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Influence of Thorny Bamboo Plantations on Soil Microbial Biomass and Community Structure in Subtropical Badland Soils

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Abstract: Vegetation in southeastern Taiwan plays an important role in rehabilitating badland soils (high silt and clay content) and maintaining the soil microbial community. The establishment of thorny bamboo (*Bambusa stenostachya* Hackel) may have had a profound impact on the abundance and community structure of soil microorganisms. However, little is known regarding the influence of bamboo on soil biota in the badland ecosystem. The present study was conducted at three badland sites in southwestern Taiwan and focused on the measurement of phospholipid fatty acids (PLFA) together with soil microbial biomass C (C_{mic}) and N (N_{mic}) contents, enzyme activities, and denaturing gradient gel electrophoresis (DGGE) assessments. The abundances of whole soil microbes as well as bacterial and fungal groups—as evident by PLFA, C_{mic} and N_{mic} contents—were much higher in the bamboo plantation soils than the bare land soils. The increased soil organic matter in bamboo plantations relative to the control largely explained the enhancement, the abundance and diversity in the soil microbial community. Principal component analysis of individual PLFA peaks separated the bamboo plantation soil from the non-plantation bare land soil. DGGE analysis also revealed a difference in both bacterial and fungal community structures between soil types. Redundancy analysis of PLFA peak abundance and soil properties indicated that microbial community structure was positively correlated with soil organic C and total N and negatively correlated with pH. This differentiation could be attributed to bamboo in suitable habitats providing an essential nutrient source for soil microbes. The pH reduction in these alkaline soils also contributed to the increase in the size of the microbial community in bamboo-regenerated soils. Together, the results of this study indicate that bamboo plantations are beneficial for soil microbial activities and soil quality in badland areas.

Keywords: phospholipid fatty acid; microbial community; soil enzyme; forest

1. Introduction

Badlands comprise a type of terrain wherein soft sedimentary rocks and clay-rich soils (a fine-grained siliciclastic sedimentary rock) have been extensively eroded by rain water [1]. Badlands are characterized as having sparse or absent plant vegetation and being adverse to cultivation, owing to high clay and calcium carbonate contents and sodium [1,2]. The badland soils are made of up to 90%

silt and clay combined and lack plant cover, largely because the soils are highly penetration-resistant, as high as 14 kg cm^{-2}, and high electrical conductivity (EC) [2–4]. In addition, Soil crusting is common on this badland soil, which enhances its bulk density and penetration resistance and seals the soil surface, decreasing infiltration and increasing runoff on hillslopes, causing the soil to become rock-hard [5].

Some studies [6,7] have indicated that vegetation in badlands can facilitate soil nutrient cycling and protection from soil erosion. In particular, bamboo, which is widely distributed in subtropical areas, is considered an important plant because it serves as an ideal economic resource for building, scaffolding material, and food [8]. Additionally, bamboo provides beneficial ecosystem services such as soil erosion control, land rehabilitation and nutrient cycling [9,10]. For example, thorny bamboo (*Bambusa stenostachya* Hackel) is resistant to hostile environments and is often planted for agroforestry applications such as wind-breaks [11]. Notably, thorny bamboo is one of the few plant species that can grow in the badlands of southwestern Taiwan. For the past few years, interest has grown in evaluating the impact of bamboo planting on soil microbial properties in badland soils [12,13].

A number of soil microbiological parameters have been used to assess the impact of revegetation on the activity, composition, and diversity of the soil microbial community [14]. Soil microbial biomass assessment represents the basic method for soil ecological studies [15] and has been widely used as index of soil fertility [16]. In addition, phospholipid fatty acid (PLFA) [17,18] measurement and denaturing gradient gel electrophoresis (DGGE) analysis [19] offer culture-independent methods to study soil microbial community structure. These methods also provide information on soil microbial characteristics such as biomass, physiology, and microbial community structure [20,21].

