RESEARCH ARTICLE

Impact of land use change on soil properties, enzyme activities, and microbial communities in the Yellow River basin's Henan segment, China

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Soil microbial communities play a pivotal role in ecosystem functioning but can be altered by land use changes. This study investigated the impacts of typical land use changes on soil properties, enzyme activities, and microbial communities in the Henan Segment of the Yellow River basin, China following the conversion from traditional farmland to artificial forests and agroforestry systems. The results indicated that the transition to artificial forests led to an increase in soil organic matter content and soil fertility. Compared with traditional farmland, artificial forests demonstrated higher levels of urease and invertase enzyme activity. The soil microbiomes of traditional farmland and artificial forests had higher proportions of *Proteobacteria* and *Actinobacteria*, whereas the agroforestry systems were enriched in *Acidobacteria*. Co-occurrence network analysis revealed that the transition from conventional farmland to artificial forest enhanced soil microbial complexity and cohesion. *Proteobacteria*, *Acidobacteria*, *Actinobacteria*, *Rokubacteria*, *Planctomycetes*, and *Gemmatimonadetes* were identified as pivotal components of the soil bacterial network during land use change. Redundancy and correlation analyses showed a negative association between certain soil microbial phyla such as *Firmicutes*, *Acidobacteria*, and *Patescibacteria*, and pH, available potassium, and available nitrogen ($P < 0.05$). Moreover, nitrogen availability and urease activity were negatively correlated among *Gemmatimonadetes*, whereas soil organic matter was positively correlated with *Chloroflexi* ($P < 0.05$). This study revealed the critical influence of land use change on the distribution of crucial bacterial groups, underscoring the importance of microecological equilibrium.

Keywords: land use change; artificial forests; soil bacterial community; co-occurrence network; Yellow River basin.

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Introduction

The Yellow River basin in China has undergone significant development. However, it is confronted with formidable ecological challenges. In recent years, with increasing emphasis on high-quality development in the region, research on the ecological environment of the Yellow River basin has emerged as a focal point of academic attention. In the Yellow River basin, land use changes are among the most pressing ecological and environmental concerns. Land use change significantly affects terrestrial ecosystems and is emerging as a global concern [1, 2]. The expansion of artificial forests has been a notable global trend. Forestry practices

characterized by short rotation cycles, and multi-generational succession can induce changes in soil properties [3]. Implementing scientific and reasonable strategies for land use practices can help mitigate negative soil impacts [4-6], conversely, unreasonable approaches might result in soil degradation, loss of biodiversity, and decreased land productivity [7]. For example, planting second-generation trees initially improves soil water retention, organic matter, and readily available nutrients. However, these benefits might diminish over time [8]. The transformation of natural forests into plantations of *Cupressus sempervirens* and *Alnus subcordata* increases soil organic carbon levels by 25% and 1.11%, respectively, while the replacement of forests with *Quercus castaneifolia*, *Acer velutinum*, or agricultural land has been associated with declines in soil organic carbon by 4%, 12.11%, and 53%, respectively [9]. Previous studies have indicated that soil degradation following such land conversions is often linked to slower litter decomposition and disrupted nutrient balances [10, 11].

Soil microbial communities are important indicators of soil health and respond quickly to environmental changes [12, 13]. Microbial communities present in soil are integral to the biogeochemical cycles of carbon, nitrogen, and phosphorus, as well as facilitate the decomposition of organic matter [14, 15]. There is evidence that plant interactions, soil properties, and land use influence soil bacterial biodiversity and composition [16-18]. The transition from pine forests to grasslands substantially alters microbial community composition, as indicated by phospholipid fatty acid profiles and physiological alterations [19]. Cultivating legumes notably increases soil microbial populations compared to cultivation of grasses or shrubs [20]. Traditional soil microorganism studies focusing on isolated strains through lab cultures fail to capture the full complexity of microbial interactions in natural settings. High-throughput sequencing now allows for an in-depth analysis of entire microbial communities *in situ*, significantly improving the understanding of soil microorganisms. Previous studies have emphasized the influence of soil properties on microbial community composition [21-23]. Hence, additional research is imperative to explore how alterations in land use affect soil microorganisms in the Henan segment of the Yellow River basin.

Soil microbes engage in complex interactions and form networks that are vital for ecosystem functions [24-26]. These networks reveal the dynamics within soil bacterial communities and increase in complexity with plant growth, leading to more modular structures closely tied to nitrogen cycling [27, 28]. Land use changes affect soil microbiome structures. However, the relationship between these changes in soil properties and bacterial community networks in the Henan Segment of China's Yellow River basin is not well understood. The present study aimed to investigate the effects of land use changes on soil physicochemical characteristics, soil microbial diversity, and community composition in the Yellow River basin of the Henan section, China. Specifically, this research focused on three common types of land use including traditional farmland, artificial forests, and agroforestry systems. This study sought to analyze the impact of these land-use modifications on soil physicochemical characteristics and assess the influence of these changes on soil microbial diversity and community composition using high-throughput sequencing. Additionally, the study aimed to investigate soil microbial co-occurrence networks and relationships and their connections to soil properties to gain insights into the factors that influenced microbial community composition. The findings of this research could inform the development of more efficient soil management techniques.

