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Heterotrophic Bacteria Play an Important Role in Endemism of *Cephalostachyum pingbianense* (Hsueh & Y.M. Yang ex Yi et al.) D.Z. Li & H.Q. Yang, 2007, a Full-Year Shooting Woody Bamboo

Tize Xia †, Lushuang Li †, Bin Li, Peitong Dou and Hanqi Yang *

Institute of Highland Forest Science, Chinese Academy of Forestry, Kunming 650233, China;
xtz7988042@163.com (T.X.); lilushuang@126.com (L.L.); libin2015caf@126.com (B.L.); kyzksdpt@163.com (P.D.)
* Correspondence: yanghanqikm@aliyun.com
† Tize Xia and Lushuang Li contributed equally to this paper.

Abstract: The previous studies show soil microbes play a key role in the material and nutrient cycles in the forest ecosystem, but little is known about how soil microbes respond to plant distribution, especially in the soil bacterial community in woody bamboo forests. *Cephalostachyum pingbianense* (Hsueh & Y.M. Yang ex Yi et al.) D.Z. Li & H.Q. Yang, 2007 is known as the only bamboo species producing shoots all year round in natural conditions. Endemic to the Dawei mountain in Yunnan of China, this species is a good case to study how soil bacteria respond to plant endemic distribution. In this work, we assayed the soil chemical properties, enzyme activity, changes in the bacterial community along the distribution range of the *C. pingbianense* forest. The results showed that soil nutrients at the range edge were nitrogen-rich but phosphorus-deficient, and soil pH value and soil urease activity were significantly lower than that of the central range. No significant difference was detected in soil bacterial diversity, community composition, and function between the central and marginal range of *C. pingbianense* forest. Notably, the relative abundance of heterotrophy bacteria, such as *Variibacter* and *Acidothermus*, in the soil of the *C. pingbianense* forest was significantly higher than that of the outside range, which may lead to a higher soil organic carbon mineralization rate. These results imply that abundant heterotrophy bacteria were linked to the endemism and full-year shooting in *C. pingbianense*. Our study is amongst the first cases demonstrating the important role of heterotrophy bacteria in the distribution formation of endemic woody bamboos in special soil habitats, and provides insight into germplasm conservation and forest management in woody bamboos.

Keywords: *Cephalostachyum pingbianense*; bacterial community; distribution range limit; soil chemical properties; soil urease

1. Introduction

Cephalostachyum pingbianense (Hsueh & Y.M. Yang ex Yi et al.) D.Z. Li & H.Q. Yang, 2007 is a rare species in the bamboo subfamily of Poaceae and is known as the only woody bamboo that produces delicious shoots all year round in the wild [1,2]. Endemic to the Dawei mountain in southern Yunnan of China, *C. pingbianense* is mainly distributed in the elevation range of 1600–2000 m [1,3]. The vertical distribution of vegetation is obvious in the Dawei mountain area [3]. The upper and lower range margins of the *C. pingbianense* forest are adjacent to the *Lithocarpus glaber* (Thunb.) Nakai, 1916 forest and *Cyclobalanopsis kerrii* (Craib) Hu, 1911 forest, respectively. Although *C. pingbianense* has been introduced and cultivated in several areas in Yunnan in the past 30 years, there is no successful record so far. Due to human interference, gregarious flowering, and genetic restriction, *C. pingbianense* faces the danger of extinction. It is urgent to study its adaptability to the environment and formulate corresponding management and protection strategies.

The formation of the geographical range boundary of the plant has always been an important topic in evolutionary biology and ecology. Based on genetics and evolution, a

gene flow hypothesis regarding plant distribution range limits deemed that the populations at range edges did not greatly adapt to their local environments due to inadequate gene flow from the range interior [4,5]. Ecologically, the plant geographic range boundary is influenced by both biotic and abiotic factors. Among abiotic factors, temperature and precipitation determine the distribution pattern of terrestrial plants worldwide [6,7]. Biological factors, such as herbivores and pollinators, affect the expansion of the plant distribution boundary [8–10]. In turn, the change of the plant distribution area also reflects the shift of external biological factors, including the symbiotic microbial community [11,12]. However, how plant distribution impacts soil bacterial communities is largely unclear.