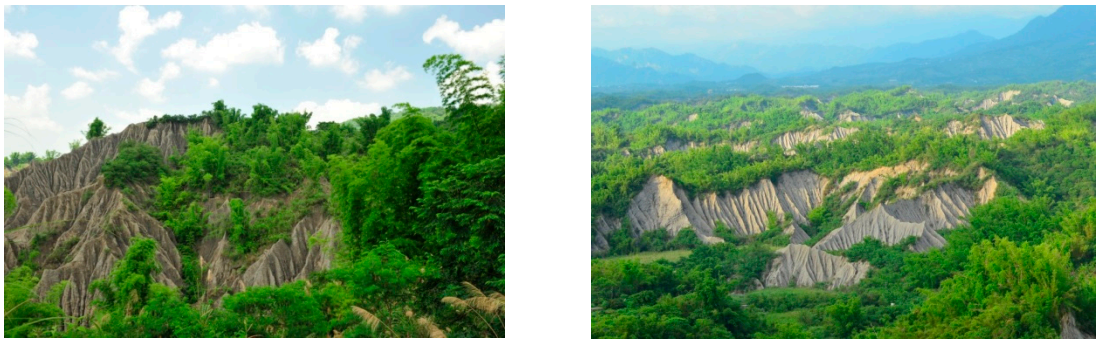
Using these methods, some studies [22,23] have shown that reforestation in degraded soils, such as red soils and karst area soils, represents an effective method for improving microbial biomass and soil quality. Li et al. [24] also found that vegetation conversion in a degraded karst area not only changed the area's carbon fraction and bioavailability but also increased its bacterial diversity. So far, little information is available regarding the effect of bamboo plantations on soil microbial activity and microbial community structure in the badland ecosystems.

We hypothesized that thorny bamboo plantations would change microbial activities as well as bacterial and fungal community composition in badland soils through ameliorating soil properties. Thus, the objective of this study was to test the above hypothesis by measuring a set of soil microbial properties, including PLFA, Gram positive (G+) and negative (G−) bacteria, fungi, and bacterial and fungal community structures in the badlands of southwestern Taiwan with and without bamboo plantations.

2. Materials and Methods

2.1. Site Description

This field study was conducted at three locations in southwestern Taiwan: Zuojhen (Site 1) (23°00′ N, 120°43′ E) in Tainan City, Longci (Site 2) (22°90′ N, 120°39′ E) in Tainan City, and Tianliao (Site 3) (22°85′ N, 120°39′ E) in Kaohsiung City. Soils in the three studied locations have high clay and silt contents, averaging 35.5% and 39%, respectively. The average elevation was 100–300 m above sea level and the mean annual temperature was approximately 25 °C. The south-facing sides of the hogbacks are composed of bare mudstone with no plant coverage. Its soils are classified as Typic Eutrustepts. Soils on the north-facing sides of the hogbacks, however, are classified as Typic Dystrudepts. These sides are dominated by thorny bamboo, bare, as seen in Zuozhen, one of the field sites in this study (Figure 1A,B). Additional information on the study sites and soil properties can be found in Shiau et al. [12] and Lin et al. [13].



(A) (B)

Figure 1. Landscape of the mudstone badland. (**A**) close up view and (**B**) view from a distance at Zuozhen (S1) in Tainan City in southwestern Taiwan. South-facing slopes are barren due to lower soil moisture and more direct sun, and north-facing slopes are covered with thorny bamboo.

2.2. Soil Sampling

Soil samples were collected at each site from bare land areas and thorny bamboo plantations. At each study site, three transects (replicates) from bamboo plantation to bare land were investigated in June 2014. Soil samples were collected at a depth of 0–10 cm using a soil auger of 4 cm diameter. We collected 10 cores at each transect of land usage type to create a composite soil sample. The soil samples were sieved (<2 mm) and roots and litter were removed. Subsamples of fresh soils were freeze-dried at −20 °C immediately after field sampling for PLFA and DGGE analysis. Soil moisture was determined by drying at 105 °C for 24 h then comparing the resulting weight to the dry weight basis. Subsamples for physicochemical properties were air-dried and ground to pass a 2 mm mesh size sieve. The organic C (C_{org}) and total N (N_{tot}) contents were determined using a Fisons NA1500 elemental analyzer (ThermoQuest Italia, Milan, Italy). The soil pH was measured at a 1:2.5 soil to water suspension using a combination glass electrode.

