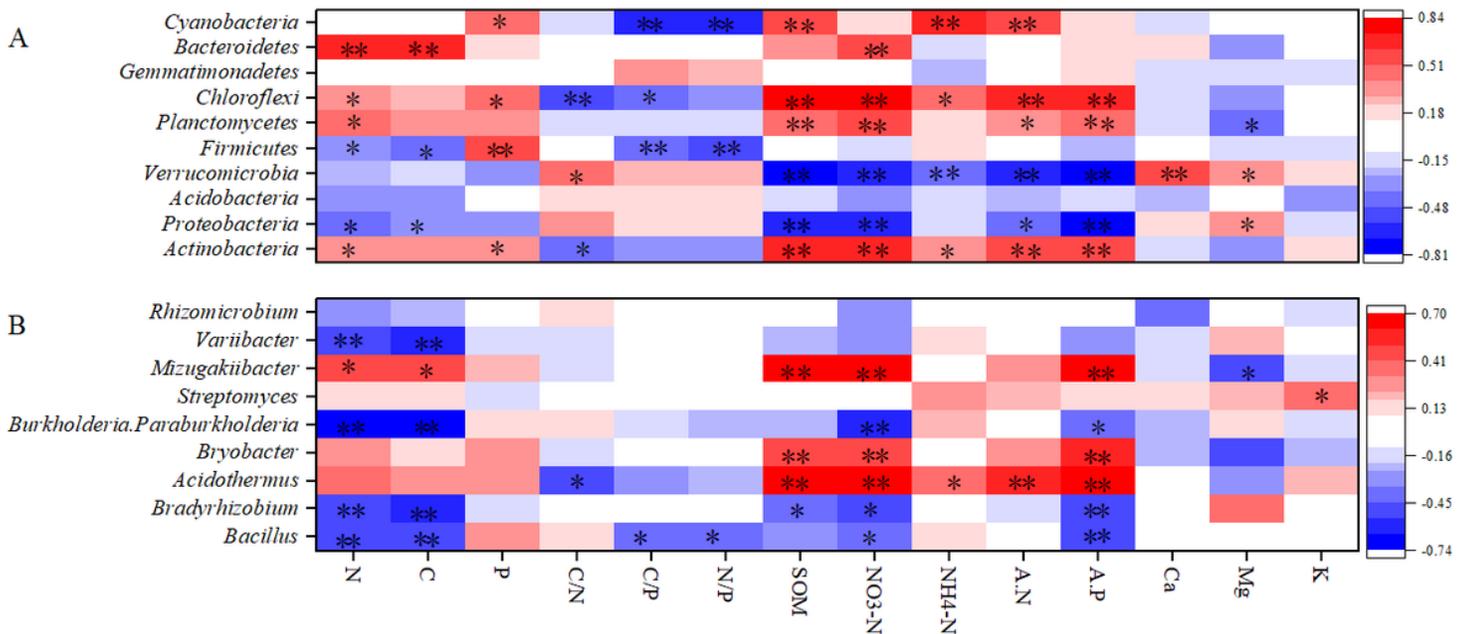


Figure 4

Spearman correlation matrix between soil physicochemical characteristics and bacterial communities at phylum level (A) and genus level (B). Note: N: soil nitrogen content, C: soil carbon content, P: soil phosphorus content, NO₃-N: soil nitrate content, NH₄+N: soil ammonium content, A.N: available nitrogen

content, A.P: available phosphorus content, Ca: soil exchangeable calcium content, Mg: soil exchangeable magnesium content, K: soil exchangeable potassium, SOM: soil organic matter.*P<0.05,** P<0.01.

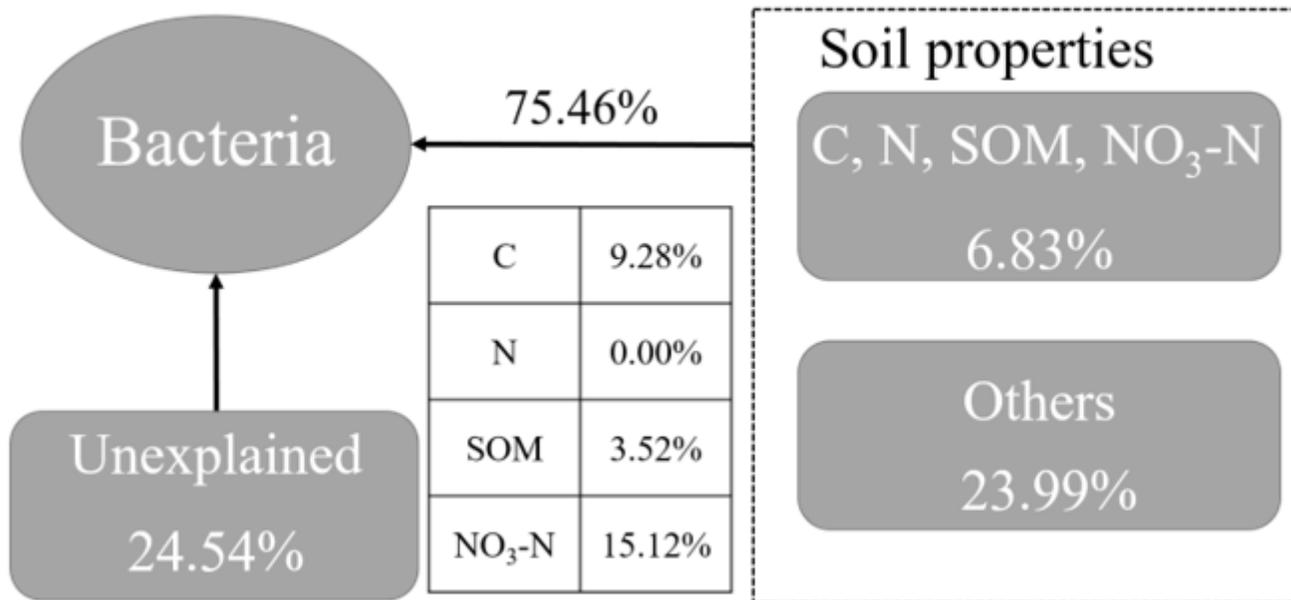


Figure 5

Variance partition analysis (VPA) of the effects of soil properties on the bacterial community structure. Soil properties include C, N, SOM and NO₃-N and interaction among them. "Others" include other soil properties.

Supplementary Files

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