Close links between plants and soil bacteria have been supported by many studies. Plants directly or indirectly affect soil bacteria through secretion and litter [13–16]. On the other hand, soil bacteria participate in nutrient cycling and inhibiting pathogens to facilitate plant growth and health [17]. Microbial distributions were once considered to follow the Bass-Becking hypothesis that "everything is everywhere, but the environment selects" [18], implying that microbes possessed high dispersal abilities. Namely, the microbial distribution pattern is mainly driven by environmental factors and is not restricted by geographical distance. However, contrary to this long-held assumption, many recent studies indicate that the distribution pattern of microbes is affected by geographical distance, environmental factors, and plant species [19]. To sum up, studies on microbial geographical distribution are not rare, but the responses of microbes to plant distribution remains largely ambiguous. In order to clarify the response of the soil microbial community to plant distribution, it is necessary to determine the changes of the soil microbial community within and beyond the plant distribution range.

As far as we know, *C. pingbianense* is strictly restricted to the tropical mountain monsoon forests in Dawei mountain [1–3], which provides a good chance to study the distribution formation of endemic woody bamboos in special soil habitats. Meanwhile, the attribute of full-year shooting demands a high material and nutrient cycling rate in *C. pingbianense* forest accordingly. As soil bacteria play a crucial role in the material and nutrient cycle in the forest ecosystem [13,15], in this study, we detected the changes of the bacterial community along distribution range limits. We investigated the soil bacterial community at the central, marginal, and outside the range of *C. pingbianense* forest through high-throughput sequencing, determined the soil and chemical properties and enzyme vitality, and analyzed the correlation between environmental factors and the soil bacterial community. We hypothesized that: (1) The soil bacterial diversity and composition are different along the distribution range of *C. pingbianense* forest; (2) Specific bacteria in the soil of *C. pingbianense* forest are associated with the endemic distribution of this rare woody bamboo.

2. Materials and Methods

2.1. Site Selection and Soil Sampling

The research location was Dawei mountain national forest park (22°54′ N, 103°42′ E) in the southern Yunnan Province of China. Dawei mountain is on the tropical edge with a tropical monsoon climate [3], characterized by wet all year round, warm in winter, and hot in summer. The annual ≥10 °C cumulative temperature is 2216 °C, and the precipitation is 1700–1900 mm. The soil type is mainly red soil below 1000 m above sea level and yellow soil above 1000 m. *C. pingbianense* is the only species of the genus *Cephalostachyum* distributed at Dawei mountain, and usually aggregates into natural bamboo forests. The vertical vegetation is clearly evidenced at Dawei mountain. The upper and lower range margins of *C. pingbianense* forest are adjacent to *L. glaber* forest and *C. kerrii* forest, respectively. The main compositions of undergrowth vegetation in the three forests are as follows: *Selaginella tamariscina* (P. Beauv.) Spring, *Polygonatum odoratum* (Mill.) Druce, and *Ophiopogon bodinieri* H. Lév. in *C. pingbianense* forest; *Ternstroemia gymnanthera* (Wight & Arn.), *Elaeocarpus sylvestris* (Lour.) Poir. 1811, and *Imperata cylindrica* in *C. kerrii* forest; *Ternstroemia gymnanthera*, *Eurya hebeclados*, and *Dryopteris simasakii* in *L. glaber* forest. We established five sites

to take soil samples: *C. kerrii* forest (1550 m, site A); the lower range limit of *C. pingbianense* forest (1650 m, site B); the range center of *C. pingbianense* forest (1850 m, site C); the upper range limit of *C. pingbianense* forest (2050 m, site D); and *L. glaber* forest (2150 m, site E). For each site, we established three 5 m × 5 m plots, totaling 15 plots. At each plot, soil samples were collected from the top 0–20 cm soil layers in 5 randomly selected locations in November 2020. The soil samples were sieved at 2 mm to remove stones and plant residues. Five samples were combined to form a single composite sample from each plot, which were then divided into three sub-samples. The first part of the soil samples was air-dried for chemical analysis, the second was stored in an icebox to determine enzyme activity within two weeks, and the third portion was stored in a dry ice box, transferred to the laboratory, and stored at −80 °C in a freezer for DNA extraction.

2.2. Soil Chemical Characterization and Enzyme Activity Measurements

Soil pH, organic matter (OM), total nitrogen (TN), total phosphorus (TP), available nitrogen (AN), and available phosphorus (AP) were determined based on Lu's methods [20]. Three soil enzyme activities (invertase, urease, and acid phosphatase) were assayed according to Guan [21]. The invertase activity was determined by the 3,5-dinitrosalicylic acid colorimetric method, calculated by the milligram number of glucose in 1 g soil after the air-dried soil was cultured at 37 °C for 24 h. Urease activity was determined by the sodium phenate-sodium hypochlorite colorimetric method, calculated by the milligram number of ammonia nitrogen in 1 g soil after culturing at 37 °C for 24 h. The colorimetric method of phenyl disodium phosphate was adopted to determine acid phosphatase activity, which was estimated by the milligram number of phenol in 1 g soil after culturing at 37 °C for 12 h.

