EFFECT OF CONVERTING NATURAL FORESTS TO PLANTATIONS ON THE SOIL BACTERIAL DIVERSITY IN A SUBTROPICAL MOUNTAINOUS AREA: CASE STUDY IN SOUTHERN CHINA

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(Received 11th Jan 2022; accepted 2nd May 2022)

Abstract. Although soil bacteria regulate biogeochemical processes, little is known about the response of their distribution and abundance to land-use changes in the subtropical region. In the present study, soil samples from four natural forests and two agricultural plantations were collected from a subtropical mountainous area of southern China. A high-throughput sequencing approach was applied to explore the soil bacterial community composition and diversity. The results showed that dominant bacterial taxa (such as *Acidobacteria*, *α-proteobacteria*, *γ-proteobacteria*, and *Planctomycea*), which accounted for >41% of the bacterial sequences, decreased with the conversion of natural forests to plantations. Structural equation modeling and canonical correspondence analysis indicated that the bacterial community and diversity responded to the decrease in soil carbon and nitrogen contents and the increase in available soil phosphorus content. Multiple statistical analyses, including hierarchical cluster, response ratio, and least discriminate analysis effect size, revealed that the community-level patterns were caused by the responses of a few taxa, particularly *Rhizobiales*, *Bacilli*, *Burkholderiales*, and *Nitrospiraceae*, which are the bacterial indicators of soil nutrient status. Our findings will help better understand the response of soil bacterial communities to reforestation and agricultural management during land-use changes in the subtropical region.
Keywords: *land-use change, soil bacterial community, subtropical acidic soil, high-throughput sequencing, reforestation, soil nutrition*

Introduction

Land-use changes impact carbon balance, nutrient cycling, and global climate change (Cordier et al., 2021; Jovani-Sancho et al., 2021). The conversion of natural forest to agricultural systems, which is the dominant type of land-use change, has been progressing continuously with high rates of 13 million ha per year (Makwinja et al., 2021). The destruction of natural forests causes rapid biomass carbon (C) loss from soil and is a major source of human-induced greenhouse gas emissions (Han and Zhu, 2020; Kim et al., 2021). Soil bacterial communities play a vital role in regulating the cycling, release, and retention of soil C and nitrogen (N) in natural forests and agricultural systems (Burkins

http://www.aloki.hu ● ISSN 1589 1623 (Print) ● ISSN 1785 0037 (Online)
DOI: http://dx.doi.org/10.15666/aeer/2004_28312844

et al., 2001; Liu et al., 2020). However, little is known regarding the response of the taxonomic composition of soil bacteria during land-use changes in subtropical areas despite the fact that the conversion of natural soils to cultivated soils has been expected to progress rapidly in the past and it is still expected to progress in the future in subtropical developing countries, particularly in Asia (Foley et al., 2005; Sheng et al., 2010).

Review of literature

Soil bacterial communities in different land-use patterns have been globally studied via phospholipid fatty acid profiles (Srivastava and Mishra, 2021; Tosi et al., 2021), DNA fingerprinting (Chave et al., 2010; Jangid et al., 2011), or culture-based methods (Ayob and Kusai, 2021), which neither identify bacterial taxonomic groups nor adequately represent the vast diversity of uncultured soil bacteria (Shen et al., 2013). Moreover, environmental and anthropogenic factors associated with the distribution and abundance of soil bacterial groups during land-use changes have been inadequately studied in the subtropical region.

Humid subtropical soils in China cover approximately 0.45 million km^2, which accounts for approximately 4% of the world's subtropical arable land surface and 37% of China's arable area (Qin et al., 2011). To support the increasing population, many natural forests have been converted to agricultural land (Kan et al., 2021). The soil in these regions is heavily weathered, acidic, and deficient in available nutrients, particularly phosphorus (P) (Han et al., 2022). These characteristics significantly influence certain soil microbial functions, including soil respiration (Sheng et al., 2010) and denitrification (Sünnemann et al., 2021). To predict the comprehensive effects of land-use change on soil microbial functions, an improved understanding of the responses of bacterial communities to land-use changes is required to complement existing knowledge about the bacterial functional groups that control biogeochemical processes. In the present study, the structure and composition of soil bacterial communities in different land-use patterns with long and clear land-use history in southeast China were identified. The studied land-use types contained four natural forests, including *Altingia gracilipes* Hemsl. (ALG), *Cinnamomum chekiangensis* Nakai (CIC), *Castanopsis fargesii* Franch. (CAF), *Tsoongiodendron odorum* Chun (TSO), and two plantations - an adjacent plantation of *Cunninghamia lanceolata* Hook. (Chinese fir) (CUL) and an economic plantation of *Citrus reticulata* (citrus orchard) (ORG). We reported previously that the conversion of natural forests to plantations negatively affects soil microbial community and diversity via phospholipid fatty acid profile, real-time quantitative polymerase chain reaction, and denaturant gradient gel electrophoresis approaches (Yu et al., 2012). Although these methods are indispensable for microbial community studies, they are insufficient for elucidating the diversity. High-throughput sequencing is a revolutionary microbial ecology tool that offers sufficient sequencing depth (Lin et al., 2012). In the present study, we applied high-throughput sequencing to investigate the response of bacterial communities to land-use changes in subtropical soil. We also explored the relationship between soil environmental factors and bacterial communities and diversities, both of which would lead to a better understanding of the ecological effects of land-use changes in subtropical China.

