Effects of Chicken Farming on Soil Phosphorus Availability and Associated Microbial Properties in Lei Bamboo (*Phyllostachys praecox*) Forest Ecosystems

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Abstract

Background: Bamboo-chicken farming (BCF) is a popular bamboo complex management model in Southeast Asia owing to its high economic benefits. However, the effects of BCF on phosphorus (P) availability and the associated microbial communities in soil remain poorly understood. In this study, we compared the soil properties, P fractions, phosphatase activities, and bacterial community compositions in the surface soil (0–20 cm) of a typical bamboo (*Phyllostachys praecox*)-chicken farming system under different grazing densities (represented as distances of 5, 15, 25, and 35 m from the henhouse, respectively). The variables were also compared with the soil measurements from an adjacent pure bamboo forest without chicken framing (control site).

Results: We observed a significant increase in soil pH, cation exchange capacity (CEC), total N (TN), total P (TP), and available potassium (AK) with increasing grazing density, while soil organic carbon (SOC) showed no significant difference between the sites. The total P accumulation of the soil was also more rapid than that of SOC and TN with increasing grazing density. Labile P and moderately labile P dominated the soil P accumulation under BCF. In particular, Resin-Pi (labile P), NaHCO_3 -Pi (labile P), and 1 M HCl-Pi (moderately labile P) increased by 100–233%, 83–183% and 414–1314%, respectively, compared with the control values. In contrast, the contribution of labile or moderately labile organic phosphorus to the total phosphorus (Pt) content decreased significantly with increasing grazing density from 38.54% (control) to 17.65% (5-m site). Phosphatase activity also increased with increasing grazing density, which suggests that BCF effectively promoted the mineralization of soil Po. A redundancy analysis showed that the changes in bacterial community structure were closely related to Resin-Pi and 1 M HCl-Pi ($r^2 = 0.938$ and 0.958 , respectively). The relative abundances of the phosphobacteria *Flavobacterium*, *Pseudomonas*, *Streptomyces*, and *Arthrobacter* increased with increasing grazing density, while the abundance of *Burkholderia* decreased at the 5-m site. Inorganic P (Resin-Pi, NaHCO_3 -Pi, and 1 M HCl-Pi) was positively correlated with the abundances of *Flavobacterium*, *Pseudomonas*, and *Arthrobacter* but negatively correlated with the abundance of *Burkholderia*; this highlights the different functional bacteria involved in P cycling.

Conclusions: We conclude that BCF generally increases soil P availability and supply, and the changes in the P forms were closely related to the changes in soil bacterial community composition. However, excessive grazing density or long-term BCF practices can cause soil nutrient imbalance, labile and moderately labile P accumulation, and P leaching. Therefore, appropriate grazing densities and/or an interval of no grazing are required under the BCF model for effective and sustainable bamboo forest management.

1. Background

Bamboo is an important component of tropical and subtropical forest ecosystems and is also a widely exploited natural resource in southern China (Phimmachanh et al., 2015; FAO, 2010). The bamboo forest industry has a long history in China, and the planting of pure forests is still the main management

method for bamboo farming (Cai et al., 2018). However, this has led to soil degradation, site productivity decline, and regional ecological and environmental deterioration (Luo et al., 1997). As a result, the bamboo forest industry has been gradually shifting toward an efficient compound management model to improve the utilization rate of bamboo forest resources and to balance economic benefits with ecological functions (Dev et al., 2017; Zhu, 2012). Because bamboo forests are usually harvested by selective harvesting methods and purely managed with a single-layer canopy (Song et al., 2011), it is advantageous to raise animals under bamboo canopies. Chicken farming in a bamboo forest was found to both increase the soil nutrient content (organic carbon, total nitrogen, total phosphorus, total potassium) and promote the growth of Moso bamboo (*Phyllostachys edulis*) (Zhu et al., 2018). However, the continuous input of chicken manure to the soil surface and the physical soil disturbance by grazing chickens increases the risks of soil surface erosion, manure leakage, biodiversity reduction, and soil degradation (Zhang et al., 2019; Cai et al., 2018). Bamboo forests and chicken farming can be mutually beneficial owing to their large ecological niche differences (Wu et al., 2013); however, the significant impact of chicken farming on soil quality must be addressed.

Phosphorus (P) is a key restrictive nutrient element in forest ecosystems (Vitousek et al., 2010; Chen et al., 2018), and its bioavailability affects plant growth and microbial properties (Tan et al., 2013; Zhao et al., 2014). However, only a relatively small amount of soil P can be absorbed and utilized by plants owing to its low mobilization (Schachtman et al., 1998). A deficiency in P inhibits photosynthesis, respiration, and other metabolic and biosynthetic processes in bamboo (Liu et al., 2015). P deficiency can also reduce enzyme activity related to carbon and nitrogen metabolism (Burman et al., 2009). Furthermore, insufficient P can cause abnormal root structures by altering the number and density of lateral roots, which affects the ecological stability of bamboo forests (Lin et al., 2014). Therefore, research on the impacts of bamboo-chicken farming (BCF) on soil P availability is necessary for ensuring the sustainable management of bamboo forests.

Different P fractions have different levels of bioavailability for plant and microbial uptake. For example, plants can directly absorb and utilize dissolved P in soil (Helfenstein et al., 2018). Inorganic phosphorus (Pi) associated with iron and aluminum minerals is a potential source of plant- and microbial-available P and is typically transformed within weeks or months (Helfenstein et al., 2018). In contrast, residual P is more stable and is considered unavailable for plant uptake (Vitousek et al., 2010). Therefore, changes in the fractions of soil P in bamboo-chicken farms (BCF) can largely determine the soil P availability, which in turn affects microbial community structure and bamboo forest production. Various factors control the dynamic changes in the content of P fractions, including soil texture (Tokural et al., 2011), management systems (Liu et al., 2019), chemical and organic fertilizers (Liu et al., 2020; Gichangi et al., 2009), and biology (Beutler et al., 2015; Li, 2001). Previous studies have shown that overgrazing may hinder the mineralization of phosphorus (Ford et al., 2016) and reduce its solubility (Sigua et al., 2014). Moreover, Li (2001) reported that long-term grazing reduced the soil P stock—particularly for organic P (Po). In addition, Li (2001) found that soil Fe-P changes were more sensitive to grazing in grassland ecosystems and could therefore be used to indicate the effect of grazing on soil. These findings highlight the need to investigate the P fractions in soil under BCF to infer the effects of grazing on soil P stocks.