2.3. DNA Extraction, PCR Amplification, and MiSeq Sequencing

FastDNA® SPIN Kit for Soil (MP Biomedicals, Santa Ana, CA, USA) was used to extract the soil DNA from 0.25 g fresh soil samples according to the manufacturer's instructions. The quality and concentration of DNA were verified with NanoDrop2000 and agarose gel. The V3V4 variable regions of bacterial 16S rRNA genes were amplified using the Primers 338F (ACTCCTACGGGAGGCAGCA) and 806R (GGACTACHVGGTWTCTAAT) [22]. The PCR amplification system (20 μL): 4 μL 5×FastPfu buffer, 2 μL 2.5 mM dNTPs, 0.8 μL forward primer (5 μM), 0.8 μL reverse primer (5 μM), 0.4 μL FastPfu polymerase, 0.2 μL BSA; 10 ng DNA template, and finally replenish to 20 μL with ddH$_2$O. The PCR conditions included an initial denaturation at 95 °C for 3 min, 35 cycles of denaturation at 95 °C for 30 s, annealing at 55 °C for 30 s, extension at 72 °C for 45 s, and then final extension at 72 °C for 10 min. Amplicon quality was visualized using gel electrophoresis. The products were sequenced on an Illumina MiSeq PE300 platform at the Shanghai Majorbio Bio-pharm Technology Co., Ltd. (Shanghai, China).

2.4. Bioinformatics and Statistical Analysis

For raw sequences, quality control was performed on paired-end raw reads using Trimmomatic (v0.33, USADEL lab, Aachen, Germany). Clean reads were merged using FLASH (v1.2.11, Johns Hopkins University, Baltimore, MD, USA). Chimeric sequences were removed using UCHIME software (v4.1, Robert C Edgar, Mill Valley, CA, USA). Effective sequences with ≥97% similarity were clustered into the same operational taxonomic units (OTUs) by UPARSE (v7.0.1090, Robert C Edgar, CA, USA). Representative sequences were chosen for each OTU, and taxonomic data were then assigned to each representative sequence according to the Silva database. The richness (number of OTUs), Shannon index, Phylogenetic diversity, and the richness estimator in Chao1 were calculated with MOTHUR (v.1.30.2, University of Michigan, Ann Arbor, MI, USA) to estimate the bacterial alpha diversity. The Kruskal-Wallis H test was performed to analyze differences in soil microbial diversity and abundance among five sites. FAPROTAX (v1.0, University of British Columbia, Vancouver, Canada) was used to predict bacterial ecological function. The rela-

tionships of the bacterial community with soil chemical properties and altitude in different soil samples were analyzed by redundancy analysis and spearman correlation analyses.

