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RESEARCH ARTICLE

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Converting croplands to orchards changes soil microbial community composition and co-occurrence patterns

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Abstract

Soil microorganisms are key to uncovering the mechanisms driving variation in soil biogeochemical processes associated with land-use change. A large number of croplands have been converted to orchards on the Chinese Loess Plateau due to the increased economic benefits which result. However, the microbial community and their functional composition remain poorly understood. In this study, soil samples were collected from croplands and orchards. Soil physicochemical properties and the community (represented by 16S rRNA for bacteria and ITS for fungi) were measured, and interactions among species and the soil organic matter (SOM) degradation via microbial metabolism and its associated genes were analyzed. Croplands converted to orchards affected bacterial and fungal community structure by increasing the relative abundance of Proteobacteria, Bacteroidetes, Firmicutes, Actinobacteria, and Ascomycota, whereas it decreased the α-diversity of bacteria and fungi. The co-occurrence network was larger and more complex within croplands than within orchards, indicating more extensive interactions and higher community stability potential. The abundance of potential genes related to cellulose and hemicellulose metabolism in orchards was higher than that in croplands, whereas the abundance of genes related to lignin decomposition was lower than that in croplands. In addition, the abundance of saprotrophic and symbiotrophic fungi in orchards was significantly lower than that in croplands (27 and 88%, respectively), whereas the abundance of pathotrophic fungi in orchards was almost six-times that in croplands. The soil organic carbon (SOC) and soil C:N in orchards were significantly lower than that in croplands. Converting croplands to orchards significantly altered the microbial community composition and their functionality, as well as decreased the complexity of interaction between microorganisms. The decreased SOC and increased soil C:N ratio could be attributed to these variations. Improved management practices should be implemented for the maintenance of soil biodiversity and SOC in orchards to avoid soil degradation and ensure sustainable development.

KEYWORDS
croplands conversion to orchards, soil microbial community, soil microbial function, soil microbial interactions, SOM degradation

1 | INTRODUCTION

Soil erosion–induced land degradation is a global issue that has especially severe consequences on the Loess Plateau of China, as well as in South Africa, subSaharan Africa, South America, and other regions (Borrelli et al., 2017; Chang, Fu, Liu, Wang, & Yao, 2012; Witt, 2014). Land-use transformation not only mitigates soil erosion–induced degradation but also improves agronomic production and enhances local economic growth. The "Grain-for-Green" rehabilitation Program has worked to convert croplands to forests and grasslands in China, representing one of the most widely applied restoration strategies initiated by humans (Chang, Fu, Liu, & Liu, 2011; Shi & Han, 2014). The ecological benefits of cropland conversion to forests and grassland have been well documented (Cao, Li, Liu, Chen, & Wang, 2018; Deng et al., 2019; Jin et al., 2017; Li et al., 2016), and include: increased soil organic carbon (SOC) sequestration (Jiang et al., 2019; Shi et al., 2019; Zhang et al., 2020) and improved microbial community diversity and function (Guo et al., 2018). Croplands have extensively been converted to orchards owing to their great economic value, and subsequently, the orchard area has increased to 4.93×10^6 ha on the global scale (Food and Agriculture Organization, 2017). China has the largest apple cultivation area (2.22×10^6 ha), approximately 50% of which is located on the Chinese Loess Plateau (National Bureau of Statistics of China, 2017). However, variations in soil quality during cropland conversion to apple orchards remain unclear.

Soil microorganisms are sensitive indicators of soil quality (Griffiths & Philippot, 2013) and are critical for maintaining soil function through processes such as organic matter decomposition and nutrient cycling (Joergensen & Wichern, 2018; Li, Zhang, Cai, Yang, & Chang, 2020; Lupwayi, May, Kanashiro, & Petri, 2018). Environmental characteristics often explain substantial variations in soil microbial community composition, including plant species, soil organic matter (SOM), and microclimate (temperature and moisture) (Chen, Niu, Hu, Luo, & Zhang, 2020; Delgado-Baquerizo et al., 2018; Hansel, Fendorf, Jardine, & Francis, 2008); however, the characteristics of the microbial community and functional composition remain unclear. Previous studies have indicated that environmental characteristics were altered after the conversion of croplands to apple orchards (Li et al., 2015; Wang et al., 2018; Wiesmeier et al., 2019), owing to the use of various agricultural management strategies as well as differences in plant properties. We have previously found that apple orchard soil has a high N content, which is a consequence of increased N fertilizer input (Wang et al., 2018). Additionally, different soil temperatures are induced by varied solar radiation interception, and the amount of soil water varies with the fraction of precipitation by stemflow or throughfall between croplands and apple orchards (Bryant, Bhat, & Jacobs, 2005; Ritter, Dalsgaard, & Eirthorn, 2005). Low carbon input into the apple orchards could induce a decrease in SOC (Wang et al., 2018; Zhang et al., 2015). In addition, high frequent tillage increases SOC decomposition, which decreases SOC in apple orchards (Li et al., 2016; Paustian, Six, Elliott, & Hunt, 2000).