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Materials and Methods

Site description and soil sampling

The study area was Wanmulin Nature Reserve in Jian'ou City, Fujian Province, China (118°08′22″–118°09′23″E, 27°02′28″–27°03′32″N) (*Fig. 1*). This nature reserve was relatively free from human disturbance for approximately 600 years. The soil is classified as red soil in Chinese soil classification (State Soil Survey Service of China, 1998), equivalent to hapludult in USDA Soil Taxonomy (Soil Survey Staff of USDA, 1999). A series of typical land-use types were selected, including ALG, CIC, CAF, TSO, CUL plantation, and ORG plantation. ALG, CIC, CAF, and TSO belong to a natural forest, which was defined as climax vegetation in mid-subtropical China. The CUL plantation developed from a partially abandoned land after the slash-and-burn of the natural forest and regenerated naturally for >20 years in the late 1980s/early 1990s. Moreover, the ORG plantation was converted from the natural forest by reforestation and terraced during the establishment of citrus trees for >15 years. Only the ORG plantation was regularly managed and fertilized primarily with chemical fertilizers. The amounts of N, P, and potassium fertilizers used per year were 310, 115, and 260 kg ha^{-1}, respectively. The soil chemical properties are shown in *Table A1*.

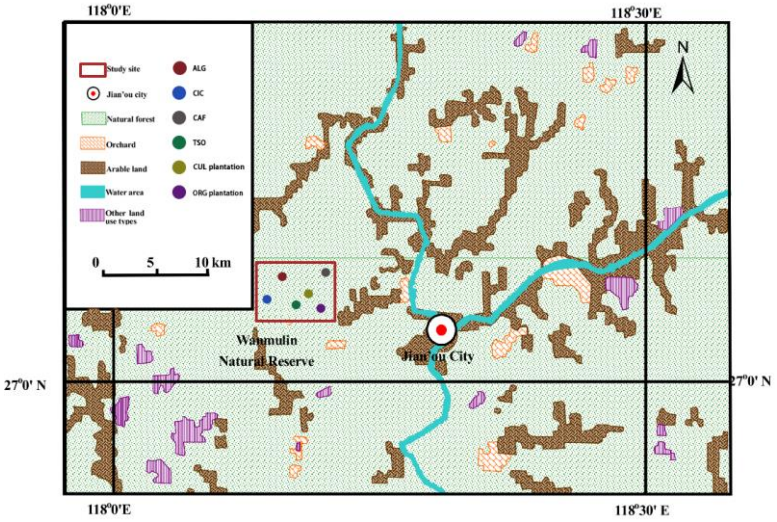

Figure 1. *Geographic location and land-use situation of the study area and sampling sites*

In September 2018, soil samples were collected from the above six land-use types. Three 45 m × 45 m plots were randomly selected from each type, and each plot had a similar slope with a minimum distance of 100 m. Five subsamples were randomly collected from the 0–20 cm soil layer of each plot, and the minimum distance between the collection points of the subsamples was 15 m. After removing the O layer of each subsample, these subsamples were then mixed into one composite sample. Finally, three discrete soil samples were formed for each land-use type. All the samples were taken to the laboratory immediately. A small portion of each soil sample was stored in a -80 °C freezer for molecular analysis. The remaining fresh soil samples were sieved (<2 mm), and stones and root residues were removed with tweezers. Fresh soils were stored at 4 °C for no more than two weeks before soil microbiological analysis. Afterward, air-dried and sieved soils were used for chemical analyses.

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DNA sequencing as well as bacterial composition and diversity analyses