3. Results

3.1. Soil Chemical Properties and Soil Enzymatic Activities

Soil chemical properties and enzyme activities were significantly different among the five sites (Figure 1). The soil samples of each site were acidic. The soil organic matter content in the *C. kerrii* forest (A) was significantly lower than that of the other four sites ($p < 0.05$), and the activities of three soil enzymes were the lowest among the five sites. The contents of available phosphorus and total phosphorus in the *L. glaber* forest soil were significantly higher than the remaining four sites ($p < 0.05$). Among *C. pingbianense* soil sites, the soil pH value, available phosphorus content, and urease activity at the range boundaries (B and D) were significantly lower than those of range center (C) ($p < 0.05$), while available nitrogen exhibited an opposite trend.
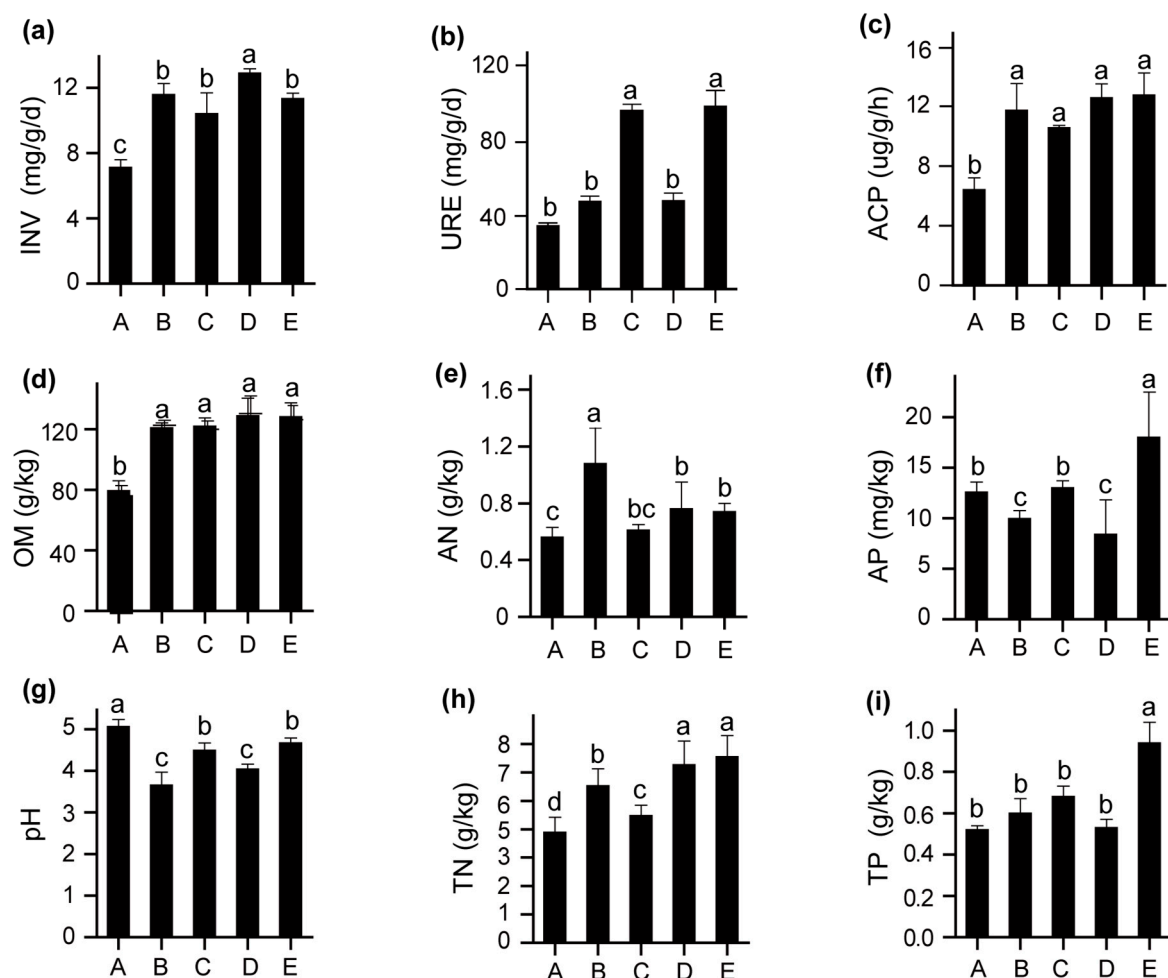

Figure 1. Soil enzyme activity and soil chemical properties. (**a**), INV, Invertase activity; (**b**), URE, urease activity; (**c**), ACP, acid phosphatase activity; (**d**), OM, organic matter content; (**e**), AN, available N content; (**f**), AP, available P content; (**g**), pH value; (**h**), TN, total N content; (**i**), TP, total P content. A, *Cyclobalanopsis kerrii* (Craib) Hu, 1911 forest; B, the lower range limit of *Cephalostachyum pingbianense* (Hsueh & Y.M. Yang ex Yi et al.) D.Z. Li & H.Q. Yang, 2007 forest; C, the range center of *C. pingbianense* forest; D, the upper range limit of *C. pingbianense* forest; E, *Lithocarpus glaber* (Thunb.) Nakai, 1916 forest. Different letters (a, b, c, d) meant significant differences at the 0.05 level.

3.2. Changes in Soil Bacterial Community Composition and Diversity

Illumina sequencing of bacterial 16S rRNA gene amplicons resulted in 316,515 effective sequences. The sequencing coverage of each sample is more than 96%, indicating that the sequencing results include most microbial groups. As shown in Table 1, the Shannon index, Chao1 index, Phylogenetic Diversity index, and Richness of bacterial community in the *C. kerrii* forest (A) soil were significantly higher than at the other four sites. There was no significant difference in soil bacterial diversity between the range center and edges of the *C. pingbianense* forest.

Table 1. Alpha diversity of soil bacterial community.