Differences in nutrient availability between croplands and apple orchards may decrease or increase the abundance of bacteria and fungi by microbial life strategies (copiotrophic/oligotrophic) (Fierer, Bradford, & Jackson, 2007; Wang, Ji, Wang, Guo, & Gao, 2017). These differences can also affect the functions of soil microorganisms, resulting in altered metabolism and genes (Guo et al., 2019; Mendes et al., 2015; Zheng et al., 2019). However, more systematic studies are needed to explore how the microbial community, along with their metabolism and SOM degradation genes, influence soil quality for sustainable utilization and development.

2 | METHODS

2.1 | Study site

This study was conducted at the Changwu State Key Agro-Ecological Experimental Station in Changwu, Shaanxi, China (35°13′N, 107°40′E, 1,220 m a.s.l.). The soil was collected from loess deposits and can be described as a loam (Cumulic Haplustoll; USDA Soil Taxonomy System) with a clay content of 22%. The long-term average annual rainfall is 568 mm, most of which mainly occurs from June to September. The average annual air temperature is 9.1°C, frost-free period is 194 days, average annual solar radiation is 5,266 MJ m^{-2}, and potential evapotranspiration is 967 mm (Huang, Shao, Zhang, & Li, 2003).

2.2 | Sample collection

Soil samples (0–20 cm) were collected from five apple orchards and five croplands in October 2018 after apples and spring maize were harvested (35°13′7″–35°14′34″ N, 107°40′33″–107°40′52″ E). The apple orchard (*Malus domestica* Borkh) was converted from cropland in the year 2000 and was approximately 2,000 m^2 with a density of 625 trees ha^{-1}. Each cropland area prior to conversion was approximately 1,000 m^2, with a rotation system, where winter wheat (*Triticum aestivum* L.) was grown 1 year with summer fallow and then 1 year broomcorn millet (*Panicum miliaceum*) was grown, followed by 1 year of spring maize. The fertilizers applied were 200 kg N ha^{-1} and 85 kg P ha^{-1} per year in the apple orchards and 120 kg N ha^{-1} and 39 kg P ha^{-1} in the croplands. For each replicate, six soil cores were randomly collected using a soil auger (d = 3 cm) and then combined to obtain one soil sample; in total, 10 soil samples were obtained (five orchards and five croplands). The samples were placed in a portable refrigerator for transport to the laboratory, after which subsamples were either stored at −80°C to analyze the bacterial and fungal composition or air-dried to determine the SOC, total nitrogen (TN), and pH.

2.3 | Soil sample analysis

The SOC was determined using the K_2CrO_7–H_2SO_4 oxidation method (Fujii, Hartono, Funakawa, Uemura, & Kosaki, 2011; Sparks et al., 1996). The soil TN was determined by acid digestion according

to the Kjeldahl method (Grimshaw, Allen, & Parkinson, 1989). The soil pH (soil:water = 1:2.5, w/w) was analyzed as described by Bao (2000).

Soil DNA was extracted using a MO BIO Power Soil™ DNA Isolation Kit (MO BIO Laboratories, Carlsbad, CA) according to the manufacturer's instructions, and a Nanodrop ND-2000 UV-VIS spectrophotometer (NanoDrop Technologies, Wilmington, DE) was used for quantification and quality checks. For bacteria, the V4 region of the 16S rRNA gene was amplified using primers 341F and 806R (Caporaso et al., 2011). Fungal communities were assessed using the ITS1 region of the rRNA operon with the primer pair ITS5 and ITS2 (Bellemain et al., 2010; Lu et al., 2013). Amplification was performed using Thermo Scientific® Phusion High-Fidelity PCR Master Mix (New England Biolabs, Hitchin, UK). After amplification, the obtained products were purified using a Qiagen Gel Extraction Kit (Qiagen, Hilden, Germany). Sequencing was performed using the Illumina HiSeq 2500 platform at Novogene Bioinformatics Technology Co. Ltd., Beijing, China.

Single-end reads were assigned to samples based on their unique barcode and truncated by cutting off the barcode and primer sequence. Quality filtering of the raw reads was performed under specific filtering conditions to obtain the high-quality clean reads according to Cutadapt (Martin, 2011) (V1.9.1, http://cutadapt.readthedocs.io/en/stable/) quality control process (–e 0.05, –q 17, –m 450, –M 550 for bacteria; –e 0.05, –q 17, –m 150, –M 350 for fungi). The sequences were compared with the relevant reference database: the Silva database for bacteria (https://www.arb-silva.de/) and the Unite database for fungi (https://unite.ut.ee/). The UCHIME algorithm (http://www.drive5.com/usearch/manual/uchime_algo.html) was used to detect chimeric sequences, and then those sequences were removed (Edgar, Haas, Clemente, Quince, & Knight, 2011; Haas et al., 2011; Kõljalg et al., 2013; Quast et al., 2013). The sequence data were deposited in NCBI (PRJNA628855).

2.4 | Statistical analysis

According to the method described by Edgar (2013), UPARSE software was used for sequence analysis. Operational taxonomic units (OTUs) were clustered with sequences ≥97% similarity. For each sample, OTU was normalized to the same least sequences (34,186 for bacterial and 38,902 for fungi) for α-diversity (Chao1, observed species, and Shannon index) analyses. The potential functional traits of bacteria and fungi were predicted using PICRUSt based on the Greengene database (Langille et al., 2013) and FUNGuild (Nguyen et al., 2016), respectively.