2.3. Biochemical Assay

Soil microbial PLFA analysis was performed using the methods described in Frostegård et al. [25]. In brief, each soil sample was extracted using a single-phase mixture of the chloroform-methanol-citrate system. Extracts were then split into neutral, glycol-, and phospho-lipids using a silica extraction column and eluting with chloroform, acetone, and methanol, respectively. Then, the phospholipids were hydrolyzed and saponified with alkaline methanol to form fatty acid methyl esters (FAMEs). The FAMEs were analyzed using capillary gas chromatography (GC) and flame ionization detection with the Thermo Finnigan Trace chromatography system (Thermo Fisher Scientific, Waltham, MA, USA). The GC operation was performed as described by Chang et al. [26]. PLFA biomarkers were grouped as bacteria (i15:0, a15:0, 15:0, i16:0, 16:1ω7c, 17:0, i17:0, cy17:0, 18:1ω7c, cy19:0), fungi (18:2ω6c), G+ bacteria (i15:0, a15:0, i16:0, i17:0), G− bacteria (16:1ω7c, cy17:0, 18:1ω7c, cy19:0), and actinobacteria (10Me18:0) [18,27].

Total DNA was extracted from 0.25 g soil sample using the PowerSoil DNA isolation kit (MO BIO Laboratories, Solana Beach, CA, USA). For amplification of bacterial 16S rRNA, polymerase chain reaction (PCR) were performed with the primer pair F968-GC and R1401 [28] as follows. The PCR mixtures were prepared with 20 µL 2X Quick Taq HS DyeMix (Toyobo Co., Ltd., Osaka, Japan), 10 pmol each primer, and 1 µL template DNA in a final volume of 50 µL. The cycling program included 2 min incubation at 94 °C, followed by 35 cycles at 94 °C for 30 s, 61 °C for 30 s, and finally a 5-min extension at 68 °C. For soil fungi, the PCR was performed with the primer pair NS1 and GC fungi [29] as follows. The PCR mixtures were prepared with 20 µL 2X Quick Taq HS DyeMix (Toyobo), 10 pmol each primer, 1 µL template DNA, and deionized water to bring the final volume to 50 µL. The cycling program was 2 min at 94 °C, followed by 35 cycles of 94 °C for 30 s, 52 °C for 30 s, and 68 °C for 5 min.

The PCR products were analyzed by DGGE as described in Reference [30]. A DGGE gel comprised 6% polyacrylamide gel and 50% to 70% denaturants for bacterial 16S rRNA and 7% polyacrylamide and 20% to 45% denaturants for fungal 18s rRNA. The electrophoresis was performed for 16 h at 60 V in 1X TAE (Tris-acetate-EDTA) buffer at a constant temperature of 58 °C for bacteria and 60 °C for fungi using a D-Code Universal system (Bio-Rad Laboratories, Hercules, CA, USA). The gel was stained with Gelstar (10 µL of Gelstar in 100 ml 1X TAE buffer) for 30 min, then DGGE band profiles were visualized under UV light. The DGGE image was analyzed using a Gel Doc XR gel imaging system (Bio-Rad).

2.4. Statistical Analysis

The statistical analyses were performed using SPSS v18.0 (SPSS Inc., Chicago, IL, USA). Data were subjected to one-way analysis of variance (ANOVA). A significance level of $p < 0.05$ was considered for all statistical analyses. Correlativity analysis was carried out between microbial parameters and soil variables. Principal component analysis (PCA) was used to test relative concentrations (mole%) of individual fatty acids with SPSS software. Multivariate pattern analyses were conducted using Canoco for Windows (Version 5.0). Redundancy analysis (RDA) was applied to comprehensively test the relations among the PLFA, with the results from our parallel studies, such as soil physiochemical properties, including electrical conductivity, bulk density, microbial biomass C (C_{mic}), soluble organic C in hot water extract (SOC_{HW}), acid hydrolysable labile pool C (AHLP-C), recalcitrant pool C (RP-C), organic C (C_{org}), N_{tot}, mineralizable N (Min-N), and metabolic quotient (qCO_2) [10], soil enzyme activities and soil bacteria compositions [13] in the badland soil through the bamboo plantation. Hierarchical cluster analysis with an unweighted pair-group method with arithmetic mean algorithm was used to process the DGGE banding pattern with Quantity One software (Bio-Rad).