Types	Shannon	Chao1	Richness	Phylogenetic Diversity
A	6.47 ± 0.07 a	3325 ± 211 a	2431 ± 174 a	210 ± 10 a
B	5.90 ± 0.08 c	2762 ± 29 b	1830 ± 44 b	154 ± 6 b
C	5.83 ± 0.09 c	2757 ± 168 b	1736 ± 138 b	148 ± 9 b
D	5.90 ± 0.04 c	2764 ± 52 b	1860 ± 31 b	155 ± 2 b
E	6.15 ± 0.05 b	2780 ± 97 b	1963 ± 58 b	163 ± 4 b

The data in the table is the mean ± standard deviation. Different letters (a, b, c) in the same column meant significant differences at 0.05 level. A, *Cyclobalanopsis kerrii* (Craib) Hu, 1911 forest; B, the lower range limit of *Cephalostachyum pingbianense* (Hsueh & Y.M. Yang ex Yi et al.) D.Z. Li & H.Q. Yang, 2007 forest; C, the range center of *C. pingbianense* forest; D, the upper range limit of *C. pingbianense* forest; E, *Lithocarpus glaber* (Thunb.) Nakai, 1916 forest.

The bacterial OTUs spanned 38 phyla, 93 classes, 189 orders, 370 families, 642 genera, and 1287 species. At the phylum level, there are 10 bacterial taxa with a >2% relative abundance (Figure 2). Among all five sampling sites, the dominant bacterial phyla (relative abundance >20%) were *Proteobacteria* and *Acidobacteria*. The relative abundance of *Actinobacteria* in the *C. pingbianense* forest soil (B–D) is about 1.4–2.4 times that in broad-leaved forest soil (A, E). The relative abundance of *Chloroflexi* and *Nitospirae* in the *C. kerrii* forest (A) was significantly higher than that in the other four sites ($p < 0.05$) (Table 2).
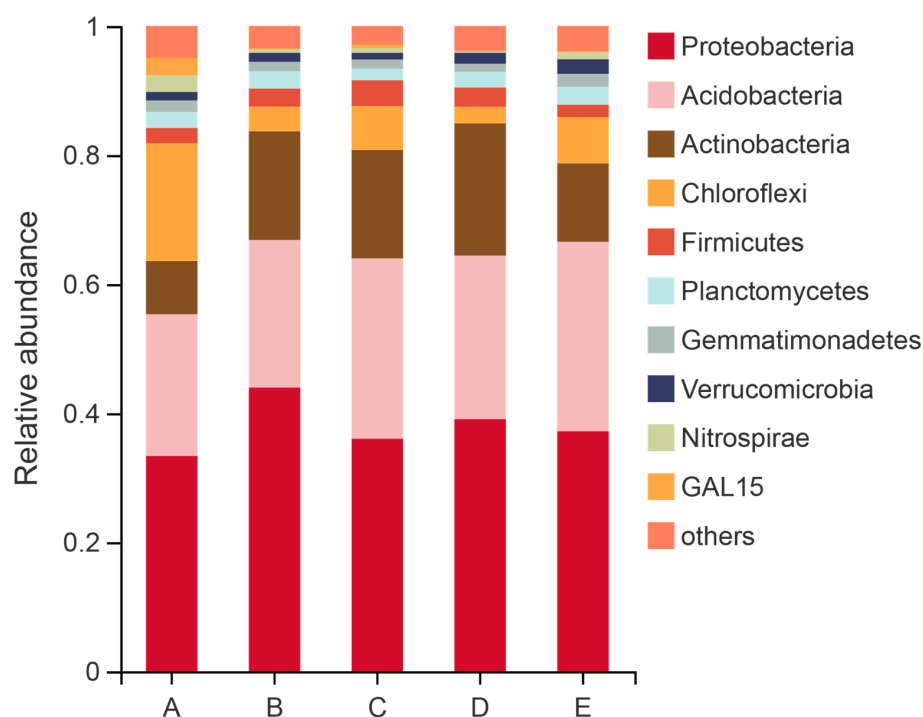

Figure 2. Bacterial community composition at the phylum level. A, *C. kerrii* forest; B, the lower range limit of *C. pingbianense* forest; C, the range center of *C. pingbianense* forest; D, the upper range limit of *C. pingbianense* forest; E, *L. glaber* forest.

Table 2. Bacterial phyla and genera with significant difference among five sites.