Microorganisms are involved in several key biogeochemical processes of P cycling, including P uptake, release, and redistribution (Richardson & Simpson, 2011; Pistocchia et al., 2018; Zhang et al., 2020). Therefore, studying the changes in microbial community structure under BCF conditions, especially P-related microorganisms, can further our understanding of the dominant mechanisms underlying the changes in soil P fractions. Furthermore, changes in microbial communities can affect soil enzymes and their activities, as enzymes in soil are mainly secreted by microorganisms (Tarafdar & Claassen, 1988; Waring et al., 2014). Acid phosphatase (ACP) and alkaline phosphatase (ALP) are non-specific enzymes that promote the bioavailability of phosphorus in soil by catalyzing the hydrolysis of ester-phosphate bonds of monoesters in orthophosphate (other than phytate) (Fraser et al., 2015; Nannipieri et al., 2010). Moreover, the ACP and ALP activities in soil have been measured to assess the conversion process of Po to Pi, as they are considered to play a major role in this process (Tarafdar & Jungk, 1987). Therefore, combining the study of the microbially mediated Pi supply pathway with P fraction change mechanisms can improve our understanding of P biogeochemical cycles and bioavailability under BCF conditions.

In this study, we aimed to determine the impact of chicken farming on soil P availability and microbial community structures in Lei bamboo (*Phyllostachys praecox*) forests. We assessed the biogeochemical changes under different grazing intensities to elucidate the relationships between the P fractions and bacterial community and to evaluate the sustainability of BCF systems. Specifically, we tested the following hypotheses: (1) chicken farming largely affects soil P status—especially the P fractions; (2) grazing density significantly affects the distribution of organic and inorganic P fractions; and (3) chicken farming significantly increases soil P availability and accelerates soil phosphatase activity, which consequently impacts the bacterial community structure in soil.

2. Materials And Methods

2.1 Experimental site

The study site is located in Jingshan Town (N 30°24', E 119°52', 125 m ASL), which is northwest of Hangzhou in Zhejiang Province, China (Figure 1). The region has a mid-latitude subtropical monsoon climate, with an average annual rainfall and temperature of approximately 1454 mm and 17.8 °C, respectively. The minimum and maximum temperatures are 2 °C in January and 39 °C in July, respectively. The experiment site is a Lei bamboo shoot production area, and its soil is classified as Ferralic Cambisol (FAO, 2006). The region is located on the sunny side of the hill with a slope of 10–15 °. The canopy closure is 80–90%, and no other plants grow on the surface. The plot has undergone short-term intensive management for two years. The BCF system has been operating for six years, and only selective logging is conducted to maintain an appropriate canopy density. The BCF area is approximately 15 ha and contains 1500–1800 chickens per hectare.

2.2 Experimental design and soil sampling

In this study, we characterized the changes in grazing intensity as the differences in grazing distance from the hen house, which is based on the chickens' habits. This technique is a common method for estimating plant and animal density and abundance (Stump et al., 2005; Manthey & Peper, 2010). A total of four sites (5, 15, 25, and 35 m distance from the hen house) and one control site (CK; > 60 m from the hen house) were assessed in the same manner. A pure bamboo forest located > 60 m from the hen house was selected as the control site as its environmental conditions and initial soil properties were similar to those of the BCF forest.

For all sites, five 2 × 2 m sampling plots were randomly selected in an S shape along the slope direction. Three samples from the same soil layer (0–20 cm) of each sampling plot were collected in mid-May 2019 and carefully mixed to form five composite samples. The composite samples were then transferred into a sterile sealed bag, placed on ice, and transported to the laboratory for pretreatment. After the samples were thoroughly mixed and hand-sieved through a 2-mm sieve, a portion of each fresh soil sample was stored at 4 °C and -80 °C for further analysis. The remaining portion of the soil sample was air-dried and stored for determining soil properties, P fractions, and phosphatase activity.

2.3 Soil basic properties

Soil pH was measured from a soil suspension (1:2.5, w/v) using a pH meter (PHS-3E; REX, China). The soil cation exchange capacity (CEC) was determined via the ammonium acetate method (Chapman, 1965). Briefly, 2 g of air-dried soil was placed in a 100 ml centrifuge tube and then centrifuged at 4000 rpm for 5 min with 50 ml of 1 mol·L⁻¹ NH₄OAc solution. The supernatant was then discarded, and the above process was repeated 3–4 times. The soil sample was then rinsed 4–5 times with 25 ml 95% ethanol. After discarding the ethanol solution, 1 g solid magnesium chloride and 2 ml liquid paraffin were added to the soil, and the NH₄⁺ content was determined using a Kjeldahl nitrogen analyzer (UDK159; Velp Scientifica; Italy). Soil organic carbon (SOC) was measured using a TOC analyzer (Multi N/C 3100; Analytik Jena, Germany), and soil alkali-hydrolysable nitrogen (AN) was determined following the alkali-diffusion method (Bremner et al., 1996). Soil available potassium (AK) was extracted with 1 mol·L⁻¹ CH₃COONH₄ at pH 7 and measured by flame photometry (FP6410 INESA, China).