Materials and methods

Study area

This study was conducted within the Yellow River basin in Henan, China located to the south of Kaifeng City (114°9’36.36”E, 34°21’18.72”N) with

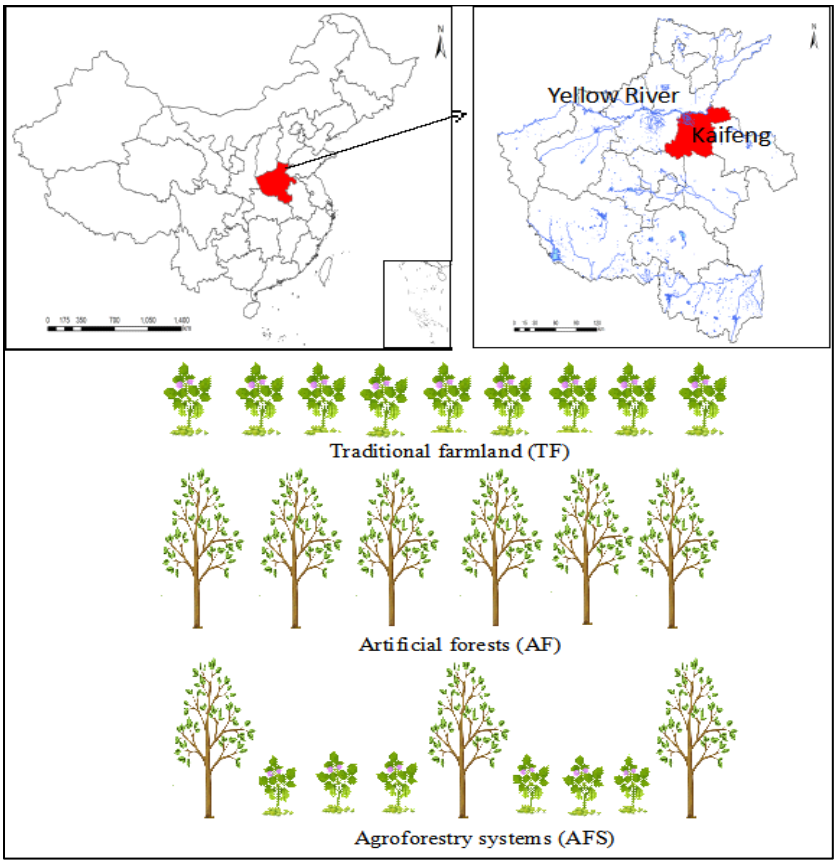

Figure 1. The study areas and monitoring site.

the temperature of 14.5°C, characterized by humidity and subtropical climate, a frost-free period approximately 221 days each year, an annual rainfall of approximately 627.5 mm. The suitable cultivation period stretches from the beginning of March to November. According to the Chinese Soil Taxonomy framework (https://www.resdc.cn/data.aspx?DATAID=145), the soil in this region is categorized as tidal, originating from alluvial deposits in the Yellow River. Historically, this region has predominantly engaged in traditional agriculture with the primary crops being wheat, corn, soybeans, and peanuts. Approximately 25 years ago, a shift occurred in some of this agricultural land, leading to the establishment of artificial forests, primarily consisting of *Populus* L., spanning an area of 6.47 hectares. By 2018, certain portions of these artificial forests covering 3.31 hectares following clear-cutting practices underwent reforestation and were combined with agricultural crops to form agroforestry systems. Hence, the different land uses within the study area are traditional farmland (TF) characterized by the cultivation of crops such as wheat, corn, soybeans, and peanuts, artificial forests (AF), mainly mono-species poplar stands dominated by *Populus* L., and Agroforestry systems (AFS), a mix of poplar and crops with the dominant plants being *Populus* L. and soybeans. The descriptions of each study area were shown in Figure 1.

Experimental design and treatment

In November 2020, the study randomly selected stands from three distinct types of land uses with a 10 m × 10 m plot for each stand. Five soil samples from each transect were mixed, and each land use type was transported to the laboratory. A portion of each soil sample was air-dried, crushed, and passed through screens of

mesh sizes of 0.85, 0.25, and 0.15 mm. A separate portion of the sample was preserved at -20°C for high-throughput sequencing analysis, which covered three land uses × three replicates. The samples were preserved in polyethylene bags for subsequent analysis.

Soil analysis

Soil pH was determined using a pHS-3E pH meter (Shanghai Leici Company, Shanghai, China) with a soil to water ratio of 1:2.5, shaking in a reciprocating shaker for 15 min at room temperature [29]. The electrical conductivity (EC) of the soil was measured using a DDS-11A digital meter (Shanghai Leici Company, Shanghai, China) with a soil to water ratio of 1:5, shaking for 30 min, and then left undisturbed for 30 min before the measurements [30]. The cation exchange capacity (CEC) was determined using 1 mol/L ammonium acetate solution (pH 7.0) to treat the soil sample after the samples being centrifuged and washed with ethanol [31]. Soil organic matter (SOM) was quantified using the potassium dichromate-sulfuric acid digestion method to oxidize soil organic matter under heating conditions and was calculated by measuring the remaining potassium dichromate [32]. Soil available nitrogen was assessed using the alkali hydrolysis and diffusion technique by treating soil samples with sodium hydroxide solution to convert readily hydrolysable nitrogen into an ammonia state, which continuously escaped and was absorbed by boric acid followed by titration with a standard acid to calculate the amount of available nitrogen in the soil. Soil available potassium was determined using the ammonium acetate extraction method, which was used as an extraction agent to extract potassium from soil by exchanging it with potassium ions [33]. Urease activity in the soil was measured by incubating 10 g of soil with a 10% urea solution for 24 h at 37°C and was reported as NH_4-N in mg/g/d, whereas invertase activity was measured by mixing 5 g of soil with 15 mL of an 8% sucrose solution and incubating at 37°C for 24 h, resulting in glucose at mg/g/d [34].

Next-generation sequencing

Three replicates of soil samples from each land use type were analyzed using a modified cetyltrimethylammonium bromide (CTAB) method to extract DNA [35]. Briefly, CTAB was used to form ion pairs with DNA, which was subsequently combined with impurities such as proteins and polysaccharides that were dissolved in water. The impurities were eliminated by centrifugation and the DNA was then precipitated. The polymerase chain reactions (PCR) were performed using the primers 338F (GTG CCA GCM GCC GCG GTA A) and 806R (GTG CCA GCM GCC GCG GTA A) and the PCR products were analyzed and purified using an AxyPrep DNA Gel Recovery Kit (Sigma-Aldrich, Inc., St. Louis, MO, USA) and characterized by 2% agarose gel electrophoresis. Using a FLx800 microplate reader (BioTek, Winooski, Vermont, USA) and the Quantity PicoGreen dsDNA Assay Kit (Thermo Fisher Scientific, Waltham, MA, USA), fluorescence quantification and library construction were carried out with the aid of the TruSeq Nano DNA LT Library Pre Kit (Illumina, San Diego, CA, USA) following the manufacturers' instructions. Illumina MiSeq Sequencing System was used for double-ended sequencing of microbial constitutive DNA. Genome sequencing was performed on the Pacific Biosciences and Illumina Novaseq platforms by Personal Biotechnology Co., Ltd., Shanghai, China, focusing on the V3-V4 region of the 16S rRNA gene for bacterial analysis.