3. Results

3.1. Microbial Community Structure

The total soil PLFA, bacteria, actinobacteria, and G+ and G− bacteria contents in bamboo plantations were significantly higher than those in bare land soils (Table 1). The highest values were observed in the bamboo plantation soil at Site 2. Fungi contents showed no significant difference between bamboo plantation and badland soils, with the exception of the bamboo plantation soil at Site 2.

Table 1. Content of phospholipid acid biomarkers (nmol g^{-1} soil) in the soils at different locations with and without bamboo plantation.

Site	Location	Vegetation	Total PLFA	Bacteria	Fungi	Actinobacteria	G+	G−	G+/G−	Fungi/Bacteria
1	Zuojhen	Bare land	1.74 c	0.198 c	0.226 b	0.037 c	0.137 c	0.039 c	3.50 a	1.33 a
		Bamboo	8.60 b	2.90 b	0.323 b	0.876 b	2.24 b	0.524 b	3.89 a	0.102 a
2	Longci	Bare land	1.50 c	0.168 c	0.257 b	0.068 c	0.236 c	0.037 c	4.38 a	1.49 a
		Bamboo	23.7 a	9.87 a	1.79 a	2.56 a	7.47 a	2.03 a	3.69 a	0.179 a
3	Tianliao	Bare land	1.79 c	0.129 c	0.464 b	0.049 c	0.103 c	0.027 c	3.72 a	3.50 a
		Bamboo	10.3 b	3.85 b	0.337 b	1.15 b	2.95 b	0.706 b	4.27 a	0.087 a

Values in each column with different letters indicate significant differences between treatments (Duncan' multiple range test, $p < 0.05$). PLFA: phospholipid fatty acids.

Soil communities, as analyzed by PCA for PLFA levels, differed significantly between bamboo plantation and bare land soils. The PLFA levels in the soil could be divided into two large clusters—bare land and bamboo plantation soils. The first and second principal components (PC1, PC2) accounted for 74.7% of the variation in PLFA levels (Figure 2). PC1 differentiated bamboo plantation soil from bare land soils, high positive loadings by the G+ bacteria (i15:0, a15:0, i16:0, and i17:0) and actinobacteria (10Me16:0 and 10Me18:0) contributed to separating bamboo plantation soil from bare land soil along the PC1 axis.

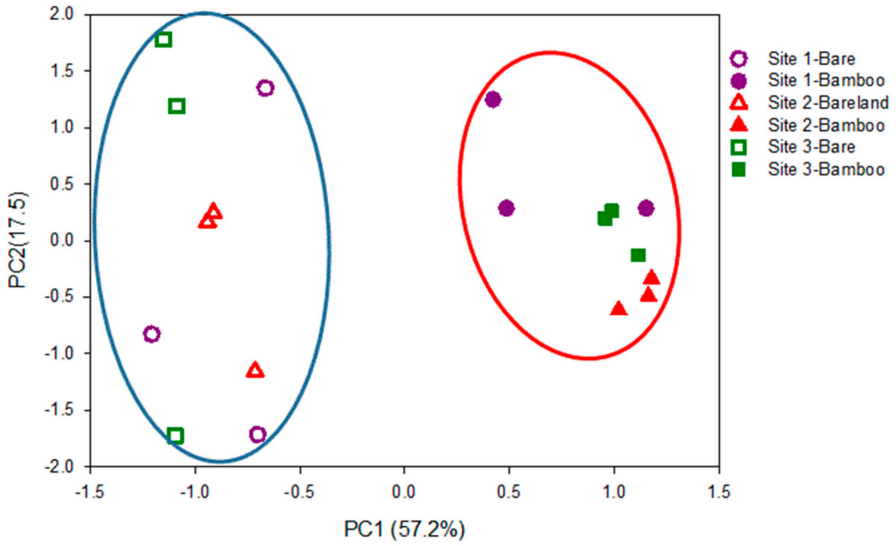


Figure 2. Score plots of the two first components (principal component (PC) in a principal component analysis) of the mole% of microbial phospholipid fatty acids (PLFA) in the soils at different locations.