2.4 Fractionation procedure for soil P

The continuous extraction method proposed by Hedley et al. (1982) and modified by Tissen and Moir (1993) was used to fractionate the soil P in this study. Briefly, the P fractions were extracted from 0.5 g air-dried soil in a 50 ml centrifuge tube via the following steps: (1) two 9 × 62 mm resin strips and 30 ml distilled water were added to the centrifuge tubes, and the phosphorus in the resin strips was extracted with 0.5 M HCl after 16 h of shaking at 160 rpm (Resin-Pi); (2) after removing the aqueous solution, 30 ml 0.5 M NaHCO₃ at pH 8.5 was added and shaken for 16 h to extract NaHCO₃-P; (3) 30 ml 0.1 M NaOH was added and shaken for 16 h to extract NaOH-P; (4) 1 M HCl-Pi was extracted by adding 30 ml 1 M HCl to

the centrifuge tube and shaken for 16 h; (5) the soil residue was further extracted with 15 ml concentrated HCl at 80 °C (conc. HCl-P); and finally, (6) P was extracted by boiling the soil residue in 8 ml concentrated H₂SO₄ and 10 drops of HClO₄ (Residual-P). The concentrations of Pi in the different extracts (Resin-Pi, 1 M HCl-Pi, and conc. HCl-P) were determined via the method described by Murphy and Riley (Murphy & Riley, 1962). The extracts that were obtained using NaHCO₃ and NaOH were first acidified with 6 ml and 1.6 ml 0.9 M H₂SO₄, respectively, before determining the Pi concentrations via the method by Murphy and Riley. The total P concentrations of the different extracts (NaHCO₃-P, NaOH-P, and conc. HCl-P) were determined by the ammonium persulfate digestion method. Finally, the Po concentration of the different extracts (NaHCO₃-P, NaOH-P, and conc. HCl-P) was calculated as the difference between total P and Pi.

2.5 ACP and ALP activities

ACP (EC 3.1.3.2) and ALP (EC 3.1.3.1) activities were determined following a modified method as described by Tabatabai and Bremner (1969). Briefly, 0.5 ml toluene was added to 1 g of air-dried soil and then shaken for 15 min. A modified universal buffer (pH 6.5 for ACP and pH 11.0 for ALP) was then added, and the sample was subsequently incubated at 37 °C for 24 h. The formation of *p*-nitrophenol was determined at 400 nm after the termination of the enzymatic reaction. ACP and ALP activities were expressed as $\mu\text{mol pNP g}^{-1} \text{ soil d}^{-1}$.

2.6 Soil DNA extraction, PCR, and high-throughput sequencing

The Fast DNA[®] Spin Kit for Soil (MP Biomedicals, U.S.A) was used to extract the soil DNA according to the manufacturer's instructions. We used 1% agarose gel electrophoresis to detect the DNA extraction quality and NanoDrop2000 to determine the DNA concentration and purity. Primers 338F (5'-ACTCCTACGGGAGGCAGCAG-3') and 806R (5'-GGACTACHVGGGTWTCTAAT-3') were used to amplify the V3-V4 hypervariable region sequences of the bacterial 16S rRNA gene (Wang et al., 2018). Polymerase chain reaction (PCR) amplification, library construction, and Illumina Miseq sequencing were performed by Shanghai Majorbio Bio-pharm Technology Co., Ltd.

2.7 Bioinformatic analysis

Trimmomatic v 0.32 was used to perform quality control on the original sequencing sequence (Lohse et al., 2012). The quality control sequence was performed double-end splicing using FLASH v 1.2.11 (Magoč et al., 2011). Chimeras 16S sequences were removed, and high-quality nucleic acid sequences were clustered into operational taxonomic units (OTUs) based on 97% similarity using UPARSE v 7.1 (Wang et al., 2017). The alignment threshold was 70%, and each sequence was classified and annotated using the

RDP classifier (<http://rdp.cme.msu.edu/>). The phosphobacterial species were identified by database screening.

2.8 Statistical analysis

We used the SPSS statistical software package version 21.0 for Windows to perform the statistical analyses in this study. A one-way analysis of variance (ANOVA) and Duncan's test were used to identify the significant differences ($p < 0.05$) between the soil samples. The alpha diversity (Shannon, Chao1, and Observed species index) of the soil bacterial communities was calculated using the Vegan package of R (ver. 3.6.3). To determine the differences in soil bacterial communities between the different sites, we used QIIME to conduct a principal coordinate analysis (PCoA) based on Unifrac distance. We conducted a redundancy analysis (RDA) on soil environmental factors and bacterial communities, which was visualized by the Vegan and ggplot2 packages of R. Finally, a Pearson's correlation analysis was used to test the correlation between soil phosphobacteria and P fractions.

3. Results

3.1 Soil properties

The BCF soil showed significantly different chemical properties to that of the control soil (Table 1). Soil pH, CEC, SOC, TN, AN, and AK were significantly higher in BCF ($p < 0.05$) than in the control. The soil pH, CEC, TN, AN, and AK were highest at the 5-m site; however, we observed no significant difference in SOC across the different sites ($p > 0.05$). The soil total P (Pt) content in the BCF was significantly higher than that of the control ($p < 0.05$) and increased with increasing grazing density. Pi accounted for approximately 60–82% of Pt and also showed similar variability to that of Pt. The Pi/Pt value significantly increased with increasing grazing density ($p < 0.05$). Compared with the control, the BCF soil had a significantly higher total Po content but lower Po/Pt values ($p < 0.05$).

Table 1

Soil properties at different grazing distances from the hen house.