Statistical analysis

Microsoft Excel 2019 (Microsoft, Redmond, Washington, USA) and SPSS (version 22.0) (IBM, Armonk, New York, USA) were used for data processing and statistical analysis. One-way ANOVA with Duncan's test was used to assess the impact of land use change on soil physicochemical characteristics and microbial diversity with land use change as an independent variable. The *P* value less than 0.05 was defined as significant difference, while *P* value less than 0.01 was defined as very significant difference. QIIME2 (2019.4) (https://qiime2.org/) and R

Table 1. Effects of land use changes on soil properties.

Soil properties	TF	AF	AFS
pH	8.04 + 0.07^{a}	8.08 + 0.04^{a}	7.94 + 0.02^{b}
SOM (g/kg)	16.83 + 1.09^{b}	18.60 + 0.65^{a}	17.08 + 0.28^{ab}
EC (cmol/kg)	76.60 + 2.41^{ab}	81.60 + 6.58^{ab}	86.80 + 5.17^{a}
CEC (g/kg)	6.75 + 6.75^{b}	8.26 + 1.11^{a}	6.79 + 0.15^{b}
Available K (mg/kg)	68.49 + 8.22^{b}	99.10 + 8.63^{a}	69.07 + 6.52^{b}
Available N (g/kg)	78.22 + 6.03^{c}	121.22 + 13.75^{a}	115.12 + 13.36^{ab}

Note: TF, AF, and AFS represented the traditional farmland, artificial forests, and agroforestry systems, respectively. The data presented are the average values with standard deviations from five repeated measurements. The letters represented a statistically significant disparity ($P < 0.05$).

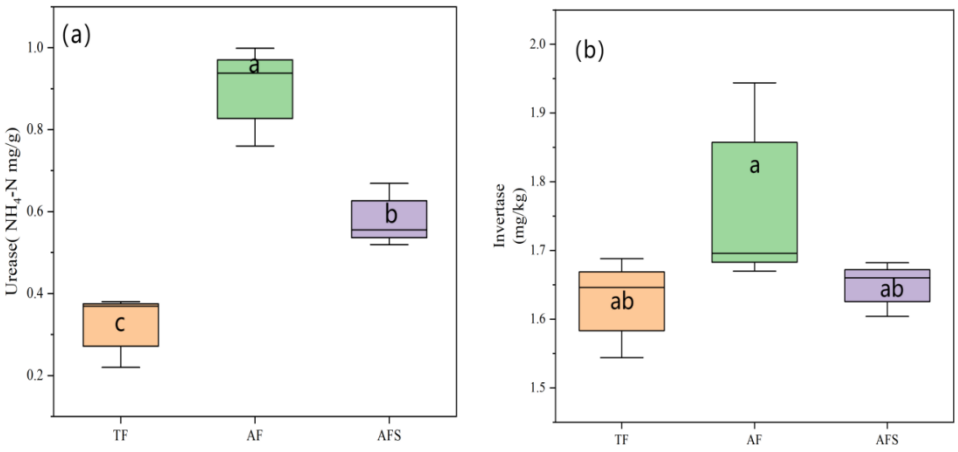

Figure 2. The impact of changes in land use on the activity of soil enzymes. The data presented were the average values with standard deviations from five replicates. Bars with different letters indicated a significant difference ($P < 0.05$).

software (version 3.6.1) (https://www.r-project.org/) were utilized to generate a Venn diagram, microbial abundance chart, co-occurrence networks, nonmetric multidimensional scaling analysis, principal coordinate analysis, and heatmap.

Results and discussion

Soil properties and enzyme activities

Land use changes significantly affected soil properties. Th results showed that AFS had lower soil pH than AF and TF. Soil EC, a marker of salinity and alkalinity, followed the order of TF < AF < AFS with AFS showing the highest EC value. Compared to TF, soil available N, available K, SOM, and CEC were significantly increased ($P < 0.05$) in AF soils (Table 1). Land use changes had the potential to affect the coverage of soil surfaces, thereby influencing soil properties [9]. The disparity in SOM content in different land types might stem from reduced organic matter input resulting from agricultural practices, as well as the potential acceleration of decomposition when soil particles containing organic matter were exposed to air [36]. Increased SOM could attract positively charged ions, which frequently resulted in a higher CEC, consistent with the findings of previous studies [37, 38]. In addition, the results aligned with the concept that soil fertility robustly correlated with land use type [39]. Among the land use types, TF exhibited the lowest available nitrogen content, which could be attributed to consistent light in farmland that boosted plant transpiration and accelerated soil water evaporation, thus inhibiting nitrogen accumulation in the soil [40, 41]. Meanwhile, the