3.2. Redundancy Analysis

To evaluate the relations among soil enzyme activities and environmental factors, an RDA was conducted using soil enzyme activities and environmental variables (Figure 3). Soil enzyme activities changed with bamboo plantation, and soil samples from the bamboo planations were well separated from badland soils by RDA analysis. Soil enzyme activities were positively correlated with soil microbial biomass, C_{org}, N_{tot}, and Min-N were negatively correlated with pH, suggesting that soil pH and C_{org} and N_{tot}, mineral N contents had strong effects on the soil enzyme activities of badland soils.

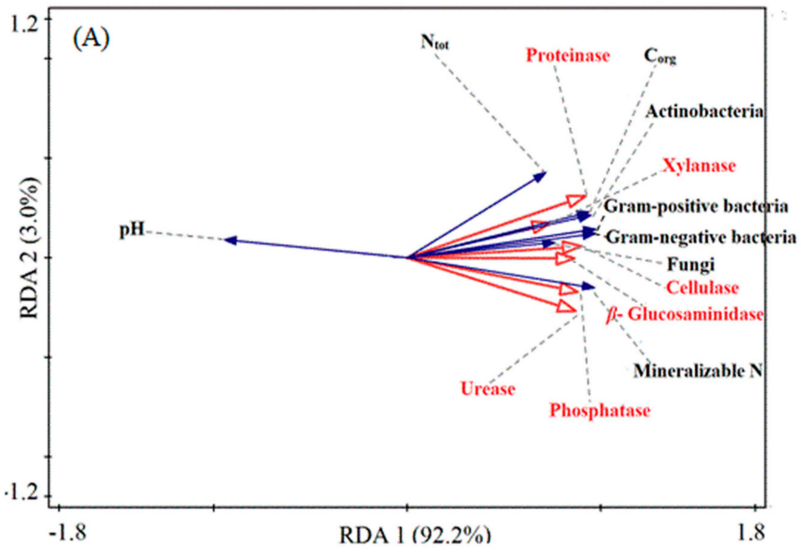


Figure 3. *Cont.*

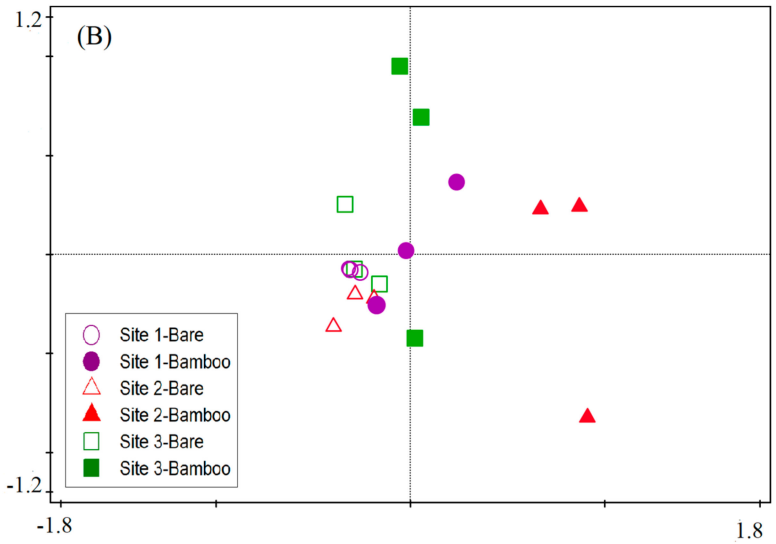


Figure 3. Redundancy analysis on soil enzyme activities, and environmental factors from soil samples collected at different locations (**A**). (**B**) shows site code for each sample. Bare land (open), Bamboo plantation (solid) soil.