	5-m	15-m	25-m	35-m	CK
pH	^b 6.69 ± 0.21a	5.75 ± 0.08b	5.66 ± 0.12b	5.77 ± 0.14b	5.02 ± 0.06c
CEC (cmol·kg ⁻¹)	18.07 ± 1.30a	17.62 ± 0.67a	15.35 ± 0.96b	15.25 ± 0.80b	13.75 ± 0.43c
SOC (g·kg ⁻¹)	41.97 ± 2.36a	42.72 ± 3.20a	41.81 ± 30.97a	41.35 ± 2.99a	36.67 ± 1.36b
TN (g·kg ⁻¹)	3.19 ± 0.32a	2.97 ± 0.12a	2.27 ± 0.27b	2.46 ± 0.16b	1.77 ± 0.12c
AN (mg·kg ⁻¹)	214.97 ± 4.96a	220.66 ± 3.66a	184.43 ± 8.35b	176.69 ± 4.98b	146.67 ± 9.55c
AK (mg·kg ⁻¹)	591.64 ± 34.78a	402.22 ± 10.48b	381.16 ± 3.10b	394.32 ± 8.30b	200.27 ± 4.77c
^a Total P (g·kg ⁻¹)	2.56 ± 0.08a	2.02 ± 0.05b	1.72 ± 0.09c	1.62 ± 0.08d	0.93 ± 0.03e
Total Pi (g·kg ⁻¹)	2.10 ± 0.08a	1.48 ± 0.04b	1.31 ± 0.08c	1.22 ± 0.06d	0.56 ± 0.03e
Pi/Pt (%)	82.00 ± 1.29a	73.04 ± 1.34c	75.97 ± 1.35b	74.88 ± 1.64b	60.61 ± 1.31d
Total Po (g·kg ⁻¹)	0.45 ± 0.03b	0.54 ± 0.03a	0.41 ± 0.03c	0.40 ± 0.04c	0.36 ± 0.02d
Po/Pt (%)	17.65 ± 1.28d	26.57 ± 1.33b	23.64 ± 1.35c	24.72 ± 1.64c	38.54 ± 1.29a
^a Total P is the cumulative value of all P fractions; total Pi is the sum of Resin-Pi, NaHCO ₃ -Pi, NaOH-Pi, 1 M HCl-Pi, and Conc. HCl-Pi; and Total Po is the sum of NaHCO ₃ -Po, NaOH-Po, and Conc. HCl-Po.					
^b Values are expressed as mean (n = 5) ± standard error. Values in the same row with different lowercase letters indicate significant differences to the other grazing sites at p < 0.05 (Duncan's test).					

3.2 Soil P fractions and phosphatase activity

Our results showed that the BCF system significantly affected the relative content of each P fraction (Figure 2). The relative content of labile P was approximately 26–28% of Pt. In comparison, the relative content of moderately labile P was 52–64% of Pt, which gradually increased with increasing grazing density. Furthermore, NaHCO₃-Pi contributed the largest proportion to labile P in the soil, accounting for

approximately 44–50%. Moreover, the relative content of Resin-Pi gradually increased with increasing grazing density, while the proportion of $\text{NaHCO}_3\text{-Po}$ in labile P gradually decreased. Chicken farming had altered the composition of moderately labile P. The proportion of NaOH-extracted P in moderately labile P decreased gradually with increasing grazing density from 86% to 40%. Correspondingly, the proportion of 1 M HCl-Pi increased with decreasing grazing distance; the proportion at 5 m was higher than those of the other sites and the control group by ~1.36-fold and 13.54-fold, respectively. Compared with the control, chicken farming reduced the relative content of sparingly labile P, but the variability in its composition was limited (the relative content of conc. HCl-Pi varied within the range of 59–68% across all sites).

Labile P, moderately labile P, and sparingly labile P increased significantly with increasing grazing density ($p < 0.05$) (Table 2). The Pi fraction (Resin-Pi and $\text{NaHCO}_3\text{-Pi}$) in labile P especially increased with increasing grazing density, and the maximum and minimum soil values of $\text{NaHCO}_3\text{-Pi}$ and Resin-Pi occurred at the 5-m site and the control, respectively. Compared with the control, we observed no significant difference in the Po fraction in labile P at 25 and 35 m ($\text{NaHCO}_3\text{-Po}$) ($p > 0.05$). In moderately labile P, the maximum and minimum P contents extracted by NaOH were observed at 15 m and the control, respectively. Although both NaOH-Pi and NaOH-Po values at 5 m were significantly lower than those at 15 m ($p < 0.05$), the 1 M HCl-Pi at 5 m increased by 116.41% and 1354.41% compared with the 15-m site and the control, respectively. In sparingly labile P, the soil at 5 m had significantly higher conc. HCl-Pi than the soils at the other sites and the control ($p < 0.05$). The conc. HCl-Po trend was not consistent with that of conc. HCl-Pi, except for 15 m; however, the values were not significantly different to those of the other sites and the control ($p > 0.05$).

Table 2

Phosphorus (P) sequential fractionation (g·kg⁻¹) in the bamboo forest soil at different grazing distances from the hen house.

P fraction	5-m	15-m	25-m	35-m	CK
^a Labile P					
Resin-Pi	^b 0.20 ± 0.01a	0.15 ± 0.01b	0.12 ± 0.01c	0.13 ± 0.01c	0.06 ± 0.01d
NaHCO ₃ -Pi	0.34 ± 0.03a	0.26 ± 0.02b	0.22 ± 0.02c	0.22 ± 0.02c	0.12 ± 0.01d
NaHCO ₃ -Po	0.14 ± 0.02a	0.13 ± 0.03a	0.11 ± 0.01b	0.09 ± 0.01b	0.09 ± 0.01b
∑ Labile P	0.68 ± 0.02a	0.55 ± 0.04b	0.45 ± 0.02c	0.44 ± 0.03c	0.26 ± 0.02d
Moderately labile P					
NaOH-Pi	0.42 ± 0.03b	0.45 ± 0.02a	0.37 ± 0.03c	0.37 ± 0.02c	0.21 ± 0.02d
NaOH-Po	0.24 ± 0.02b	0.30 ± 0.02a	0.23 ± 0.01ab	0.24 ± 0.03b	0.20 ± 0.02c
1 M HCl-Pi	0.99 ± 0.08a	0.46 ± 0.02b	0.45 ± 0.04b	0.36 ± 0.02c	0.07 ± 0.01d
∑ Moderately labile P	1.65 ± 0.05a	1.21 ± 0.04b	1.05 ± 0.08c	0.97 ± 0.07d	0.48 ± 0.03e
Sparingly labile P					
conc.HCl-Pi	0.16 ± 0.01a	0.15 ± 0.01b	0.15 ± 0.01ab	0.13 ± 0.01c	0.11 ± 0.01d
conc.HCl-Po	0.08 ± 0.01b	0.11 ± 0.01a	0.07 ± 0.02b	0.07 ± 0.02b	0.07 ± 0.01b
∑ Sparingly labile P	0.24 ± 0.01ab	0.25 ± 0.01a	0.22 ± 0.02bc	0.20 ± 0.01c	0.18 ± 0.01d
Non-labile P					

^a P fractions were classified according to Liao et al. (2020) and Crews and Brookes (2014).