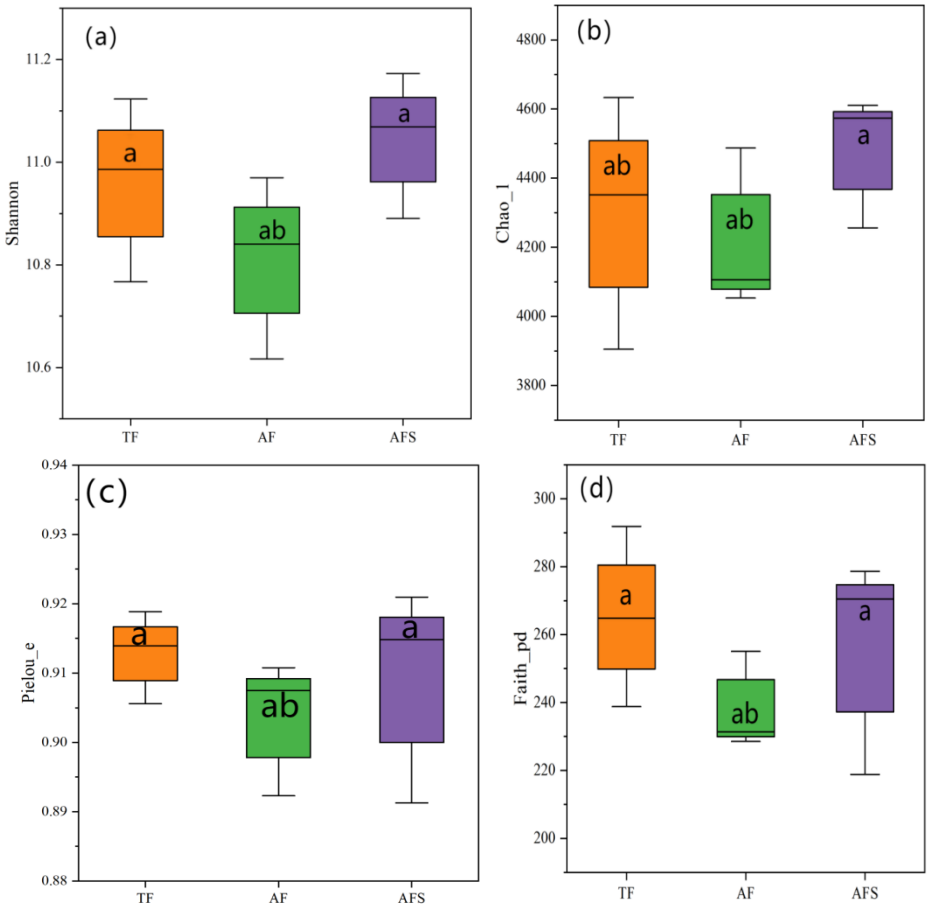

Figure 3. Effects of land use changes on soil microbes' alpha diversity index. TF, AF and AFS were the traditional farmland, artificial forests, and agroforestry systems, respectively. Data was means ± SD of three replicates. Bars with different letters indicated a significant difference ($P < 0.05$).

increased soil surface temperature due to intense light could accelerate nitrogen mineralization [42]. Furthermore, agricultural practices conducted in farmlands had the potential to reduce the size and shape of soil clusters, consequently affecting the concentrations of soil nutrients [43]. Soil enzymes play a vital role in determining soil productivity and biochemical processes. In the present study, soil urease activity exhibited a range of 0.32 to 0.90 NH_4-N mg/g with AF soil having the highest and TF the lowest (Figure 2a). Soil invertase activity was also high in the AF soils of 1.67 mg/kg compared to TF of 1.63 mg/kg. The results showed that land use changes had a marked impact on soil enzyme activities. TF soils exhibited the lowest enzyme activity, indicating a less favorable environment for these biochemical processes. AF soils had higher activities possibly due to the presence of decomposable organic matter enhancing soil fertility, thus improving soil fertility and stimulating enzyme activity [44, 45]. AFS soil showed higher enzyme activity than TF, but lower than AF with significant variability, which was consistent with a previous study [46].

Diversity of microorganisms in the soil

The alterations in land use affected the alpha diversity of soil bacteria (Figure 3). Shannon index ranged from 10.81 to 10.96, the Chao_1 index changed from 4,215.52 to 4,296.47, the Faith_pd index changed from 238.33 to 265.19, and the Pielou_*e* index ranged from 0.9035 to 0.9128. Microbial beta diversity was evaluated using non-metric multidimensional scaling analysis (NMDS). The stress value of the NMDS

analysis was calculated as 0.028, indicating a high level of reliability. In the NMDS analysis plots, land use changes could be clearly differentiated with TF clustering towards the left side of the abscissa and exhibiting distinct separation from AF and AFS. The AF and AFS groups clustered more closely than the TF group (Figure 4). These results indicated that soil microbial characteristics were greatly affected by land use type. The NMDS analysis yielded a stress value of 0.028, suggesting a high degree of reliability. The NMDS analysis plots showed clear differentiation of land use changes with TF clustering on the left side of the x-axis and showing distinct separation from AF and AFS, which clustered more closely together than the TF group suggesting that the soil microbiome was significantly affected by the different types of land use.

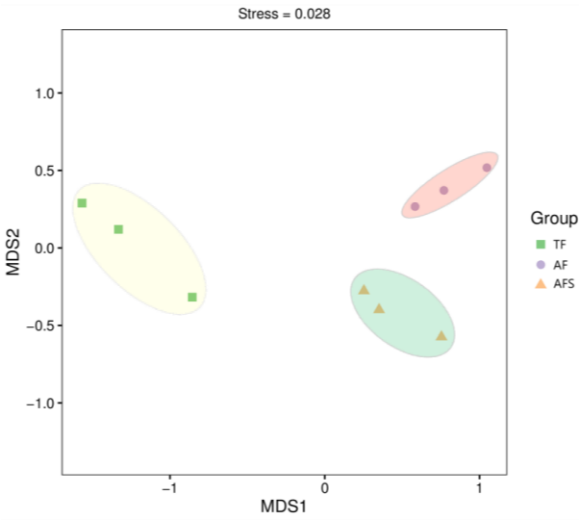

Figure 4. Effects of land use changes on soil microbes' beta diversity. TF, AF, and AFS were the traditional farmland, artificial forests, and agroforestry systems, respectively.