Bacteria with Significant Differences	A (%)	B (%)	C (%)	D (%)	E (%)
Actinobacteria	8.24 ± 1.74 b	16.84 ± 0.94 ab	16.80 ± 2.79 ab	20.46 ± 1.49 a	12.13 ± 3.76 b
Chloroflexi	18.22 ± 4.14 a	3.83 ± 3.23 b	6.82 ± 2.58 b	2.61 ± 0.21 b	7.20 ± 2.87 b
Gemmatimonadetes	1.76 ± 0.48 a	1.45 ± 0.46 a	1.42 ± 0.65 a	1.23 ± 0.31 b	2.04 ± 0.26 a
Nitrospirae	2.61 ± 0.52 a	0.56 ± 0.63 b	0.75 ± 0.48 b	0.21 ± 0.04 b	1.63 ± 0.42 b
Variibacter	4.33 ± 1.45 b	8.60 ± 1.12 a	8.34 ± 1.25 a	8.37 ± 0.12 a	6.66 ± 0.45 ab
Acidothermus	2.27 ± 0.83 b	6.94 ± 0.75 ab	7.59 ± 1.91 ab	9.59 ± 2.02 a	4.19 ± 1.23 b
Acidibacter	1.88 ± 0.28 b	2.89 ± 0.62 ab	2.53 ± 0.43 ab	3.03 ± 0.74 a	2..02 ± 0.39 b
Roseiarcus	0.69 ± 0.15 b	3.21 ± 1.53 a	1.76 ± 0.38 ab	2.28 ± 0.23 ab	1.13 ± 0.39 b
Nitrospira	2.61 ± 0.52 a	0.56 ± 0.63 b	0.75 ± 0.48 b	0.21 ± 0.04 b	1.09 ± 0.56 b

The data in the table is the mean ± standard deviation. Different letters (a, b) in the same line meant a significant difference at the 0.05 level. A, *C. kerrii* forest; B, the lower range limit of *C. pingbianense* forest ; C, the range center of *C. pingbianense* forest; D, the upper range limit of *C. pingbianense* forest; E, *L. glaber* forest.

Among the bacterial genera of the top 20 genera with relative abundance, *Variibacter*, *Acidothermus*, *Acidibacter*, *Roseiarcus*, *Nitrospira* varied significantly among five sites (p < 0.05) (Table 2). Meanwhile, the relative abundance of *Acidothermus*, *Roseiarcus*, and *Variibacter* in the *C. pingbianense* forest (B–D) is higher than that of broad-leaved forests (A, E). At the phylum and genus level, there was no significant difference in the relative abundance of soil bacteria between the range center(C) and the range boundaries (B, D) of *C. pingbianense* forest.

3.3. Ecological Function of Soil Bacterial Community

FAPROTAX was used to predict the ecological functions of the soil bacterial community. The relative abundance of the bacterial community related to chemoheterotrophy, aerobic_chemoheterotrophy, cellulolysis, nitrogen_fixation, nitrification, aerobic_nitrite_oxidation, predatory_or_exoparasitic varied significantly among five sites (p < 0.05) (Figure 3). In addition, the relative abundance of bacterial community related to chemoheterotrophy and cellulose hydrolysis in the *C. pingbianense* forest soil was higher than that in the broad-leaved forest soil, while the relative abundance of the bacterial community related to nitrification and aerobic nitrite oxidation was lower in *C. pingbianense* forest soil.

3.4. Relationships between Soil Chemical Properties, Altitude, and Soil Bacterial Community

To determine relationships between the bacterial community and soil chemical properties and altitude, redundancy analysis was carried out. The results showed that soil organic matter (R^2 = 0.7351, p = 0.001), soil pH (R^2 = 0.6231, p = 0.006) and soil available nitrogen (R^2 = −0.6955, p = 0.028) significantly affected soil bacterial community (Figure 4).