The results from RDA also showed similar patterns as those observed from the PCA analysis (Figure 4). Soil labile C to C_{org} (i.e. AHLP-C/C_{org} and SOC_{HW}/C_{org}) were both positively related to the bamboo soils, while soil recalcitrant C pools to C_{org} (RP-C/C_{org}) and metabolism quotient (qCO_2) were positively related to bare land soils. In summary, distinctive soil physiochemical chemical properties and the available labile C and N between the bamboo plantation soils and the bare land soils were responsible for the development of soil bacteria, fungi and actinobacteria communities. These available C and N contents were also positively correlated with soil bacterium communities such as gemmatimonadetes (Gemmatimonas), acidobacteria (Gp1, Gp4 and Gp6), and actinobacteria (Gailla), but negatively correlated with gammaproteobacteria (Thiohalophilus) and Actinobacteria (Amycolatopsis).

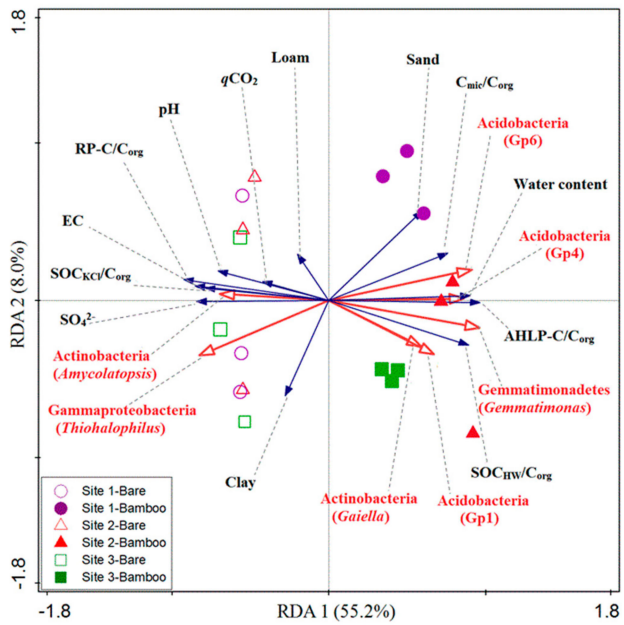


Figure 4. Redundancy analysis on the soil physiochemical properties and soil bacterium community contents in the soils at different locations.

3.3. Denaturing Gradient Gel Electrophoresis (DGGE) Analysis

Dendrograms of genetic similarity obtained by DGGE analysis of bacterial communities in the bare land soil samples clustered more differently than those from bamboo plantations (Figure 5). Specifically, the microbial communities in the bare land and bamboo plantation soils clearly comprised two different groups. Similarly, cluster analysis of the fungal communities showed two main clusters: soil samples from bamboo plantations and those from bare land (Figure 6).

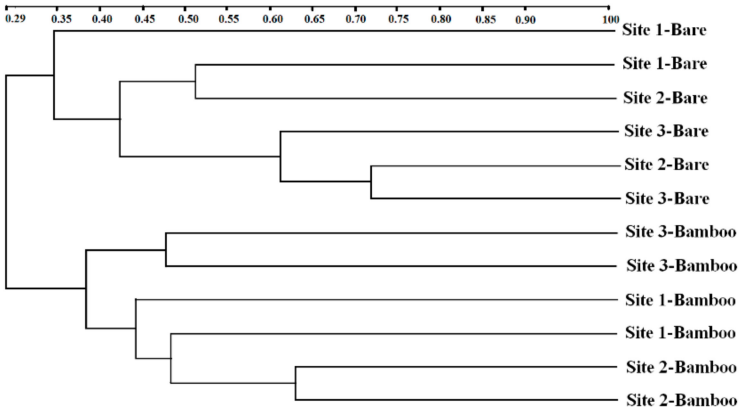


Figure 5. Cluster analysis of bacterial community structures from the soils studied at different locations measured by the unweighted pair group method with arithmetic mean.