^b Values are expressed as the mean (n = 5) ± standard error. Values in the same row with different lowercase letters indicate significant differences to the other grazing sites at P < 0.05 (Duncan's test).

P fraction	5-m	15-m	25-m	35-m	CK
Residual-Pt	0.01 ± 0.00a	0.01 ± 0.00b	0.01 ± 0.00c	0.01 ± 0.00c	0.01 ± 0.00b
^a P fractions were classified according to Liao et al. (2020) and Crews and Brookes (2014).					
^b Values are expressed as the mean (n = 5) ± standard error. Values in the same row with different lowercase letters indicate significant differences to the other grazing sites at P < 0.05 (Duncan's test).					

Chicken farming affected the activity of ACP and ALP in soil (Figure 3). The activity of soil ACP was significantly higher in BCF than in the control ($p < 0.05$) (Figure 3a), but no significant differences were observed between the different sites ($p > 0.05$). The highest ALP activity was observed at the 5-m site ($9.97 \mu\text{mol } p\text{NP g}^{-1} \text{ soil d}^{-1}$), which was significantly higher than the other sites and the control ($p < 0.05$) (Figure 3b). Compared with the control, the ALP activity at 15, 25, and 35 m significantly increased by 66.43%, 26.96%, and 69.61%, respectively ($p < 0.05$).

3.3 Soil bacterial community structure

Except for 25 m, we observed no significant difference between the alpha diversity index of the different sites and the control ($p > 0.05$) (Figure S1). We used a PCoA to compare the bacterial communities between the sites and the control based on unweighted and weighted Unifrac distances (Figure S2). The unweighted PCoA clearly separated the BCF and control bacterial communities (Figure S2a). Moreover, the 15-, 25-, and 35-m sites were tightly clustered, whereas the 5-m site notably deviated from the group. The sample aggregation in the weighted analysis was similar to that in the unweighted analysis. The combined axis of PCo1, PCo2, and PCo3 accounted for 28.94% and 74.81% of the total change in the unweighted and weighted PCoA, respectively. The ANOSIM results also revealed significant differences in the bacterial community composition between the different sites ($p < 0.05$).

In all the soil samples, the dominant bacteria phyla with average relative abundances of > 1% were Proteobacteria (38.91%), Acidobacteria (16.27%), Actinobacteria (10.61%), Bacteroidetes (7.89%), Chloroflexi (7.05%), TM7 (6.11%), Gemmatimonadetes (3.71%), AD3 (1.67%), Firmicutes (1.08%), and Verrucomicrobia (1.07%) (Figure S3). We performed a one-way ANOVA to compare the individual taxa at the phylum level (Figure 4). Compared with the control, the relative abundance of Proteobacteria and TM7 had significantly increased in BCF ($p < 0.05$), except at the 5-m site. The relative abundances of Acidobacteria and Bacteroidetes in the 15-, 25-, and 35-m sites did not significantly differ from that of the control ($p > 0.05$). However, their relative abundances in the 5-m site were significantly different to those of the other sites and the control ($p < 0.05$). The relative abundance of Gemmatimonadetes was significantly higher at the 5-m and 15-m sites compared with the 25-m and 35-m sites and the control ($p < 0.05$). Soils under BCF conditions had a lower relative abundance of AD3 compared with the control soil

($p < 0.05$). Furthermore, the relative abundance of Firmicutes was similar in the BCF sites and the control, except at 5 m ($p > 0.05$).

Seven dominant phosphobacteria genera (average relative abundance $> 0.1\%$) were detected in the topsoil of the BCF sites and the control, including *Flavobacterium* (1.55%), *Burkholderia* (0.59%), *Pseudomonas* (0.40%), *Bacillus* (0.30%), *Streptomyces* (0.21%), *Arthrobacter* (0.20%), and *Paenibacillus* (0.10%). The relative abundance of *Flavobacterium* at the 5-m site was significantly higher than those of the other sites and the control ($p < 0.05$) (Table 3). *Flavobacterium* abundances at 15, 25, and 35 m were 0.55, 1.32, and 2.12 times the control values, but the differences were not significant ($p > 0.05$).

Compared with the control, the relative abundance of *Burkholderia* was significantly lower in the 5-m site ($p < 0.05$) but showed no significant differences at 15 and 25 m ($p > 0.05$). The relative abundance of *Pseudomonas*, *Streptomyces*, *Arthrobacter*, and *Paenibacillus* increased significantly in the BCF soils, but only the relative abundances of *Pseudomonas* and *Paenibacillus* at 25-m significantly differed from the other sites ($p < 0.05$). Furthermore, we observed no clear difference in the relative abundance of *Bacillus* between the different sites and the control.