Total DNA was extracted from 0.5 g fresh soil using FastDNA® SPIN Kit for soil (MP Biomedicals, CA, USA) as per the manufacturer's instructions. An aliquot of soil DNA extract (2 μL) was used to partially amplify the bacterial 16S rRNA gene using the barcoded primers 519F and 907R as per the protocol from (Shen et al., 2013). Triplicate reaction mixtures per sample were pooled, purified using QIAquick PCR Purification kit (QIAGEN, Hilden, Germany), and quantified using Agilent 2100 Bioanalyzer (Agilent Technologies, CA, USA) and Qubit 2.0 Fluorometer (Invitrogen, CA, USA). MiSeq (Illumina, CA, USA) coupled with paired-end 250-bp kits were used to generate the sequencing data. Prior to analyses, primer sequences were removed, which resulted in the average sequencing reads of 251 bp. The sequences were processed and analyzed using the Quantitative Insights into Microbial Ecology (QIIME) 1.9.1-dev pipeline with default parameters, unless otherwise noted. In brief, sequences were quality-trimmed (>25 quality score and 200 bp in length) and assigned to soil samples based on unique 5-bp barcodes. Sequences were denoised (Reeder and Knight, 2010) and then binned into operational taxonomic units (OTUs) using *de novo* UCLUST (Edgar, 2010) with a 97% identity threshold. The most abundant sequence from each OTU was selected as the representative sequence for that OTU. Taxonomy was assigned to bacterial OTUs against a subset of the Silva database. OTU representative sequences were aligned using PyNAST via QIIME, and a phylogenetic tree was subsequently constructed using FastTree2 (Price et al., 2009) to support phylogenetic diversity calculations.

The richness of phylotypes was calculated to compare community-level bacterial diversity at a single level of taxonomic resolution. We estimated phylogenetic diversity using Faith's index (Faith, 1992). In this diversity analysis, 1,119,018 bacterial sequences that passed QIIME's quality filtering were included. In total, 9,200–34,353 sequences per sample were obtained (mean = 12,612; median = 12,984). Because an even sampling depth is required for beta diversity calculations, we reduced the datasets to the lowest number available to adjust for differences in survey effort among samples. We calculated both diversity metrics using a randomly selected subset of 9,200 sequences per soil sample. This approach allowed us to compare general diversity patterns among sites, even though it is unlikely that we surveyed the complete diversity in each community (Shaw et al., 2008). Weighted pairwise UniFrac distances (Ramírez et al., 2020) were calculated for community comparisons via QIIME and visualized using nonmetric multidimensional scaling plots as implemented in PRIMER v6.

Statistical analyses

Significant differences in each variable were determined using Tukey's honestly significant difference test at 95% confidence level in SPSS 16.0 (SPSS Inc., IL, USA). Based on the subset of 1,200 16S rRNA gene sequences per soil sample, clustering analysis heatmaps were created in Cluster 3.0 and generated in Java TreeView 1.1. The response ratios of bacterial classes under different land-use soils were analyzed as per the statistical method applied in the literature (Luo et al., 2006). Significant taxonomic differences at the family level were also tested using the least discriminate analysis (LDA) effect size (Segata et al., 2011). This method employs the factorial Kruskal–Wallis sum-rank test ($\alpha = 0.05$) to identify taxa with significant differential abundances among categories (using one-against-all comparisons); this was followed by LDA to estimate the effect size of each differentially abundant feature. Significant taxa were then used to

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generate taxonomic cladograms, which illustrated differences among different land-use soils. Canonical correspondence analysis was performed in Canoco 4.5 for Windows. To identify the various species of each bacterial phylum and their discriminating characteristics, similarity percentage (SIMPER) analysis (Clarke, 1993) was performed using the "simper" function of the "vegan" library in R 3.0 software (Dixon, 2003). Structural equation modeling (SEM) was performed in Amos 18.0 (SPSS Inc., IL, USA). The land-use patterns were fit as 1 or 2 to represent natural forests and plantations. Fertilization was fit as 0 or 1 to represent whether fertilization was present in different land-use soils. We tested how effectively the models fit our data using the maximum likelihood chi-square goodness-of-fit test.

Results

The taxonomic distribution of soil bacteria differed among the land-use types (*Fig. 2*). The dominant phyla across all soil samples included *Acidobacteria*, *Actinobacteria*, and *Proteobacteria*, which accounted for >61% of the bacterial sequences from each of the soils. *Bacteroidetes*, *Chloroflexi*, *Cyanobacteria*, *Firmicutes*, *Gemmatimonadetes*, *Nitrospirae*, and *Planctomycetes* were present in most soils but at relatively low abundances, and some rare bacteria were also identified. The conversion of natural forests to plantations changed the relative abundance of some bacteria; for example, the *Acidobacteria* phylum decreased by ~3.1%, *α-proteobacteria* decreased by ~3.4%, and *β*- and *δ-proteobacteria* increased by >1.1%.