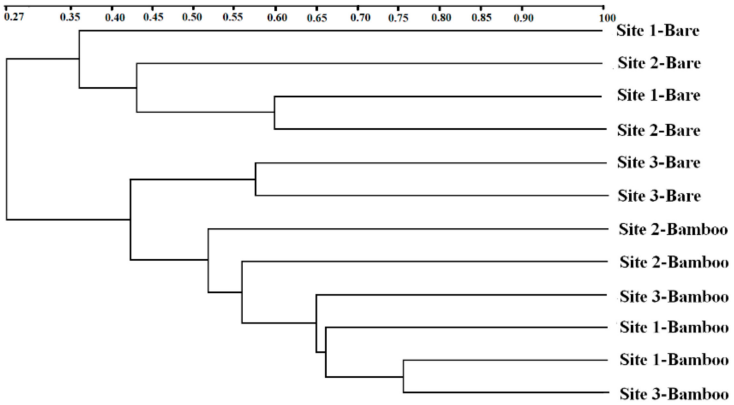


Figure 6. Cluster analysis of fungal community structure from the soils studied at different locations measured by the unweighted pair group method with arithmetic mean.

4. Discussion

Our results indicate that bamboo plantations tended to have higher C_{org} and N_{tot} contents and microbial abundances than bare land soils. Tian et al. [31] suggested that planting bamboo in degraded soils would result in the storage of more soil C_{org} and also have a positive effect on soil biodiversity. For example, badland soils often contain high Na^+ and Ca^{2+}, which can raise the soil pH. Some studies [32,33] have shown that vegetation provides the biological stability to lower exchange Na^+. In addition, plant roots could uptake Na^+ and release H^+, which may replace Na^+ in the soil [34]. In the present study, we observed that C_{org} was higher and pH lower in bamboo plantation soils than adjacent bare land soils. Notably, Beets et al. [35] indicated that lower soil pH could lead to the formation of humic acid and enhance the accumulation of C_{org}. The lowering of soil pH in the bamboo plantation may also contribute to the higher content of C_{org}. Furthermore, the soil microbial biomass was also increased by bamboo, and this could be due to the increased C_{org} caused by the input of litter from the bamboo. Additionally, penetration of the bamboo rooting system might help to create porosity, reduce the bulk density and wash the salts away from the soil [13].

Some studies showed that soil enzyme activities were correlated with C_{org} [36,37] and microbial biomass [36]. Our results showed that soil enzyme activities were positively correlated with C_{org}, increasing with bamboo planation (Figure 3). A similar result was also found by Zhou et al. [38], which showed that soil enzyme activities in karst soil increased when bamboo was planted and had positive correlations with C_{org}. The results indicated that planting bamboo improved soil nutrition and enzyme activity compared with bare land soils. In addition, the enzymes' activities were negatively correlated with pH, as described above, and the planting of bamboo resulted in a higher soil humic acid accumulation.

Furthermore, the PCA analysis for PLFA content clearly distinguished the bamboo plantation from the bare land soils, largely because of the PC1 axis (Figure 2). The G+ bacteria and actinobacteria provided the highest contribution to the PC1 score, which suggests that the content of G+ bacteria is an important factor response to the effect of bamboo plantation in these badland soils. In particular, the community-level PLFA profiles are useful to detect soil microbial community responses to various land uses or disturbances in ecosystems [39,40]. We found that the bamboo plantation provided a higher quantity of labile compounds than the bare land soils and increased soil microbial biomass and total PLFAs. Furthermore, the G− bacteria content was significantly higher in bamboo plantation than in bare land soils. Notably, the G− bacteria content has been reported to increase with substrate availability [41,42]. Lin et al. [11] also found that planting bamboo in the badland soil increased the abundance of *Alphaproteobacteria* compared with the bare land soils. Additionally, some studies [43,44] indicated that drought-tolerant microbes, such as G+ bacteria and actinobacteria, could be protected inherently against low moisture during drought stress and adapt to low levels of available organic matter. Hence, G+ bacteria might adapt to inferior conditions more effectively than G− bacteria, which may explain the important roles that G+ bacteria and actinobacteria appear to play in these badland systems. The result coincided with our previous study—Lin et al. [13] found that actinobacteria abundance comprises almost 50% of all pyrosequences in the same badland, suggesting that the stress of rapid drying and lack of water infiltration made this phylum dominant in this badland system.

In comparison, the fungi showed no significant response to bamboo plantation, with the exception of Site 2, which had higher fungi content under bamboo plantation. The ratio of fungi to bacteria showed an increasing trend in bare land soils (Table 1). Notably, several studies have shown that the microbial community structure responds to soil fertility and that fertile soils favor bacteria, whereas less fertile soils favor fungi [45]. Thus, the high availability of labile C in the bamboo plantation soil likely allows bacteria to be more competitive than fungi.