Co-occurrence network of bacteria and fungi was constructed by OTU abundance (>0.1%) using the routine CoNet in Cytoscape 3.4. To build the network, the Pearson's and Spearman's correlation coefficients and the Bray–Curtis (BC) and Kullback–Leibler (KLD) dissimilarity indices were combined to estimate the correlations between OTUs. The threshold for edge selection was set to 1,000 top and bottom. During randomization, 100 iterations were calculated for edge scores. In the following bootstrap step, 100 iterations were calculated, and unstable edges were filtered out (p-level threshold of 0.05). The BROWN METHOD was chosen as the p value merging method, and the Benjamini–Hochberg procedure was selected for multiple test correction. The network was analyzed by NetworkAnalyzer in Cytoscape. The Gephi platform was used to visualize the network (Bastian, Heymann, & Jacomy, 2009; Newman, 2003, 2006). The values of topological features were evaluated by path length, diameter, degree, density, clustering coefficient, and modularity.

Soil properties and microbial/genes abundance data between croplands and orchards were compared using analysis of variance (ANOVA) followed by a least significant difference (LSD) test ($p < 0.05$). All these statistical analyses were performed with STATISTICAL ANALYSIS SYSTEM ver. 8.0 (SAS Institute Inc., Cary, NC) unless otherwise indicated.

3 | RESULTS

3.1 | Soil physicochemical properties

The TN was significantly higher in orchards than in croplands, whereas the SOC, soil microorganism biomass carbon (SMBC), and soil C:N ratio were significantly lower in orchards than in croplands (Table 1). The SOC was 7.3% greater, SMBC was 15% greater, and soil C:N ratio was 30% higher in croplands than in orchards. However, the TN was 19% higher in orchards than in croplands.

3.2 | Soil microbial diversity and community structure

Proteobacteria and Ascomycota were the dominant bacterial and fungal phyla in both croplands and orchards, but their relative abundance was significantly higher in orchards than in croplands (Table 2). Alphaproteobacteria, Deltaproteobacteria, Bacteroidetes, Firmicutes, and Actinobacteria abundances were also higher in orchards than in croplands, while Acidobacteria, Gemmatimonadetes, Nitrospirae,

TABLE 1 Soil properties of the croplands and orchards system

Soil properties	Croplands	Orchards
Soil organic carbon (g kg^{-1})	7.90 ± 0.32a	7.36 ± 0.70b
Total nitrogen (g kg^{-1})	0.95 ± 0.05b	1.13 ± 0.05a
Soil microorganism biomass carbon (mg kg^{-1})	156.85 ± 10.8a	136.17 ± 35.0b
Soil C:N ratios	8.32 ± 0.6a	6.51 ± 0.04b
pH	8.08 ± 0.19a	8.11 ± 0.06a
Available phosphorus (mg kg^{-1})	20.00 ± 1.31a	24.69 ± 1.11b

Note: All data are presented as mean ± *SE*, data that do not share a letter are significantly different between cropland and orchard ($p < 0.05$).

TABLE 2 Relative abundances of soil bacterial and fungi communities in croplands and orchards

	Index/taxonomy	Croplands	Orchards
Bacteria	Chao1estimator of richness	3,958 ± 106a	3,562 ± 334b
	Observed species	3,241 ± 87a	3,083 ± 280a
	Shannon's diversity index	10.02 ± 0.05a	9.95 ± 0.18b
	Proteobacteria		
	Alphaproteobacteria	13.62 ± 0.90b	17.01 ± 1.19a
	Deltaproteobacteria	6.83 ± 0.54a	4.63 ± 0.67b
	Gammaproteobacteria	9.82 ± 0.83a	10.25 ± 2.69a
	Bacteroidetes	7.93 ± 0.55b	10.25 ± 2.69a
	Firmicutes	1.13 ± 0.25b	2.38 ± 1.40a
	Acidobacteria	19.97 ± 1.25a	15.35 ± 2.85b
	Actinobacteria	17.75 ± 1.75b	20.51 ± 6.44a
	Gemmatimonadetes	6.55 ± 0.41a	6.26 ± 2.31a
	Nitrospirae	1.36 ± 0.12a	1.08 ± 0.10b
Fungi	Chao1estimator of richness	1,936 ± 123a	1,616 ± 136b
	Observed species	1,605 ± 113a	1,276 ± 114b
	Shannon's diversity index	7.70 ± 0.49a	6.67 ± 0.53a
	Ascomycota	24.84 ± 2.35b	38.74 ± 5.33a
	Basidiomycota	11.33 ± 1.28a	10.18 ± 8.16a
	Mortierellomycota	7.41 ± 1.83a	4.79 ± 2.07b
	Mucoromycota	2.56 ± 0.84a	0.16 ± 0.05b
	Glomeromycota	2.01 ± 0.52a	0.12 ± 0.01b

Note: All data are presented as mean ± *SE*, data that do not share a letter are significantly different between cropland and orchard ($p < 0.05$).

Basidiomycota, Mortierellomycota, Mucoromycota, and Glomeromycota abundances were lower in orchards than in croplands.