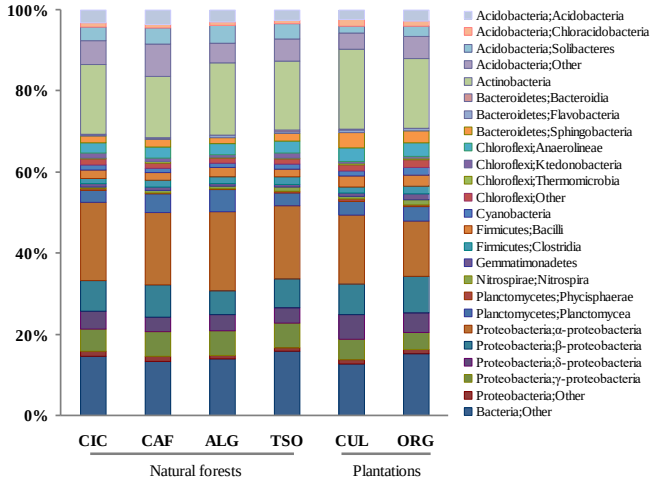

Figure 2. *Taxonomic distribution of bacterial communities derived from 16S rRNA genes across different land-use soils. CIC, CAF, ALG, and TSO were four natural forests that represent Cinnamomum chekiangensis, Castanopsis fargesii, Altingia gracilipes, and Tsoongiodendron odorum, respectively. CUL and ORG represent the Cunninghamia lanceolata and Citrus reticulata plantations, respectively*

Based on the OTU table at the phylum level, a hierarchical cluster analysis heatmap was created to monitor the responses of bacterial phyla to land-use patterns (*Fig. 3*). In this figure, color keys represent the deviation from the mean of each OTU number. Less abundant bacterial phyla in different land-use soils are displayed in green, whereas predominant bacterial phyla are shown in red. The six different land-use types were

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classified into two major linkage clusters. One cluster comprised CAF, CIC, TSO, and ALG, which were natural forests. The other cluster comprised CUL and ORG, which were plantations. By contrast, bacterial communities were classified into two major clusters. One consisted of *Bacteroidetes*, *Cyanobacteria*, and *Gemmatimonadetes*, which were less dominant in natural forests than in plantations. Other bacterial phyla, including *Chloroflexi*, *Proteobacteria*, *Acidobacteria*, *Planctomycetes*, and other rare bacteria, were clustered together and were more dominant in natural forests than in plantations.

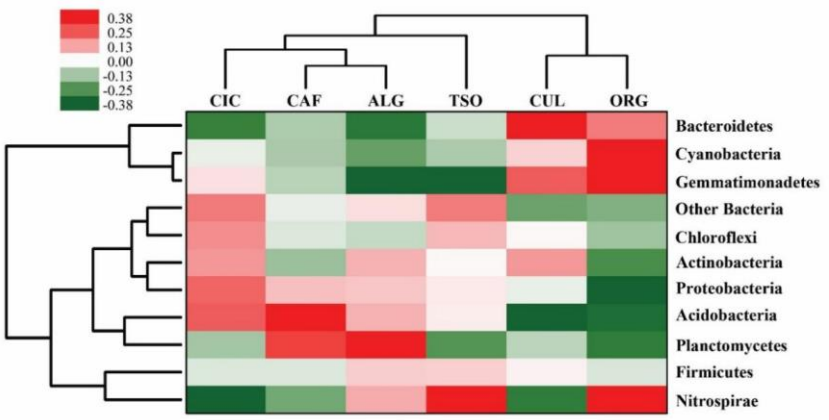

Figure 3. *Hierarchical clustering and heatmap display of the relative abundance of the bacteria based on 16S rRNA gene amplicon sequencing in different land-use soils. Color intensity increases with relative abundance. CIC, CAF, ALG, and TSO were four natural forests that represent Cinnamomum chekiangensis, Castanopsis fargesii, Altingia gracilipes, and Tsoongiodendron odorum, respectively. CUL and ORG represent the Cunninghamia lanceolata and Citrus reticulata plantations, respectively*

According to the sequence size of each bacterial class, response ratios were calculated to statistically resolve the changed bacterial constituents in response to the conversion of natural forests to CUL and ORG plantations (*Fig. 4*). The 95% confidence interval (CI) between natural forests and the CUL plantation ranged from 0.07 to −0.01, which overlapped with 0. This suggested that the conversion of natural forests to the CUL plantation did not induce a significant change in the bacterial community composition. While the 95% CI between the natural forests and ORG did not overlap with 0, it indicated that the conversion of natural forests to an ORG plantation significantly influenced the composition of the soil bacterial community. By contrast, most of the dominant bacterial classes, including *α-proteobacteria*, *γ-proteobacteria*, *Ktedonobacteria*, *Solibacteria*, *Acidobacteria*, and *Planctomycea*, decreased with the conversion of natural forests to plantations. These decreased bacterial classes accounted for >41% of bacterial sequences across all soil samples. Other bacterial classes, including *β-proteobacteria*, *δ-proterobacteria*, *Nitrospira*, *Cyanobacteria*, and *Actinobacteria*, were lower in natural forests than in plantations.