Table 3

Relative abundances of the dominant phosphobacteria genera (average relative abundance $> 0.1\%$) in soil at different distances from the hen house.

phyla	genera	5-m	15-m	25-m	35-m	CK
Bacteroidetes	<i>Flavobacterium</i>	3.80 ± 1.57a	0.49 ± 0.21b	0.73 ± 0.35b	0.99 ± 0.25b	0.32 ± 0.13b
Proteobacteria	<i>Burkholderia</i>	0.41 ± 0.12c	0.81 ± 0.21a	0.75 ± 0.16ab	0.55 ± 0.19b	0.83 ± 0.21a
	<i>Pseudomonas</i>	0.42 ± 0.09b	0.38 ± 0.07b	0.62 ± 0.16a	0.35 ± 0.10b	0.13 ± 0.04c
	<i>Streptomyces</i>	0.20 ± 0.05b	0.32 ± 0.07a	0.20 ± 0.04b	0.23 ± 0.03b	0.10 ± 0.04c
Actinobacteria	<i>Arthrobacter</i>	0.29 ± 0.11a	0.23 ± 0.11a	0.22 ± 0.20a	0.16 ± 0.06ab	0.02 ± 0.02b
	<i>Bacillus</i>	0.26 ± 0.08a	0.35 ± 0.12a	0.27 ± 0.03a	0.35 ± 0.05a	0.35 ± 0.15a
Firmicutes	<i>Paenibacillus</i>	0.07 ± 0.02c	0.11 ± 0.02b	0.14 ± 0.02a	0.13 ± 0.01ab	0.05 ± 0.01d

3.4 Correlating P fractions with the bacterial community

The results of the Pearson correlation analysis inferred the relationship between soil parameters and the dominant bacteria phyla (Figure S4). Among the different soil chemical properties, Proteobacteria and TM7 only significantly positively correlated with the SOC content. In contrast, except for SOC, Bacteroidetes significantly positively correlated with the other soil chemical variables (pH, CEC, TN, AN, and AK). Gemmatimonadetes significantly positively correlated with pH, CEC, SOC, TN, AN, and AK. However, contrary to Gemmatimonadetes, AD3 significantly negatively correlated with all the soil basic properties. Furthermore, Proteobacteria and TM7 showed significant and extremely significant positive correlations with NaOH-P, respectively. We also observed a strong positive relationship between Bacteroidetes and all the Pi fractions. Gemmatimonadetes also showed a significant positive correlation with the Pi fractions, except conc. HCl-Pi. Actinobacteria showed a strong significant negative correlation with Resin-Pi and 1 M HCl-Pi and a significant negative correlation with NaHCO₃-Pi and conc. HCl-Pi. Moreover, AD3 showed a strong significant negative relationship with the Pi fractions and a significant negative correlation with NaHCO₃-Po and NaOH-Po.

The relative abundances of *Flavobacterium*, *Pseudomonas*, *Streptomyces*, *Arthrobacter*, and *Paenibacillus* were mostly correlated with the changes in P fractions (Figure 5). *Flavobacterium* showed a significant positive correlation with Resin-Pi and a strong significant positive correlation with NaHCO₃-Pi and 1 M HCl-Pi. *Pseudomonas* significantly positively correlated with Resin-Pi, NaHCO₃-Pi, and 1 M HCl-Pi, and showed a strong significant positive correlation with NaOH-Pi and conc. HCl-Pi. *Streptomyces* significantly positively correlated with Resin-Pi, NaHCO₃-Pi, conc. HCl-Pi, and conc. HCl-Po, and showed a strong significant correlation with NaOH-Pi and NaOH-Po. *Arthrobacter* showed a strong significant correlation with Resin-Pi, NaHCO₃-Pi, 1 M HCl-Pi, and conc. HCl-Pi, and a significant positive correlation with NaOH-Pi. *Paenibacillus* only significantly correlated with NaOH-Pi. *Burkholderia* had a negative correlation with all P fractions, with a strong significant negative correlation with Resin-Pi, NaHCO₃-Pi, and 1 M HCl-Pi, and a significant negative correlation with NaOH-Po and conc. HCl-Pi.

The RDA showed that the soil chemical properties and P fractions explained 44.79% of the variations in soil bacterial community structure (Figure 6). According to the Monte Carlo permutation test (permutation = 999), the Pi fractions, Po fractions (except conc. HCl-P), soil properties, and phosphatase were significantly correlated with the structure of bacterial communities. In Figure 6, a longer arrow represents a stronger relationship between the soil variables and bacterial community composition. Therefore, according to the variance of r^2 , Pi fractions had a stronger correlation with bacterial community changes than Po fractions (Table S1). Furthermore, among all soil parameters, AK and pH showed the strongest correlation with the changes in bacterial community ($r^2 = 0.963$ and 0.962 , respectively), followed by 1 M HCl-Pi and Resin-Pi in the Pi fractions ($r^2 = 0.958$ and 0.938 , respectively).

4. Discussion

4.1 Effect of BCF on P fractions

Labile Pi (Resin-Pi and NaHCO_3 -Pi) is the main source of P for plant growth and can be directly absorbed and utilized by plants (Fu et al., 2020). In our study, we found that the soil labile Pi content in BCF increased significantly compared with the control and also increased with higher grazing density. This trend may be attributed to the soil adsorption of P from manure accumulation (Neufeldt et al., 2000). The increase in P content from manure is more significant for labile Pi than other P fractions (Maranguit et al., 2017), as labile Pi typically accounts for > 40% of the Pt in chicken manure (Yan et al., 2015; Pagliari & Laboski, 2012). The NaOH-Pi in moderately labile P usually represents the partially dissolved Fe/Al phosphate in the soil solution, as well as phosphate anions adsorbed on the surface of Fe/Al oxides (Cross & Schlesinger, 2001). Moreover, Fe and Al mineral contents are relatively high in acidic soils (pH < 5) (McGroddy et al., 2008); thus, NaOH-P generally dominates the composition of moderately labile P in Subtropical China. However, BCF altered the composition of moderately labile P in this study, and 1 M HCl-Pi gradually dominated with increasing grazing density. This observation can be linked to three possible phenomena: 1) the deposition of chicken manure gradually increases soil pH with increasing grazing density (Somda et al., 1997), which reduces the adsorption performance of iron-aluminum oxides (Yan et al., 2019) and prevents it from complexing with more free phosphorus; 2) the stability of HCl-extracted P is strongly dependent on soil pH, and HCl-extracted P pools in high-pH soils tend to contain highly stable calcium phosphate minerals (Hou et al., 2019; Helfenstein et al., 2020); and 3) the higher Ca^{2+} in chicken manure may complex with dissolved Pi in the soil to form 1 M HCl-Pi (Sugiyama et al., 2016).