Soil microbial community

Soil microbes are integral components of ecosystems and serve as pivotal indicators of the soil environmental quality [47-49]. The structure of the soil microbial population in the study area was illustrated in Figure 5a. The TF soil had the highest number of unique microbes of 7,403 (31.03%), while AF and AFS had 6,405 (26.84%) and 6,510 (27.28%) unique species, respectively. The shared core of all the samples comprised 1,060 microbes (4.44%). The overlap microbes between AF and AFS soils (1,186 species, 4.97%) was higher than that between TF and AF (495 species, 2.07%) or TF and AFS (801 species, 3.36%). Microbial sequences were categorized into 32 phyla, 106 classes, 258 orders, 385 families, and 718 genera using a 97% similarity threshold. In addition, *Proteobacteria*, *Actinobacteria*, *Acidobacteria*, *Chloroflexi*, *Gemmatimonadetes*, *Bacteroidetes*, *Rokubacteria*, *Patescibacteria*, *Latescibacteria*, *Planctomycetes*, *Firmicutes*, *Verrucomicrobia*, and *Nitrospirae* contributed 26.21, 25.81, 23.13, 9.81, 4.57, 2.22, 2.08, 1.42, 1.01, 0.75, 0.71, 0.56, and 0.41%, respectively (Figure 5b). All dominant bacterial phyla were markedly affected by land use changes. Land use change had a significant impact on the predominant bacterial phyla. *Proteobacteria* displayed the highest relative abundance in the TF soil followed by *Actinobacteria* and *Acidobacteria*, which were beneficial for soil health and decomposition. *Actinobacteria* and *Acidobacteria* were the most abundant in AF and AFS soils followed by *Proteobacteria*. The significant contribution of these microorganisms to soil ecosystems underscored their remarkable ability under various environmental conditions [50, 51]. Principal coordinate analysis (PCoA) at the phylum level revealed a distinct separation of soil microbial communities across the two axes, accounting for 48.9% of the total variance in the soil microbe composition (Figure 5c). TF, AF, and AFS showed significant separation with each land use change predominantly located in different quadrants. The results showed that land use changes had a notable influence on soil microorganisms. Adonis analysis (R^2 = 0.476, P = 0.003) further confirmed this significant impact (Table 2). In addition, TF soil microbial communities formed a distinct group, whereas those of AF and AFS tended to cluster together (Figure 5d). These results were consistent with the composition and distribution of bacterial communities. It was evident from these patterns that land use changes had an impact on

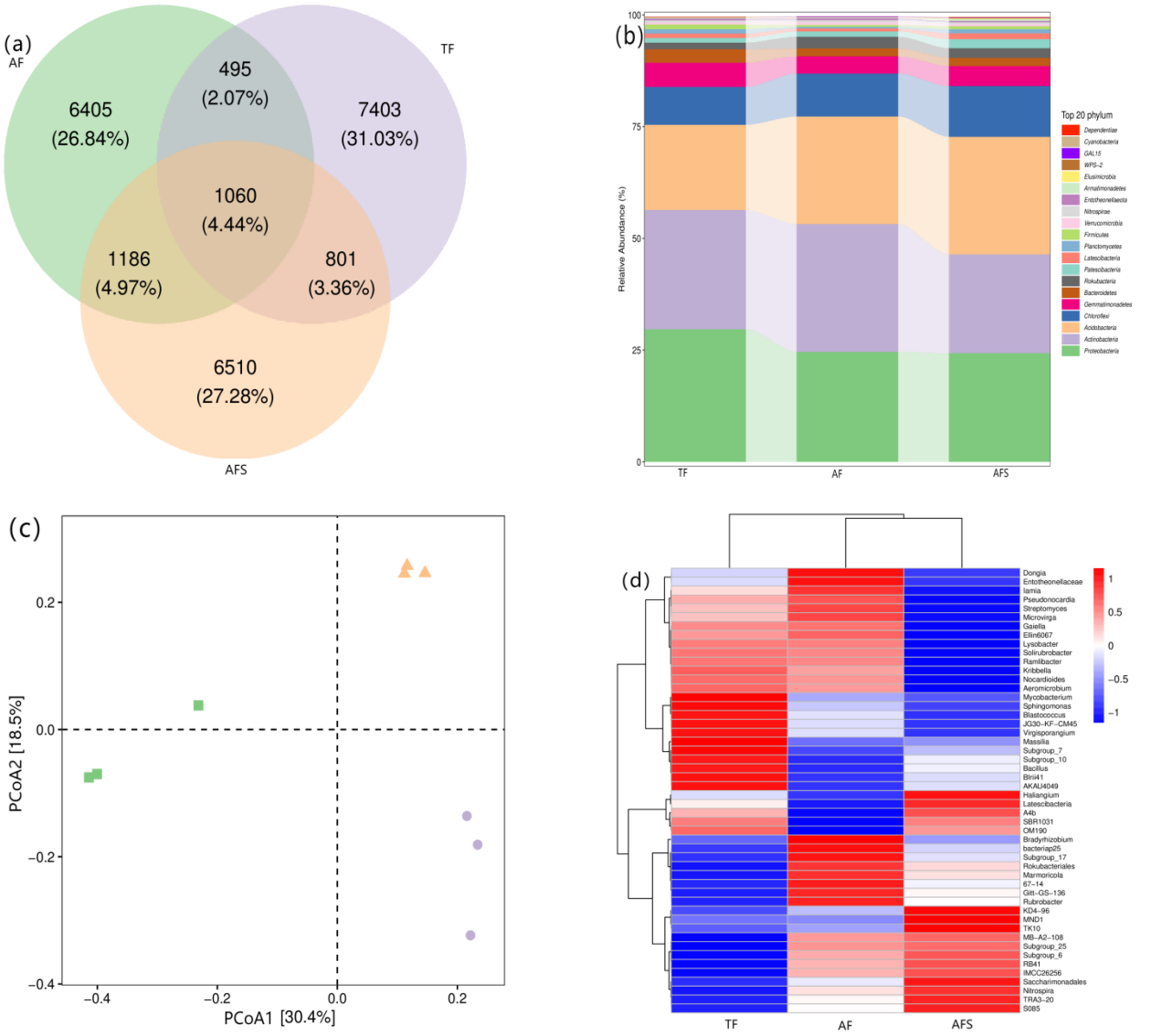

Figure 5. Impacts of land use changes on the soil microbiome. TF, AF, and AFS represented the conventional farmland, artificial forests, and agroforestry systems, respectively.