The LDA effect size was performed on the basis of the sequence size at the family level in natural forests and plantations (*Fig. 5*). This analysis confirmed the observation that the conversion of natural forests to plantations significantly influenced the composition of the bacterial community at the phylum and class levels. Furthermore, the LDA effect size analysis illustrated changes in the bacterial composition at the family level. For example, *Acidobacteriaceae*, *Solibacteraceae*, *Acidimicrobiales*,

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Bradyrhizobiaceae, *Rhizobiales*, *Rhodospirillales*, and *Burkholderiales* were more dominant in natural forests than in plantations, whereas *Nocardioidaceae*, *Sphingobacteriales*, *Bacilli*, and *Nitrospiraceae* were less dominant in natural forests.

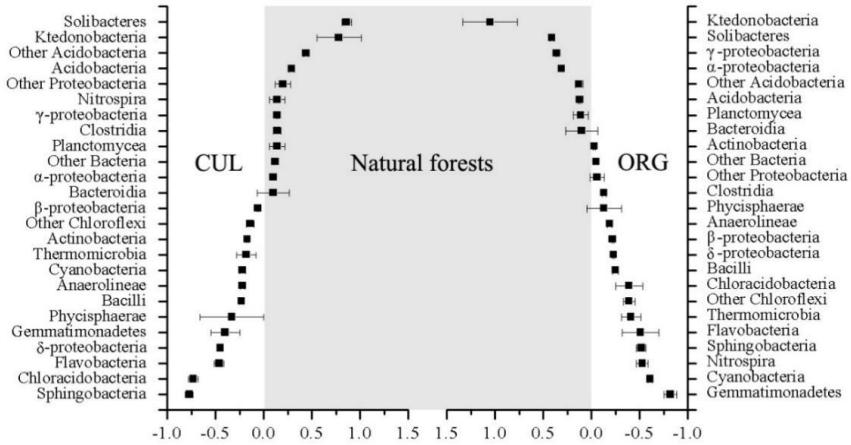

Figure 4. *Significant changes in bacterial classes between natural forests and plantations according to the response ratio method at a 95% confidence interval. CIC, CAF, ALG, and TSO were four natural forests that represent Cinnamomum chekiangensis, Castanopsis fargesii, Altingia gracilipes, and Tsoongiodendron odorum. CUL and ORG represent the Cunninghamia lanceolata and Citrus reticulata plantations, respectively*

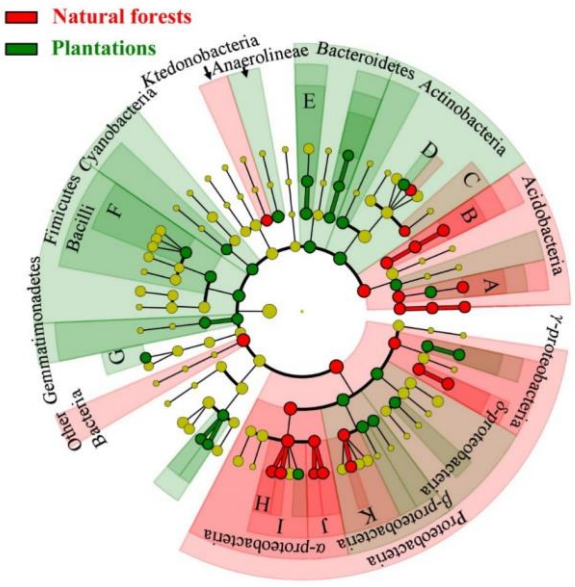

Figure 5. *LDA effect size taxonomic cladogram comparing soil bacterial communities between natural forests and plantations. Significantly discriminant taxon nodes are colored, and branch areas are shaded as per the highest-ranked variety of that taxon. For each detected taxon, the corresponding node in the taxonomic cladogram is colored as per the highest-ranked group for that taxon. If the taxon is not significantly differentially represented among sample groups, the corresponding node is colored yellow. Highly abundant and select taxa are indicated as A, Acidobacteriaceae; B, Solibacteraceae; C, Acidimicrobiales; D, Nocardioidaceae; E, Sphingobacteriales; F, Bacilli; G, Nitrospiraceae; H, Bradyrhizobiaceae; I, Rhizobiales; J, Rhodospirillales; and K, Burkholderiales*

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Discussion

The conversion of natural forest to agricultural systems is closely associated with the sustainable use of soil resources (Hasan et al., 2020; Kan et al., 2021), and the soil microbial community is well established as the key biological indicator for assessing soil health. Thus, using the high-throughput sequencing method in a subtropical mountainous area of southern China, we investigated how soil bacterial communities are affected by land-use changes. The results showed that the composition and diversity of the bacterial community are significantly negatively influenced by the conversion of natural forests to agricultural plantations.