Phosphatase is closely related to the transformation of Po and Pi (Amador et al., 1997) and significantly influences P cycling rates in soil (Sardans et al., 2006). In this study, the activities of both ALP and ACP significantly increased in BCF, which may be linked to manure input and litter disturbance by grazing chickens. These processes increase the soil available nutrients (Williams & Haynes, 1990; Lindsay & Cunningham, 2009), which stimulates phosphatase activity. Furthermore, ALP at 5-m was significantly higher than that of the other sites, while ACP showed no significant differences. This may be attributed to the pH sensitivity of amino acid functional groups in the different phosphatases (Dick et al., 2000); ACP activity is known to be much higher in acidic soils, while ALP activity is much higher in alkaline soils (Katsalirou et al., 2016; Luo et al., 2017). Phosphatases are thought to play a major role in the mineralization of Po to Pi (Nannipieri et al., 2012; Tarafdar & Jungk, 1987). In agreement, we found that the Pi fractions were significantly correlated with both ALP and ACP in this study. However, ALP was only significantly positively correlated with NaHCO_3 -Po of the Po fractions, as NaHCO_3 -Po may be more easily hydrolyzed by the enzyme compared with other Po fractions (Luo et al., 2017).

4.2 Effect of BCF on the P-associated bacterial community structures

Marcos et al. (2019) found that grazing can alter soil properties by affecting litter decomposition, manure deposition, and soil compaction, thereby altering soil microbial compositions. In this study, we found that

BCF increased the relative abundance of Proteobacteria, likely owing to an increase in soil available nutrients and carbon (Goldfarb et al., 2011; Fierer & Jackson, 2006; Fierer et al., 2007). In addition, previous studies have shown that most Proteobacteria and Actinobacteria are oxygen-dependent (Emerson et al., 2010; Hamamura et al., 2006). Therefore, relatively high grazing density can lead to soil compaction, which decreases the soil oxygen content (Martínez & Zinck, 2004; Shah et al., 2017); this may explain the relatively low abundance of Proteobacteria and Actinobacteria at the 5-m site (Figure 4). Furthermore, Wang et al. (2016) found that the relative abundance of Actinobacteria correlated with the soil C:N ratio. In our study, the TN content increased with increasing grazing density, but SOC showed no significant change, indicating a gradual decrease in the C:N ratio. This may be another reason for the significantly lower Actinobacteria abundance at the 5-m site. Bacteroides was more abundant in the BCF soils, especially at 5 m, which may be owing to the high abundance of Bacteroides in the digestive system of chickens under BCF conditions (Zhang et al., 2020). Bacteroides is also involved in the degradation of complex carbohydrates and has been significantly positively correlated with soil respiration (Thomas et al., 2011; Wang et al., 2016). Therefore, the gradual increase in Bacteroides with increasing grazing intensity may aggravate the loss of SOC. Costello (2007) found that members of AD3 have oligotrophic or micronutrient-requiring characteristics. Thus, our results show that chicken farming significantly reduces the relative abundance of AD3, which suggests that BCFs may be able to alleviate soil nutrient deficiency.

In this study, we observed significant differences in the relative abundance of phosphobacteria (e.g., *Flavobacterium*, *Pseudomonas*, *Streptomyces*) between the BCF and control soils. *Flavobacterium* is a relatively common bacteria (Soltani et al., 2010) that stimulates plant growth and promotes the developmental plasticity of plant roots through auxin production (Verbon & Liberman, 2016; Zhao et al., 2019). *Flavobacterium* is also a highly active phosphobacteria that dissolves phosphate by producing organic acids (Nahas, 1996; Cunningham & Kuiack, 1992). We found that the relative abundance of *Flavobacterium* was significantly related to Pi (Resin-Pi, NaHCO₃-Pi, and 1 M HCl-Pi) (Figure 5), which suggests that the bacteria enhances soil P bioavailability. Moreover, the significant enrichment of *Pseudomonas* and *Arthrobacter* in BCF soils may help to mobilize sparingly labile P, as their relative abundances were significantly positively correlated with recalcitrant and labile P. The significant positive correlation between *Streptomyces* and the Pi fraction and the lower labile Po fractions (such as NaOH-Po and conc. HCl-Po) suggests that the bacteria was involved in the mineralization of lower labile Po as well as the microbial immobilization of Pi to lower labile Po. Similar results were observed by Battni et al. (2017; 2016). In our study, the significant negative correlation between *Burkholderia* and the P fractions may be linked to the accumulation of chicken manure, which alkalizes the originally acidic soil. Although chicken manure increases the soil P content, a more alkaline soil is known to inhibit the activity of *Burkholderia* (Pereira et al., 2013; Stopnisek et al., 2014). *Bacillus* is one of the most important phosphobacteria (Hayat et al., 2010) and has strong resistance to hostile environments (Zhang, 1990). In this study, the relative abundance of *Bacillus* did not differ significantly between the different sites and the control and was not significantly correlated with soil properties. This suggests that the soil

environment in the BCF sites did not influence *Bacillus* activity, which supports its high resistance to changing environments.

4.3 Effect of BCF on phosphorus availability and sustainable land use

BCF significantly enhanced the adsorption capacity for cations (CEC) and improved the fertilizer retention capacity in soil (Ge et al., 2014). Additionally, the increased soil CEC under higher grazing densities may be due to the finer soil texture (Elliott et al., 1986; Teague et al., 2011). We observed no significant difference in SOC between the different grazing densities, which may be due to a number of factors: 1) higher grazing densities may damage the soil structure, which increases the loss of water-soluble organic carbon (Zhan et al., 2020); 2) the accumulation of chicken manure increases soil pH under higher grazing density, which weakens the adsorption capacity of iron and aluminum oxides and influences the sequestration of passive organic carbon (Yan et al., 2019); and 3) the increase in Pi fractions alleviates P limitation for soil microbial metabolism, which enhances soil respiration (Spohn & Schleuss, 2019).