Table 2. Adonis analysis based on sample distance matrix.

	Df	Sums of Sqs	Mean Sqs	F. Model	R^2	Pr (> F)
Treat	2	0.911365	0.455682	2.721236	0.475638	0.003
Residuals	6	1.004725	0.167454	NaN	0.524362	NaN
Total	8	1.916090	NaN	NaN	1.000000	NaN

Note: Df was the degree of freedom. Sums of Sqs and Mean Sqs were the sum of squares of deviation and the mean square error, respectively. F. Model represented the test value of F statistics. R^2 was the proportion of variances and residuals accounted for by group interpretations to the total variance. Pr (> F) was the *P* value obtained by the permutation test.

microorganism composition, particularly those microbes crucial for soil material transformation.

Co-occurrence network of microbial communities

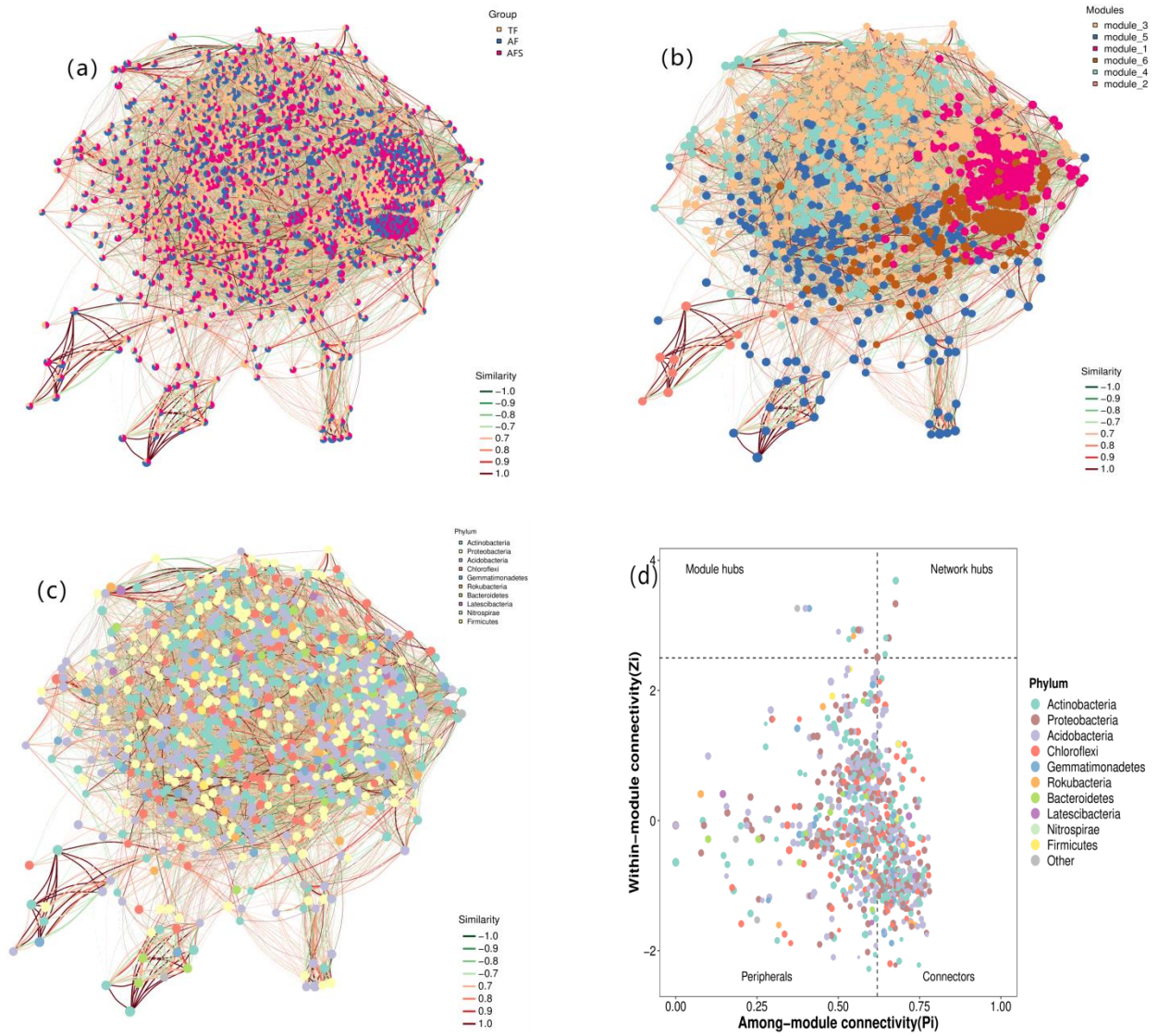

Figure 6. Molecular ecological network and Zi-Pi diagram of TF, AF, and AFS. TF, AF, and AFS were the traditional farmland, artificial forests, and agroforestry systems, respectively.

Co-occurrence network analysis (Figure 6) and topological data (Table 3) revealed distinct structural and interaction patterns among soil bacterial communities with land use changes. Soil bacterial networks transitioning from cultivated land to forestry systems were more positively than negatively connected. Compared with TF, the number of vertices, edges, betweenness centralization, modularity, average nearest neighbor degree, and closeness centrality significantly increased in AF and AFS, displaying more complex networks. Despite the lower degree of bacterial community interaction and connection tightness in TF, limited interactions still formed a highly modular bacterial interaction network. In the current study, *Proteobacteria*, *Actinobacteria*, *Rokubacteria*, *Acidobacteria*, *Planctomycetes*, and *Gemmatimonadetes* played central roles in both the co-occurrence networks and the overall bacterial community. *Proteobacteria* and *Actinobacteria* functioned as the central hub and primary network module in

Table 3. Topological properties of molecular ecological network of soil bacterial communities.