According to results of the spearman correlation analysis (Figure 5), soil pH was positively correlated with autotrophic bacteria (e.g., *Nitrospira*) and was negatively correlated with heterotrophic bacteria (e.g., *Acidothermus*) (p < 0.05). However, compared with soil pH, the soil organic content, total nitrogen, and available nitrogen had an opposite correlation with bacterial groups. Meanwhile, there was a significant positive correlation between available phosphorus and *Gemmatimonas*, and available nitrogen was significantly positively correlated with *Candidatus_Solibacter* and *Bradyrhizobium* (p < 0.05). No significant correlation between soil bacterial community and altitude was detected.
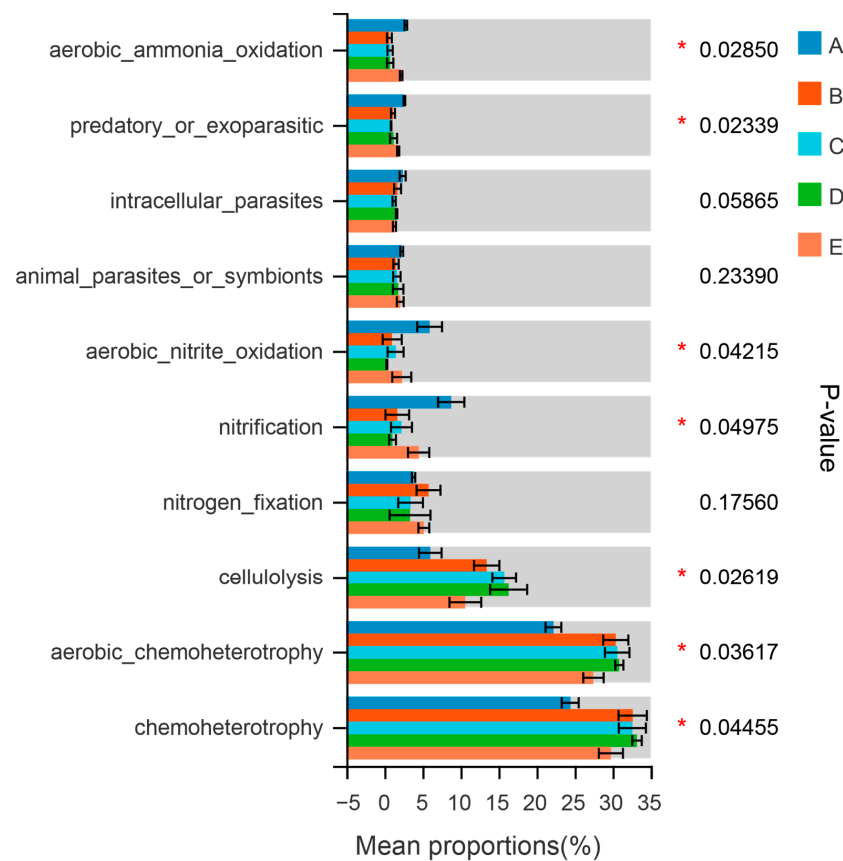
Figure 3. Differences in ecological functions of soil bacteria among 5 sites. A, *C. kerrii* forest; B, the lower range limit of *C. pingbianense* forest; C, the range center of *C. pingbianense* forest; D, the upper range limit of *C. pingbianense* forest; E, *L. glaber* forest. * $0.01 < p \leq 0.05$.
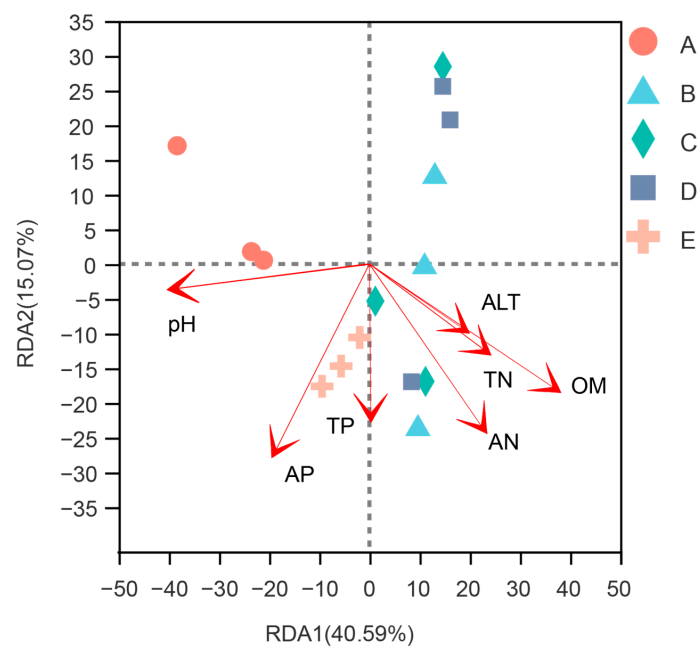