Both bacterial and fungal species richness and diversity significantly decreased after croplands were converted to orchards (Table 2). The Chao1 estimator of richness in croplands was greater than 11 and 20% for bacteria and fungi, respectively. The observed species of fungi in croplands were 26% greater than in orchards, whereas no significant changes were observed for bacteria. The Shannon's diversity index for bacteria in croplands was significantly higher than in orchards, whereas there was no significant difference for fungi.

3.3 | Microorganism co-occurrence patterns in croplands and orchards

The topological properties commonly used in network analysis were calculated to describe the complex patterns of interrelationships between bacteria and fungi at the applied analysis threshold (Table S1). The network pattern of croplands contained shorter characteristic path lengths, lower clustering coefficients, and a lower modularity index compared to that of the orchards. The nodes in the network were assigned to 13 bacterial phyla and 7 fungal phyla (Figure 1). Among these, Proteobacteria, Ascomycota, and Acidobacteria were widely distributed in croplands and orchards, whereas Nitrospirae and Aphelidiomycota were found only in orchards (Figure 1). In addition, when the distribution of nodes was modularized, all nodes were grouped into 11 modules in croplands and 9 modules in orchards (Figure S1).

The co-occurrence network in orchards had less nodes and edges compared with croplands. The numbers of total, positive, and negative links in orchards were 14, 10, and 23% lower than in croplands, respectively. The positive bacterial–bacterial taxa (B–B) and positive fungal–fungal taxa (F–F) links in orchards were slightly higher than those in croplands, whereas negative B–B, F–F, and bacterial–fungal taxa (B–F) links were higher in croplands than in orchards. Network analysis further showed that the keystone taxa belonged to the orders Pleosporales, Gemmatimonadales, Cytophagales, Erysipelotrichales, and Clostridiales in orchards and Chitinophagales, Caulobacterales, Rhizobiales, and Solirubrobacterales in croplands.

3.4 | Relative abundances of genes for soil carbon cycling

Genes were annotated according to six groups based on KEGG pathway analysis. Of the top 10 genes related to carbon reactions, *glc*D, *kat*G, *ahp*C, and *gpx* were significantly lower in orchards than in croplands, whereas *mal*Z, *bgl*X, and E3.2.1.22B were significantly higher in orchards than in croplands (Figure 2). The top five trophic modes