Although ratios of soil G+/G− and cyclopropane fatty acids to monoenoic precursor fatty acids are useful indicators for interpreting the physiological stress that microbial communities endure [46,47], low values obtained in bare land soils caused large variation and did not show significant difference between soils.

Dendrograms of soil bacteria and fungi based on PCR-DGGE showed primary differences in microbial communities between bamboo plantation and bare land soils (Figures 5 and 6). These findings support our hypothesis. Specifically, bamboo plantations provide an available C source and restore soil microbial communities, particularly bacteria. In this study, the DGGE findings agreed with the PCA of PLFAs, showing distinct compositions of the bacterial and fungal communities between bamboo plantation and bare land soil.

The results from this study and the soil physiochemical and bacterium composition data previously collected at the same study locations clearly show that thorny bamboo plantations improved the overall quality of badland soils. Soil properties such as EC, SO_4^{2-}, water content and bulk density were dramatically improved after bamboo was planted [11]. Furthermore, the soil labile C and N provided by bamboo litters helped reducing environmental stresses found in the original badland soils.

In addition, as shown in Lin et al. [13] and the RDA (Figures 3 and 4) from this study, the improvement in soil quality through bamboo plantation is directly linked to changes in the soil bacterium compositions. As seen from the RDA, the biomass of soil microbial communities and soil

labile C to C_{org} (i.e., AHLP-C/C_{org} and SOC_{HW}/C_{org}) were both positively related to the bamboo soils, showing that the labile C sources significantly increased microbial biomass. On the other hand, soil recalcitrant C pool to C_{org} (RP-C/C_{org}) and metabolism quotient (qCO_2) were positively related to bare land soils, indicating that microbes were under greater stress in the bare land soils [12].

Subdivision 1 of acidobacteria (Gp1) can use carbohydrates such as glucose, xylose and lactose, but are unable to digest fucose or sorbose [48]. As plant cell walls are composed majorly by glucose, xylose and lactose [49,50], the organic matter provided by bamboo may favor the development of acidobacteria (Gp1) community. Acidobacteria were found in soils with low pH and strongly correlated with pH [51]. Acidobacteria may be classified as oligotrophic bacteria and is well adapted to resource-limited environments with low plant productivity [52]. However, Fierer et al. [53] also indicated that certain acidobacteria might be like copiotrophic bacteria and show high abundance of high substrate availability in soils. In this study, acidobacteria were negatively correlated with pH and dominant in bamboo plantation soils. Furthermore, acidobacteria are also important to N mineralization, especially nitrate and nitrite reductions [54,55]. As the bamboo plantation provided C and N sources with litter for soil microorganisms, the observed enzyme activities, mineralizable N, and labile fractions of C_{org} explains the increase in soil bacteria, fungi and acidobacteria biomass in the bamboo plantation soils. Moreover, these fundamental changes provided a favorable environment for bacteria such as *Gemmatimonas* and *Gailla*, which were previously found in soils with high pH and resisted the impact of drainage [56,57]. In addition, the community of sulfur reducing bacteria, *Thiohalophilus*, was positively correlated with the SO_4^{2-} concentration and inhabited in bare land soils [13,58].

5. Conclusions

The present study shows a higher abundance of soil microbial community in bamboo than bare land soils, suggesting that the stress of poor physicochemical properties in the badland soils were ameliorated by the bamboo plantation. PCA for PLFA content, RDA for soil bacterial community and cluster analysis for DGGE all revealed that changes in both the bacterial and fungal community structure were associated with bamboo plantation. Planting bamboo in badland soils increased C_{org} composition, particularly the labile C pool. Therefore, bamboo plantations in badland soils increases microbial biomass and activities by changing soil physicochemical properties and promoting diversity of microbial communities. PLFA indicators and acidobacteria based on pyrosequencing of 16S rRNA genes were all positively correlated with C_{org} and negatively correlated with soil pH. Overall, our findings show that bamboo plantations in the badlands improves soil quality and soil community, especially for acidobacteria.

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