Properties	TF	AF	AFS
Vertice	684	754	778
Edge	27298	36600	38964
Betweenness centralization	1932979	2571859	3249515
Modularity	0.480	0.612	0.613
Average nearest neighbor degree	101	123	126
Average path length	2.377	2.308	2.293
Closeness centrality	74.628	82.019	85.315
Degree assortativity	0.605	0.531	0.551
Density	0.117	0.129	0.129
Diameter	3.230	3.317	3.173
Clustering coefficient	0.685	0.672	0.673

the soil bacterial network with Zi ≥ 2.50 and Pi ≥ 0.62. *Acidobacteria* acted as the module center for network modules 3, 4, and 5. *Rokubacteria* was the module center of network module 3, while *Planctomycoetes* and *Gemmatimonadetes* were the module centers of network module 5. Previous studies have documented the influence of land use changes on the quality of soil [52, 53]. The conversion of cultivated land to forest land significantly enhanced soil nutrient status and increased the availability of soil resources, thereby promoting greater complexity and cohesiveness within soil microbial co-occurrence networks [54, 55]. This was evidenced by the observed progressive increase in the number of positive correlation connections within these networks. Compared to TF, AFS with high levels of available nitrogen exhibited a higher abundance of nodes and connections within molecular ecological networks, as well as shorter average path lengths. These results indicated that differences in microbial relationships could be important signs that affected soil fertility, highlighting the profound impact of land use change on the biological and chemical characteristics of the soil. Furthermore, this study revealed that each module within the microbial interaction network possessed distinct functionalities. Specifically, artificial forests, characterized by a higher soil available N content, displayed a significantly greater number of nitrogen cycling-related network modules than traditional farmlands. *Actinobacteria* and *Proteobacteria*, which served as core members of the artificial forest module, were pivotal in nitrogen biogeochemical cycling. Similarly, key taxa such as *Proteobacteria*, *Acidobacteria*, and *Actinobacteria* in the TF and AFS soil networks primarily contributed to the soil carbon and nitrogen cycles. Transformation of farmland into forest led to a notable increase in soil organic carbon and total nitrogen levels. Furthermore, *Rokubacteria*, *Planctomycetes*, and *Gemmatimonadetes*, which were identified as the key organisms in the bacterial networks in this study, had not been extensively studied in soil ecology. Further research is required to understand their unique functions and impact. The results indicated that changes in soil use were closely linked to the characteristics of microbial interaction networks and their modules. The conversion of farmland to artificial forests enhanced the complexity and cohesion of microbial communities.

Redundancy analysis

Redundancy analysis (RDA) showed that the first four principal axes accounted for 79.3% of the total variation in the soil microbial community, indicating that changes in land use were the primary drivers of the evolution of the soil microbial community. The cumulative explained variance of 49.74% was primarily due to the first and second axes, which accounted for 28.01% and 21.73% of the variation, respectively. Soil microbial communities responded significantly to

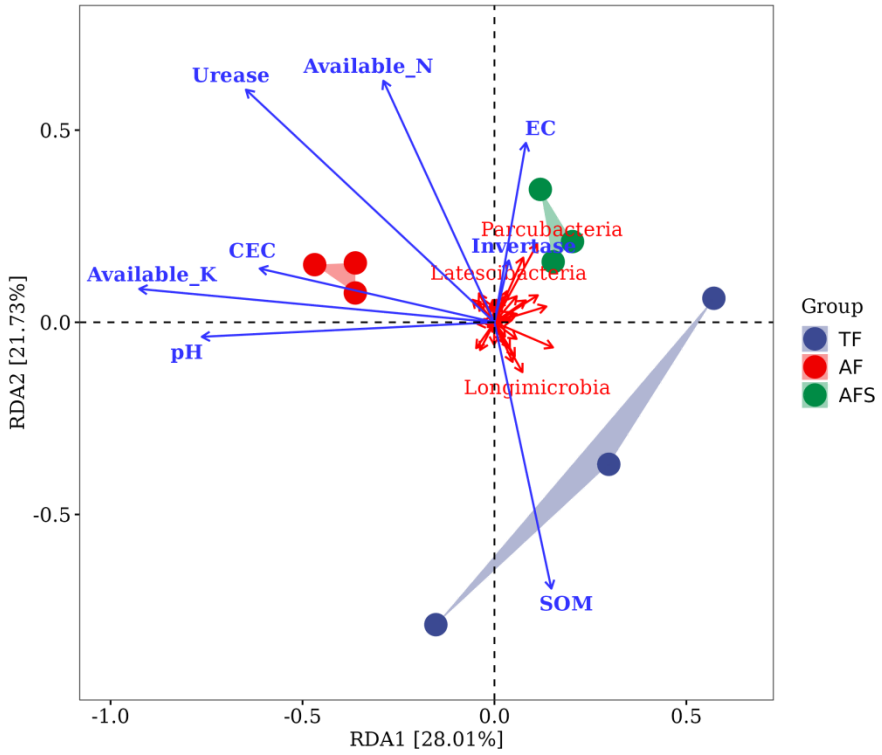

Figure 7. RDA analysis of soil microorganisms with soil properties. TF, AF, and AFS were the traditional farmland, artificial forests, and agroforestry systems, respectively. The blue arrows represented environmental variables. The red arrows depicted soil microbes. The length of the arrows signified the relative importance of each environmental factor in explaining variations in bacterial community structures, while the angles between the arrows reflected the degree of correlation between them.

factors such as soil available K and N concentrations, urease activity, SOM, and pH as evidenced by the lengths of their respective vectors (Figure 7). The correlation between the prevalence of genera and soil physicochemical properties was examined using Pearson's correlation analysis (Supplementary Table 1s). The findings indicated significant negative correlations between certain soil microbial phyla including *Firmicutes*, *Acidobacteria*, *Patescibacteria* and soil pH, available potassium, available nitrogen ($P < 0.05$). Additionally, phyla such as *Gemmatimonadetes* exhibited significant negative correlations with available nitrogen and urease activity, whereas *Gemmatimonadetes* and *Chloroflexi* were positively correlated with soil organic matter and available potassium content ($P < 0.05$), respectively. These findings indicated that soil characteristics were crucial for influencing the prevalence of important bacterial genera, highlighting the importance of maintaining stability in microecosystems. Land use changes could have a significant impact on soil microbial communities, leading to changes in the structure and function of microbial populations, which in turn could affect the transformation and cycling of soil nutrients [56, 57].