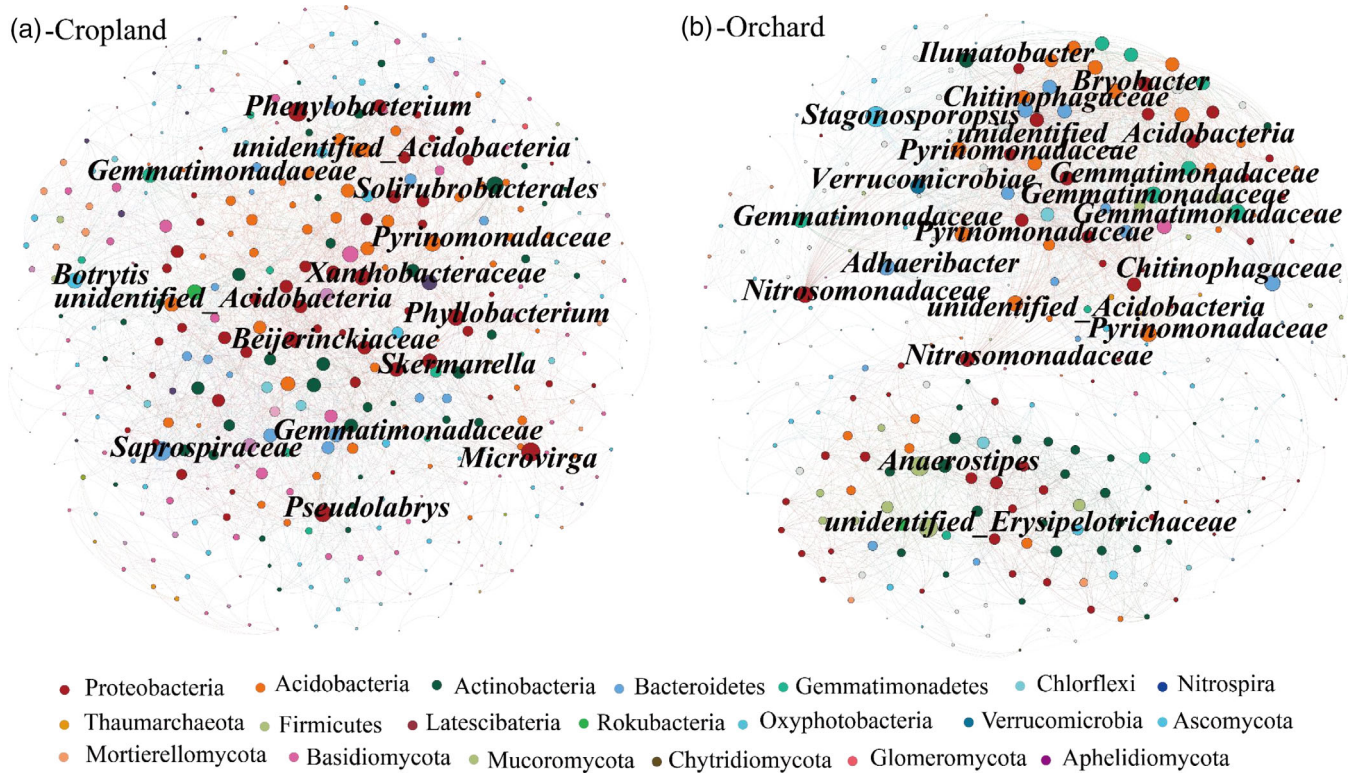

FIGURE 1 Co-occurrence networks among microbial communities of croplands (a) and orchards (b). A node represents an operational taxonomic unit (97% sequence identify threshold, OTU). Nodes were coloured according to phylum, the size of each node is proportional to the degree of connectivity, and the connection lines present the interaction between two nodes [Colour figure can be viewed at wileyonlinelibrary.com]

for fungi were saprotroph, pathotroph, pathotroph–saprotroph, symbiotroph, and pathotroph–saprotroph–symbiotroph. Saprotroph and symbiotroph soil fungi in orchards were significantly lower than in croplands (27 and 88%), whereas pathotroph fungi in orchards reached almost six-times the level of that in croplands (Figure 3).

4 | DISCUSSION

4.1 | Changes in the soil microbial community structure

Microbial communities can respond rapidly to environmental changes caused by ecosystem transformation (Barnett, Youngblut, & Buckley, 2020; Jangid et al., 2011; Tosi et al., 2016). Microbial community composition, interaction, and function were all affected in the conversion of croplands to orchards (Table 2, Figures 1–3). First, these changes affect resource availability (Fierer et al., 2007). Bacterial and fungal diversity were positively correlated with abundances of SOC and SMBC but negatively correlated with TN and soil C:N ratio (Figure 4). The lower SOC found in the orchard (Table 1), which was due to the lower root C input (0.75 vs. 1.1 t ha^{-1} yr^{-1}, unpublished data), may directly decrease soil microbial diversity within the system. Second, litter in the orchards was removed to avoid diseases, which significantly decreased its litter C input compared to that in croplands (Wang et al., 2018). Third, compared with the orchards (monoculture soil), the croplands were on a rotation system, which increased plant diversity and complexity. Previous studies have shown that a higher plant diversity leads to a greater soil microbial diversity (Guo et al., 2019; Jiang et al., 2016). Fourth, the frequent tillage in orchards was another reason for the low soil microbial diversity. Just before sowing of plants each year, tillage was undertaken five- to seven-times in the orchards and one- to two-times in the croplands to control weeds. As less-tilled soils are cooler and moister than intensely tilled soils (Johnson & Hoyt, 1999), the soil microbial diversity was decreased in orchards. Similarly, Miura et al. (2016) and Li, Zhang, et al. (2020) also suggested that the soil microbial diversity in conventional tillage soils was lower than that in no-tillage soils. Additionally, soil bacterial diversity was negatively correlated with the TN content; this result was consistent with that of a previous study which showed that nitrogen decreased bacterial diversity (Li, Nie, & Pendall, 2020). However, in contrast to the study by Li, Nie, and Pendall (2020), soil fungal diversity was also significantly negatively correlated with TN content.

Soil microbial community composition can be affected by cropland conversion to orchards because of the high mineral nutrient content in orchards (Table 2, Figure 4). The higher abundance of Alphaproteobacteria, Gammaproteobacteria, Bacteroidetes, and