Soil stoichiometry directly reflects the soil's fertility status and indirectly reflects the plant's nutritional status (Fan et al., 2015). Plant leaves with N:P ratios of < 14 indicate N limitation for plant growth, while N:P ratios of > 16 indicate P limitation (Koerselman & Meuleman, 1996; Drenovsky & Richards, 2004). Fan et al. (2015) showed that soil N:P ratios were strongly correlated with plant N:P ratios. This suggests that the different rates of increase of soil N and P with increasing grazing density may have impacted plant growth in this study. Additionally, Yang et al. (2017) demonstrated that a decrease in soil N:P exacerbates N limitation for plant growth and affects the coupled relationship between N and P in soil; this further suggests that the reduced soil N:P from excessive grazing may cause N limitation for plant growth. Furthermore, Tipping et al. (2016) found that lower C:P and C:N ratios may increase the risk of soil nutrient loss. Previous studies have shown that the risk of P loss in soil is closely related to P availability (Liu et al., 2012; Stutter & Richards, 2018; Liu et al., 2019). Therefore, the lower C:N and C:P ratios and the higher labile and moderately labile P contents under higher grazing densities indicate a possible risk of P leaching. In our study, the gradual decrease in the relative content of Po, the increased phosphatase activity, and the increased abundance of phosphobacteria with increasing grazing density suggest that chicken farming promotes the mineralization of Po to Pi. However, further long experiments in this ecosystem are required to determine whether the decrease in Po will eventually lead to P deficiency and become a limiting factor in the P cycle.

Among the different soil properties, pH had the highest impact on bacterial community structure, likely owing to the narrow pH range for optimal bacterial growth (Ragot et al., 2016; Tian et al., 2020). Similar results were observed in previous studies (Geisseler & Scow, 2014; Zhang et al., 2019). Potassium can activate a large number of enzymes (Dotaniya et al., 2016) and is therefore important for microbial metabolism and growth processes; this also explains the large influence of available potassium on the bacterial community structure. Furthermore, our results revealed a strong association between the Pi

fractions (especially 1 M HCl-Pi and Resin-Pi) and the soil bacterial community structures, which may be due to the dominance of heterotrophic microorganisms that depend on exogenous nutrients for growth (Beauregard et al., 2010). Therefore, unstable P levels in soil can have profound effects on the soil microbial community structure (Zhang et al., 2020; Langenheder & Prosser, 2008). In addition, under BCF conditions, Pi fractions (Resin-Pi, NaHCO₃-Pi, and 1 M HCl-Pi) and Po fractions (NaOH-Po and conc. HCl-Po) changed significantly, which affected the relative abundance of phosphobacteria (such as *Flavobacterium*, *Pseudomonas*, *Streptomyces*, and *Arthrobacter*; Figure 5); this likely further influenced the overall soil microbial composition.

5. Conclusion

We found that chicken farming in bamboo forests significantly altered both the soil P distribution and the soil bacterial community structure. Labile and moderately labile P significantly increased with increasing grazing intensity, which suggests that chicken farming effectively enhances soil P bioavailability. Furthermore, grazing intensity could cause the redistribution of soil P and promote the mineralization of Po, as evidenced by an increase in the relative contents of labile and moderately labile P, a decrease in the relative content of Po, an increase in phosphatase activity, and changes in phosphobacteria abundance. Our results suggest that phosphobacteria regulated the soil P cycle, mineralized lower labile Po (*Streptomyces*), and converted insoluble phosphate to soluble phosphate (*Pseudomonas* and *Arthrobacter*). Overall, our findings indicate that BCF can alleviate P deficiency in subtropical forests and increase the soil P supply capacity and potential. However, high grazing density or long-term BCF practices can lead to soil nutrient imbalances and P leaching, which impacts the sustainability of BCF systems.

Abbreviations

BCF: Bamboo-chicken farming; P: Phosphorus; Pt: Total phosphorus; Po: organic phosphorus; Pi: Inorganic phosphorus; ASL: Above sea level; CEC: Cation exchange capacity; SOC: Soil organic carbon; AN: Alkali-hydrolysable nitrogen; AK: Available potassium; TN: Total nitrogen; ACP: Acid phosphatase; ALP: Alkaline phosphatase; PCoA: Principal coordinate analysis; RDA: Redundancy analysis.

Declarations

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Not applicable.

Authors' contributions

Z.Z. and X.Z. conceived the study. X.G., S.L., X.Z. and C.Y. performed the fieldwork. X.G., F.B and S.L. measured the soil samples and collaborated with data analysis. X.G. drafted the manuscript and performed statistical analyses. All authors read and approved the final manuscript.

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Availability of data and materials

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

Ethics approval and consent to participate

Not applicable.

Consent for publication

Not applicable.

Competing interests

The authors declare that they have no competing interests

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Figures

Figure 1

Location map of the experimental site: Jingshan Town, northwest of Hangzhou in Zhejiang Province, southeast China. Note: The designations employed and the presentation of the material on this map do not imply the expression of any opinion whatsoever on the part of Research Square concerning the legal status of any country, territory, city or area or of its authorities, or concerning the delimitation of its frontiers or boundaries. This map has been provided by the authors.

Figure 2

Percentage of each phosphorus (P) fraction in labile P (a), moderately labile P (b), sparingly labile P (c), and total P (d) at the different grazing sites.

Figure 3

Acid phosphatase (a) and alkaline phosphatase (b) activity in the bamboo forest soil under different grazing distances from the hen house. The error bars indicate the standard error of the mean (n = 5). According to Duncan’s test, the different letters indicate significant differences at p < 0.05.

Figure 4

Differences in the dominant phyla (average relative abundance > 1%) of soil bacteria at different distances from the hen house.

Figure 5

Pearson correlation analysis between soil phosphorus fractions and the phosphobacteria genera.

Figure 6

Redundancy analysis of the selected soil properties, phosphorus fractions, and phosphatase for bacterial community structures.

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