Soil microbial communities are strongly distributed as per soil chemical properties under different land-use patterns (Srivastava and Mishra, 2021; Tosi et al., 2021). To demonstrate the effects of land-use, fertilization, soil pH, and nutrient concentrations on the diversity of bacterial taxonomic groups, SEM was constructed on the basis of bacterial diversity (*Table A2*) and soil chemical variables (*Table A1*; chi-square = 315, $P < 0.001$) (*Fig. 6*). Bacterial diversity was highly correlated with soil organic C, which accounted for the effects of soil pH, land use, and other chemical variables ($\lambda = 0.981$). The total N, available P, and the C/N ratio had significant effects on the bacterial diversity across different land-use soils. According to canonical correspondence analysis, the soil C and N contents were key factors for classifying natural forests (CIC, CAF, ALG, and TSO) and the CUL and ORG plantations into three main areas (*Fig. 7*). The available P also played an important role in distinguishing between the soil bacterial communities of ORG and other land-use patterns. These results are consistent with those of our previous study (Yu et al., 2012). These differentiations among the soil C, N, and available P between natural forests and the ORG plantation primarily resulted from differences in the nutrient supply. Unlike chemical fertilization in the ORG plantation, the dominant pathway for nutrient return to soil in natural ecosystems is from leaf litterfall, which contains high C and N contents (Price et al., 2009). The CUL plantation, which is a type of coniferous forest, has significantly lower annual litterfall than the natural broad-leaved forests (Yang et al., 2009; Yu et al., 2012). When the soil C and N content decreased as a result of the conversion of natural forests to plantations, the readily decomposable organic C and N were lost preferentially (Qin et al., 2011). These fractions support a majority of the heterotrophic microbial biomasses that have been reported in soils (Degens et al., 2000), and their loss could decrease soil microbial richness and diversity via disproportionate declines in catabolic functions. However, as P is absent in subtropical acidic soil (He et al., 2008), it is reasonable to say that available P plays an important role in separating ORG from other land-use soils.

Multiple statistical analyses, i.e., hierarchical cluster analysis heatmap, response ratio, and LDA effect size, showed that the distribution of the soil bacterial community significantly differed between natural forests and plantations. However, the differences among natural forests, CUL plantation, and ORG plantation were inconsistent. For example, according to the 95% CI, the differences in bacterial communities between natural forests and the ORG plantation were significant, but the difference in bacterial communities between natural forests and the CUL plantation were insignificant (*Fig. 4*). Moreover, the ratio of *Proteobacteria* and *Acidobacteria*, which is a broad indicator of nutrient status (Smit et al., 2001), in the ORG plantation (2.76 ± 0.18) was significantly lower than that in the CUL plantation (3.80 ± 0.27; $P < 0.05$). These inconsistent results suggest that certain agricultural practices, such as fertilization, herbicide, and irrigation, in the ORG plantation have a greater effect on the soil bacterial community composition

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than on naturally regenerated plantations in the subtropical region (Chave et al., 2010; Sheng et al., 2010). By contrast, the *Proteobacteria* phylum, which was the dominant bacteria in soil ecosystems (Smit et al., 2001; Sheng et al., 2010), made a primary contribution that differentiates the bacterial community of natural forests from that of plantations at the phylum level according to SIMPER analysis (*Table A3*). A previous study showed that the *Proteobacteria* phylum was associated with C and N cycling in soil ecosystems (Smit et al., 2001). Thus, when the concentration of *Proteobacteria* decreased with the conversion of natural forests to plantations, soil C and N cycling weakened concomitantly. At the class level, *β-proteobacteria* appeared to be less abundant in natural forests than in plantations and were capable of ammonium oxidation, denitrification, and polyphosphate accumulation (Naeem and Wright, 2003), which indicated the important role of this group in soil nutrient cycling in land-use changes. At the family level, the conversion of natural forests to plantations decreased the concentrations of *Acidobacteriaceae*, *Solibacteraceae*, *Acidimicrobiales*, *Bradyrhizobiaceae*, *Rhizobiales*, *Rhodospirillales*, *Burkholderiales*, and others and increased those of *Nocardioidaceae*, *Sphingobacteriales*, *Bacilli*, *Nitrospiraceae*, and others according to LDA effect size (*Fig. 5*). These bacterial taxa were closely associated with the accumulation and decomposition of soil organic matter, mineralization, and transformation of N and P and other nutrient utilization (Uroz et al., 2010; Knelman et al., 2012; Huang et al., 2013). Therefore, the responses of the soil microbial community to the conversion of natural forests to plantations can influence nutrient cycling and sustainable soil use (Ramírez et al., 2020; Xiao et al., 2021).