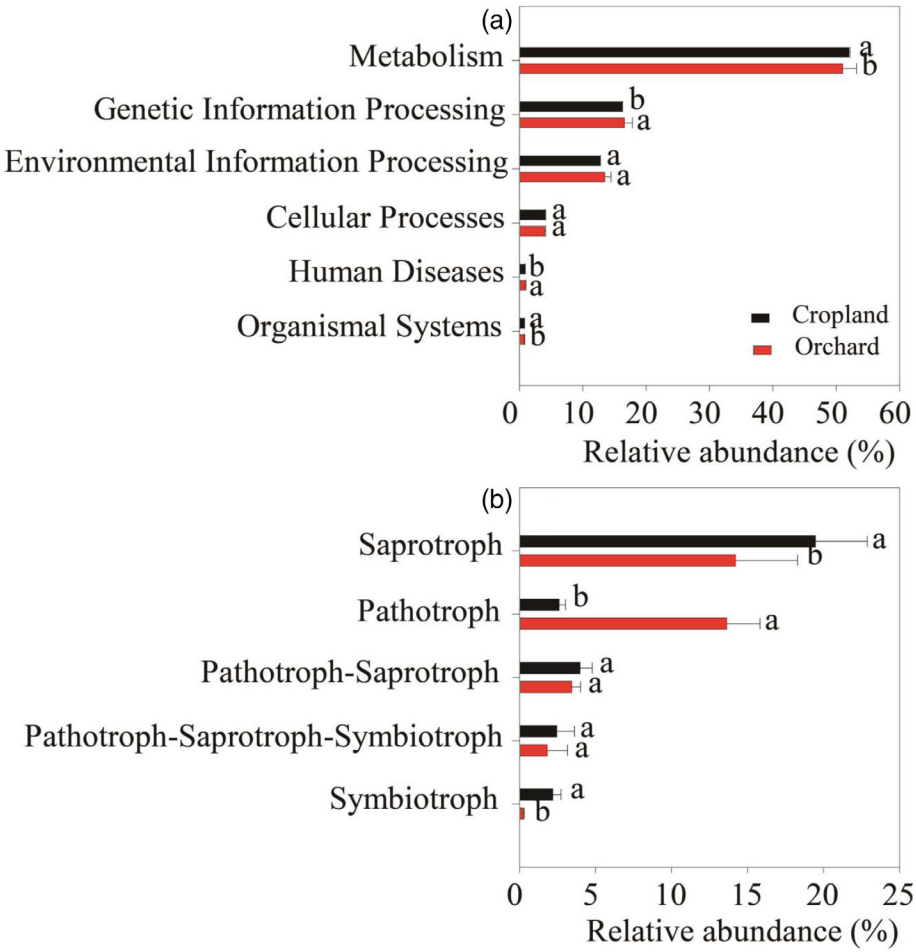

FIGURE 2 Relative abundances of bacterial groups (a) and fungal groups (b) in croplands and orchards [Colour figure can be viewed at wileyonlinelibrary.com]

Actinobacteria in bacteria and Ascomycota in fungi in orchards than in croplands was primarily due to higher nitrogen content (1.13 vs. 0.93 g kg^{-1}, Figure 4a). These results are in accordance with previous studies showing that nitrogen application in soil promoted the abundance of copiotrophic microorganisms (*r*-strategists, e.g., Actinobacteria, Bacteroidetes, and Gammaproteobacteria) (Fierer et al., 2012), and that Ascomycota growth was closely correlated with nitrogen availability (Manici & Caputo, 2010). However, this variation between croplands and orchards was the opposite for the copiotrophic groups, which preferred environments with high organic C content (Banerjee et al., 2016; Fierer et al., 2007; Trivedi, Anderson, & Singh, 2013). This may be related to the high levels of nitrogen promoting organic C (low C:N) (Table 1). Eilers, Lauber, Knight, & Fierer (2010) and Goldfarb et al. (2011) indicated that copiotrophic microorganisms also prefer labile substrate supplies and soil with high C availability. Moreover, there may be high Proteobacteria and Firmicutes in orchards because gram-positive bacteria have been found to use substantial amounts of SOC (Kramer & Gleixner, 2006; Potthast, Hamer, & Makeschin, 2012). Olsen P was another indicator of high Alphaproteobacteria, Gammaproteobacteria, Bacteroidetes, Actinobacteria, and Ascomycota abundances in orchards, which was not consistent with the results of Li, Tremblay, Bainard, Cade-Menun, and Hamel (2020) and Pan et al. (2014). These divergent results indicated that the effects of phosphorus on the microbial community are variable and possibly site dependent. Overall, changes in soil edaphic nutrient factors were the primary reason for changes in soil microbial properties after cropland conversion to orchards.

4.2 | Changes in co-occurrence network patterns after cropland conversion to orchards

The distinct compositions of cropland and orchard networks reflect the different roles of environmental factor assembly in bacterial and fungal community composition in specific croplands and orchards (Figure 1 and Figure S1). Here, a higher complex microbial co-occurrence network was found in croplands than in orchards, which should therefore result in higher community stability and interactions in croplands (Mougi & Kondoh, 2012). The shorter path length in croplands (2.986 vs. 3.29) suggested that croplands may respond rapidly to environmental changes through efficient pathways (Table S1). Higher clustering coefficients and modularity values indicate that orchards have fragmented niches for environmental adaption of soil microorganisms (Table S1; Faust & Raes, 2012). A comprehensive comparison of all network characteristics showed that community