Conclusion

This study evaluated how changing conventional farmland to artificial forests and agroforestry systems affected soil characteristics and microbial populations in the Henan Segment of the Yellow River basin, China. The conversion of traditional farmland to artificial forests significantly enhanced soil organic matter contents and soil fertility. The conversion of traditional farmlands resulted in the formation of distinct microbial communities in the soil.

Proteobacteria and *Actinobacteria* were more abundant in traditional farmlands and artificial forests, whereas *Acidobacteria* was more abundant in agroforestry systems. The shift from agricultural land to artificial forests or agroforestry areas had enhanced the complexity and cohesiveness of microbial co-occurrence networks in the soil. *Actinobacteria*, *Proteobacteria*, *Rokubacteria*, *Planctomycetes*, and *Gemmatimonadetes* were identified as the key organisms in the bacterial networks in the present study. Analyses of redundancy and correlation showed a significant negative correlation between *Firmicutes*, *Acidobacteria*, *Patescibacteria* and soil pH, available potassium, available nitrogen, respectively. *Gemmatimonadetes* and *Chloroflexi* were positively correlated with soil organic matter and available potassium content, respectively. The results confirmed that soil fertility, soil organic matter, and pH were critical factors that drove microbial community differences across land use types, which highlighted the advantage of converting farmlands to forests to improve biomass and soil quality. Subsequent studies may explore the functional roles of soil microbial communities to enhance the comprehension of their contributions to ecosystem processes within the context of changing land use patterns.

Acknowledgments

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Supplementary

Table 1S. Correlations between abundant taxa and soil variables.

	pH	SOM	CEC	EC	Available N	Available K	Urease	Invertase
Acidobacteriia	-0.277	0.276	-0.521	-0.442	-0.503	-0.667*	-0.191	0.157
Chloroflexi	0.245	0.057	0.246	-0.045	0.354	0.781*	0.454	0.204
Gemmatimonadetes	-0.246	0.697*	-0.452	-0.535	-0.685*	-0.537	-0.784*	-0.317
Firmicutes	-0.733*	-0.15	-0.232	0.074	0.294	-0.357	-0.329	0.103
Patescibacteria	0.284	0.474	-0.237	-0.605	-0.759*	-0.385	-0.108	-0.478
AKAU4049	-0.377	0.126	-0.279	0.383	0.006	-0.373	-0.694*	-0.167
Anaerolineae	-0.621	0.058	-0.596	-0.133	-0.233	-0.792*	-0.29	0.082
AT_s3_28	-0.249	-0.443	0.004	0.833**	0.59	0.043	0.086	-0.284
Babeliae	0.669*	-0.12	-0.483	0.265	0.11	-0.688*	-0.453	0.082
Bacilli	-0.459	0.536	-0.565	-0.291	-0.532	-0.704*	-0.867**	-0.166
Bacteroidia	-0.415	0.798**	-0.531	-0.192	-0.447	-0.21	-0.706*	-0.055
BD2_11_terrestrial_group	-0.362	-0.454	-0.1	0.758*	0.556	-0.166	-0.103	-0.15
Blastocatellia	0.111	-0.703*	0.277	0.528	0.328	-0.021	0.429	0.085
Chthonomonadetes	0.535	-0.488	0.583	0.107	0.192	0.453	0.759*	-0.173
Clostridia	-0.223	0.375	-0.619	-0.17	-0.672*	-0.773*	-0.334	-0.118
Deinococci	-0.415	0.543	-0.486	-0.407	-0.649	-0.715*	-0.59	-0.022
Deltaproteobacteria	-0.588	-0.113	-0.555	0.324	0.032	-0.737*	-0.449	0.041
FCPU426	-0.547	-0.182	-0.545	0.339	0.073	-0.699*	-0.301	0.081
FFCH16263	0.571	-0.59	0.867**	-0.147	0.51	0.796*	0.922**	0.142
Fibrobacteria	-0.672*	0.22	-0.209	-0.072	-0.173	-0.448	-0.467	0.053
Fimbriimonadia	-0.589	0.046	-0.615	0.2	-0.27	-0.914**	-0.523	0.142
GAL15	0.298	-0.625	0.525	0.286	0.693*	0.708*	0.891**	0.072
Gitt_GS_136	0.804**	-0.308	0.693*	-0.49	-0.149	0.363	0.706*	0.051
Ignavibacteria	-0.124	0.830**	-0.471	-0.504	-0.894**	-0.512	-0.706*	-0.206
MB_A2_108	0.545	-0.457	0.289	0.024	0.218	0.246	0.724*	0.126
NC10	0.291	-0.659	0.416	0.568	0.759*	0.534	0.625	-0.21
OLB14	-0.772*	0.064	-0.528	0.001	-0.306	-0.922**	-0.549	0.225
Phycisphaerae	-0.29	0.513	-0.572	-0.489	-0.774*	-0.847**	-0.566	0.021
Rubrobacteria	0.41	-0.826**	0.808**	0.099	0.472	0.485	0.875**	0.234
S0134_terrestrial	-0.142	0.386	-0.161	0.039	-0.431	-0.334	-0.694*	-0.303
Subgroup_17	-0.086	-0.622	0.26	0.601	0.763*	0.228	0.264	-0.139
Subgroup_6	0.095	-0.712*	0.258	0.764*	0.725*	0.218	0.357	0.04
Thermoplasmata	-0.818**	0.067	-0.257	-0.009	0.038	-0.478	-0.476	0.088
WPS_2	-0.275	-0.162	-0.398	0.181	-0.032	-0.668*	-0.241	0.112