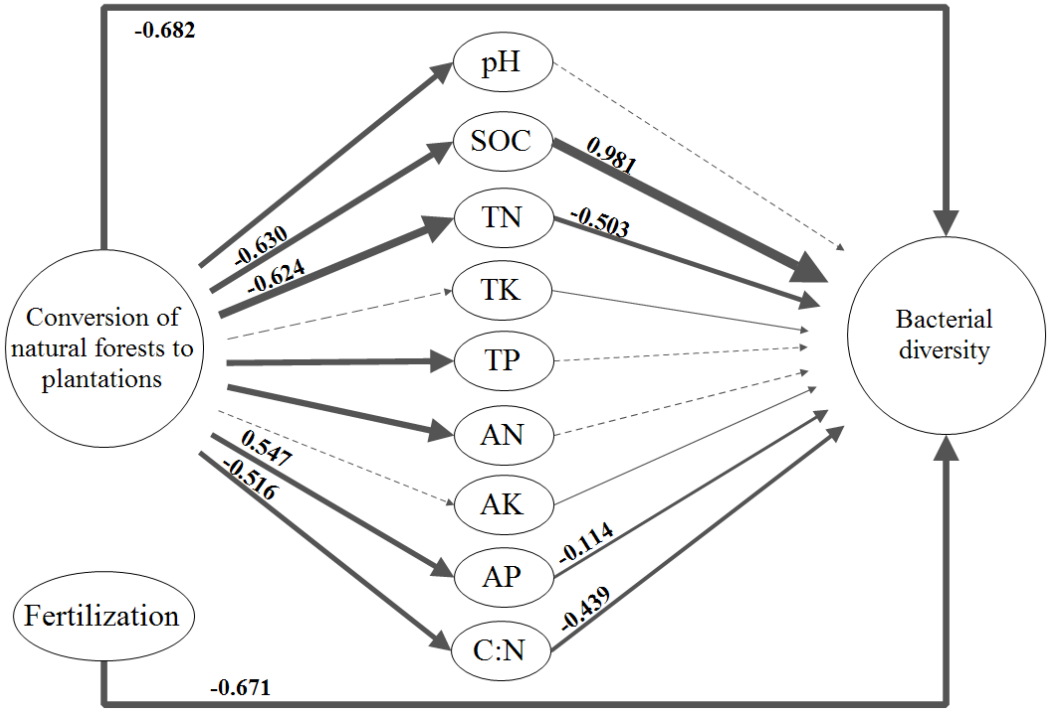

Figure 6. *Structural equation model showing the causal influences of natural forests to plantations conversion and soil chemical variables on soil bacterial diversity. The width of arrows indicates the strength of the causal effect. The numbers above the arrows indicate path coefficients (λ), and insignificant pathways are represented by dashed lines (λ ≤ 0.05)*

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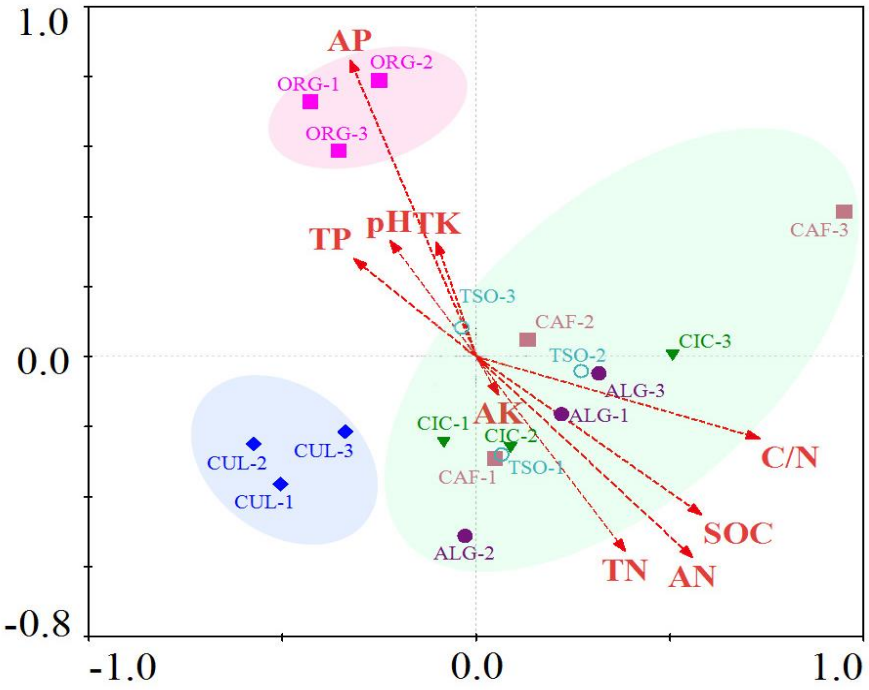

Figure 7. *Canonical correspondence analysis relating bacterial sequence patterns and land-use patterns with soil properties such as soil organic C (SOC); total N (TN), P (TP), and K (TK) contents; available N (AN), K (AK), and P (AP) contents; and the C/N ratio. CIC, CAF, ALG, TSO, CUL, and ORG represent Cinnamomum chekiangensis, Castanopsis fargesii, Altingia gracilipes, Tsoongiodendron odorum, Cunninghamia lanceolata, and Citrus reticulata plantation, respectively*

Conclusion

In summary, our findings address the lack of knowledge regarding the composition and control over bacterial communities in subtropical China as well as the impact of land-use changes on the bacterial community and diversity. As a result of changes in soil C, N, and available P contents, the conversion of natural forests to plantations alters bacterial community composition and significantly decreases bacterial diversity. The negative responses of soil bacterial communities and the conversion of natural forests to agricultural plantations are not conducive to the conservation of soil nutrition and sustainable use of soil.