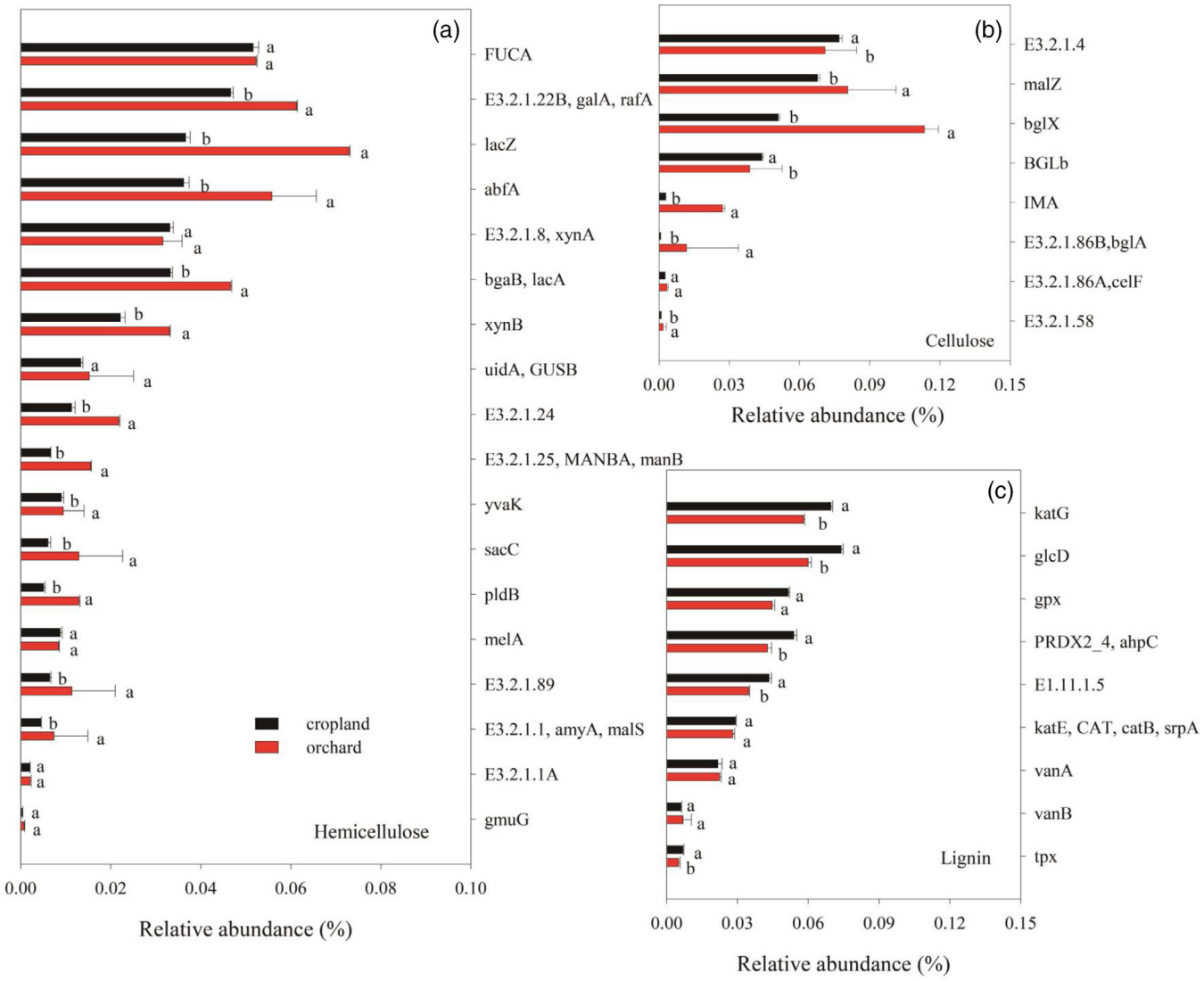

FIGURE 3 Relative abundances of genes related to plant polymer degradation in croplands and orchards [Colour figure can be viewed at wileyonlinelibrary.com]

stability and response to environmental disturbance decreased after croplands were converted to orchards.

Network topology represents complex biological interactions in an ecosystem where species are linked by positive and negative interactions (Thomas et al., 2016). Cropland conversion to orchards decreased both positive and negative links, which indicated that the co-occurrence between synergistic and antagonistic microbial groups was weakened by conversion (Yu, Deem, Crow, Deenik, & Penton, 2018; Zhang, Zhang, Liu, Shi, & Wei, 2018). The proportion of negative B–F links increased from 44% in croplands to 50% in orchards (Table S1), possibly due to competition for higher quality organic C and nutrients between bacteria and fungi (Chow, Kim, Sachdeva, Caron, & Fuhrman, 2014; Fuhrman, 2009; Steele et al., 2011). The higher proportion of negative B–F links in orchards was also affected by the increase in Ascomycota, which is a saprotrophic fungus (croplands vs. orchards: 24.84% vs. 38.74%). de Boer, de Ridder-Dulne, Gunnewiek, Smant, & Van Veen (2008) stated that saprotrophic fungi in the rhizosphere may result in an increase in bacteria with antifungal properties.

4.3 | Changes in microorganism function involved in SOM degradation

Cropland conversion to orchards not only influenced the soil microbial communities but also altered the functional group abundance of organic matter degradation (Figure 2). The relative abundance of cellulose and hemicellulose in orchards was higher than in croplands, whereas the relative abundances of lignin genes in orchards were lower than in croplands. For the top 10 genes involved in carbon reactions, the genes that encode glucosidase—which is related to cellulose and hemicellulose—such as α-glucosidase (*malZ*), β-glucosidase (*bglX*), and α-galactosidase (E3.2.1.22B) were higher in the orchards than in the croplands. A previous study also found the genes related to