In the following research, we will further reveal the driving factors of the dynamic changes in the microbial community structure during this land-use transition, as well as the shift in the feedback patterns generated by the changing microbial communities and vegetation types.

Acknowledgements. This research was funded by the High-end Research Training Project for Professional Leaders of Teachers in colleges in Jiangsu Province, grant number 2020GRFX038, and the investigation was funded by the Youth Support Project in Jiangsu Vocational College of Agriculture and Forestry, grant number 2020kj004.

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APPENDIX

Table A1. *Soil chemical properties under different land-use soils in subtropical China*

	CIC	CAF	ALG	TSO	CUL	ORG
pH	4.08(0.19)a	4.65(0.40)b	4.12(0.08)a	4.00(0.42)a	4.60(0.17)b	4.67(0.05)b
Soil organic C (g/kg)	29.3(3.53)b	29.1(14.0)b	63.2(2.71)c	33.3(7.94)b	21.9(5.75)b,c	8.8(0.42)a
Total K (g/kg)	15.6(1.83)b	14.0(4.94)a,b	8.80(0.39)a	13.5(0.92)a,b	10.5(4.82)a,b	16.0(0.55)b
Total P (g/kg)	0.68(0.08)a	0.61(0.43)a	0.49(0.10)a	0.52(0.12)a	1.03(0.48)a	0.93(0.25)a
Total N (g/kg)	2.74(0.34)c	1.77(0.09)b,c	3.80(0.25d)	2.99(0.46)c	2.02(0.42)b	1.36(0.03)a
Available K (mg/kg)	107(23.2)a,b,c	131 (69.4)b,c	55.7(6.78)a,b	37.7(3.31)a	157(78.9)c	64.3(34.4)a,b
Available N (mg/kg)	232(14.1)b,c	209(70.4)b	292(9.6)c	255(28.8)b,c	209(47.7)b	124(7.51)a
Available P (mg/kg)	2.89(0.49)a,b	2.85(1.35)a,b	4.02(0.89)b	3.97(1.36)b	1.94(0.79)a	18.19(0.94)c

The numbers in brackets are standard deviations. Different letters in a line mean significant difference at 5% level. CIC, CAF, ALG, and TSO are four natural forests, representing *Cinnamomum chekiangensis*, *Castanopsis fargesii*, *Altingia gracilipes*, and *Tsoongiodendron odorum*, respectively. CUL and ORG represent *Cunninghamia lanceolata* plantation and *Citrus reticulata* plantation, respectively

http://www.aloki.hu ● ISSN 1589 1623 (Print) ● ISSN 1785 0037 (Online)
DOI: http://dx.doi.org/10.15666/aeer/2004_28312844

Table A2. *Bacterial diversity indices*

	Average abundance		Average contribution	Ratio	Percent contribution
	Natural forests	Plantations			
Proteobacteria	437	392	1.88	2.54	23.0
Actinobacteria	236	205	1.30	1.44	15.8
Acidobacteria	115	143	1.14	2.15	14.0
Bacteroidetes	55	47	0.57	1.62	6.93
Planctomycetes	50	50	0.48	1.13	5.84
Firmicutes	49	54	0.39	1.40	4.83
Chloroflexi	68	71	0.39	1.46	4.76
Cyanobacteria	16	24	0.33	2.03	4.09
Nitrospirae	7	14	0.28	2.67	3.41
Gemmatimonadetes	12	19	0.26	1.07	3.23

Table A3. *SIMPER analysis of dissimilarity*

Soil samples		Phylogenetic diversity	Chao1	Shannon
Natural Forests	CIC	109(2.5)c	5904(295)b,c	9.41(0.04)b
	CAF	107(1.4)c	5700(169)b,c	9.43(0.02)b
	ALG	119(1.7)c	6222(569)c	9.54(0.09)b
	TSO	108(1.6)c	5738(109)b,c	9.45(0.03)b
Plantations	CUL	102(1.9)b	5283(140)a,b	9.11(0.06)a
	ORG	93.6(1.1)a	4747(189)a	9.06(0.07)a

All indices were calculated using the subset of 1,200 sequences per soil sample. The numbers in brackets are standard deviations. Different letters in a row mean significant difference at 5% level. CIC, CAF, ALG, and TSO are four natural forests, representing *Cinnamomum chekiangensis*, *Castanopsis fargesii*, *Altingia gracilipes*, and *Tsoongiodendron odorum*, respectively. CUL and ORG represent *Cunninghamia lanceolata* plantation and *Citrus reticulata* plantation, respectively

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