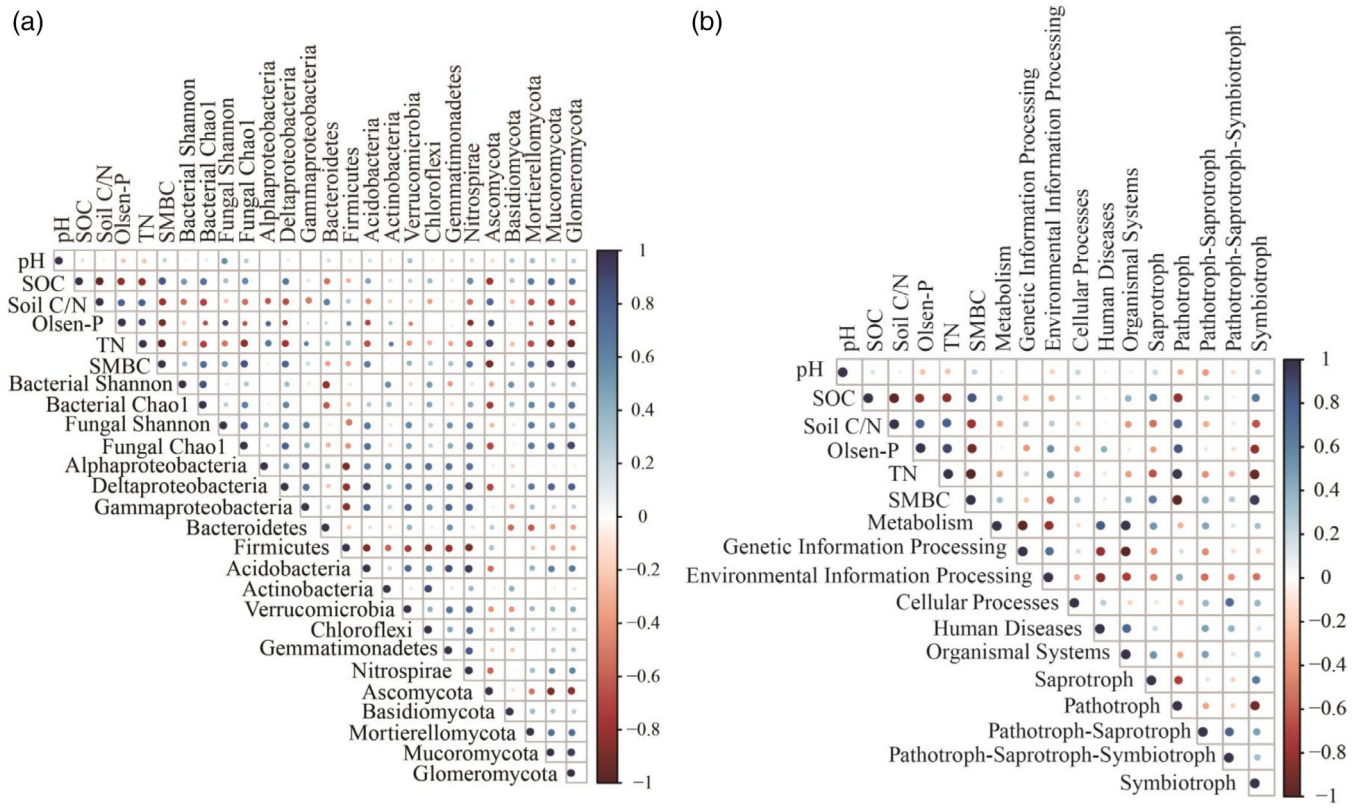

FIGURE 4 Correlations between selected soil physicochemical properties and the relative abundance of microbial community properties (a) and functional properties (b). The colour scheme indicates Spearman *r* values. SMBC, soil microorganism biomass carbon; SOC, soil organic carbon; soil C/N, ratio of SOC and TN; TN, soil total nitrogen [Colour figure can be viewed at wileyonlinelibrary.com]

cellulose and hemicellulose metabolism were higher in covered crop orchards than in uncovered orchards (Zheng, Zhao, Gong, Zhai, & Li, 2018). However, the genes that encode oxidase and peroxidase, which degrade lignin, such as glycolate oxidase (*glcD*), catalase/peroxidase (*katG*), alkyl hydroperoxide reductase subunit C (*ahpC*), and glutathione peroxidase (*gpx*), were higher in the croplands than in the orchards. This could be attributed to the higher fresh organic matter in croplands (root C input). In addition, Proteobacteria, Acidobacteria, Actinobacteria, Bacteroidetes, and Ascomycota were the major microorganisms related to SOM degradation (Fierer et al., 2007; Harreither et al., 2011; Schmidt, Horn, Kolb, & Drake, 2015; Wongwilaiwalin et al., 2013). The members of these taxonomic groups (except for Acidobacteria) were higher in the orchards than in the croplands. The significantly higher nitrogen and phosphorus contents in the orchards due to the high amounts of nitrogen (300 kg ha^{-1}) and phosphorus fertilization (385 kg ha^{-1}) may be the reason for higher plant degradation and taxonomic group abundance.

5 | CONCLUSIONS

Converting croplands to apple orchards decreased microorganism richness and diversity and network complexity. SOM degradation genes showed divergent variation in croplands and apple orchards, which increased the abundance of cellulose and hemicellulose but decreased the abundance of lignin. Cropland conversion to orchards also decreased the proportion of saprotroph and symbiotroph fungi. Soil nutrient factors were the primary drivers of altered soil microbial communities. Overall, our findings showed that conversion of croplands to orchards significantly altered the soil microbial community and function and decreased the complexity of interaction between species.

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CONFLICT OF INTEREST

The authors declare no conflicts of interest.

DATA AVAILABILITY STATEMENT

The data that support the findings of this study are available from the corresponding author upon reasonable request.

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SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section at the end of this article.

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