Figure 4. Redundancy analysis between soil chemical properties, altitude, and bacterial community. A, *C. kerrii* forest; B, the lower range limit of *C. pingbianense* forest; C, the range center of *C. pingbianense* forest; D, the upper range limit of *C. pingbianense* forest; E, *L. glaber* forest. OM, organic matter content; AN, available N content; AP, available P content; TN, total N content; TP, total P content; ALT, altitude.
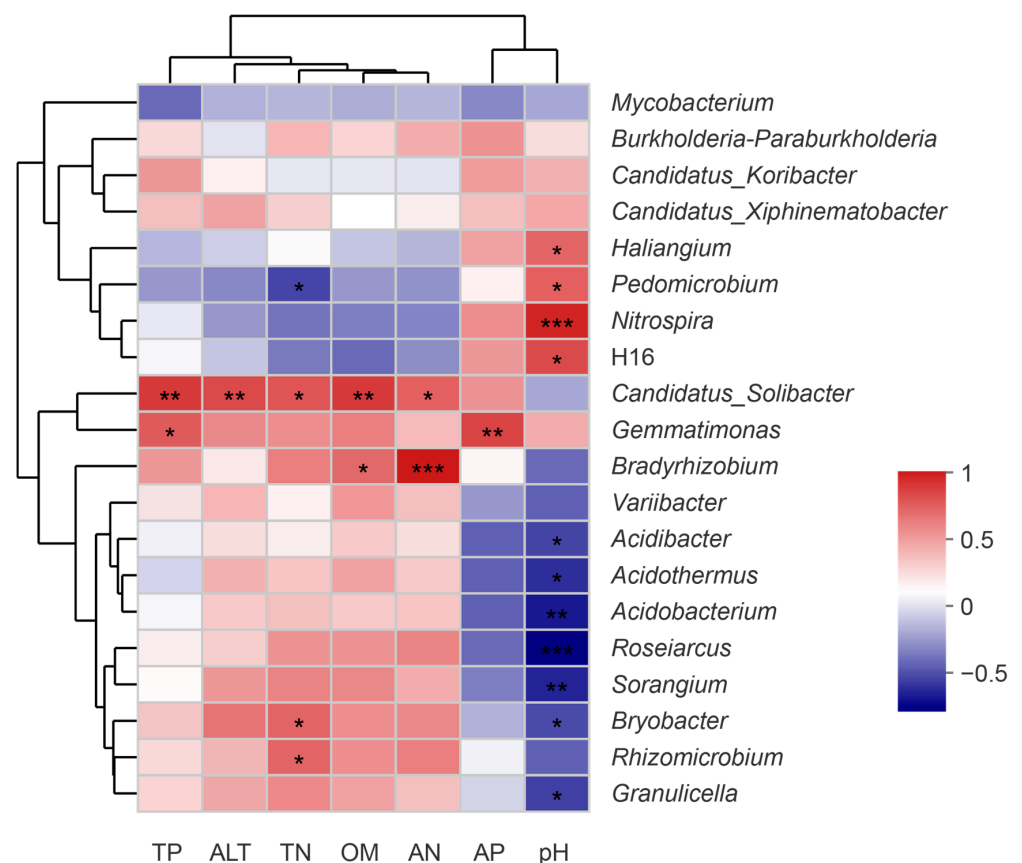
Figure 5. The Spearman correlation analysis between soil chemical properties, altitude and bacterial genus. Top 20 abundant bacterial genera are listed. * $0.01 < p \leq 0.05$; ** $0.001 < p \leq 0.01$; *** $p \leq 0.001$. OM, organic matter content; AN, available N content; AP, available P content; TN, total N content; TP, total P content; ALT, altitude.

4. Discussion

4.1. Soil Chemical Properties and Soil Enzymatic Activities

Soil chemical properties and enzyme activities were significantly different among the five sites. Concerning soil pH, the pH values of three sites in *C. pingbianense* forest were lower than those in two broad-leaved forests. Within *C. pingbianense* forest, the soil pH values of the range boundary (pH = 3.7–4.0) were significantly lower than that of the range center (pH = 4.5). Woody bamboos generally prefer acidic soil with a pH value of 4.5–5.8 [23–25]. However, phosphorus deficiency and aluminum toxicity are two interrelated problems in acid soil. Phosphorus usually reaches its maximum availability when the soil pH value is 5.5–7.0 [26]. With the soil pH value decrease, the mineral aluminum in the soil can be transformed into ionic aluminum, which will inhibit the growth of plant roots [27]. At the same time, ionic aluminum can combine with free phosphorus to form insoluble salt, which reduces the soil's available phosphorus content [28]. The soil pH value and available phosphorus content at the boundaries of *C. pingbianense* forest were significantly lower than those at the range center. It is, therefore, suggested that the low soil pH value and available phosphorus content limit the growth and distribution expansion of *C. pingbianense* at the range boundaries, and it may indicate that nutrient resorption efficiency of *C. pingbianense* is lower here, resulting in higher soil available nitrogen content at the range boundaries than at the range center.

Soil organic matter is positively correlated with soil invertase, urease, and phosphatase [29]. Among five sites, the lowest organic matter content was detected in *C. kerrii* forest soil, which was probably caused by its lowest soil enzyme activities. On the other hand, forest soils of *C. pingbianense* and *L. glaber* had similar soil enzyme activities and

organic matter content. Urease activity is generally positively correlated with the available nitrogen [30,31]. However, among three sites of *C. pingbianense* forest, the soil of the range center had higher urease activity but lower available nitrogen content than those of range limits. The trend of urease activity at those three sites was consistent with their soil pH value, implying that urease activity was significantly affected by soil pH.

4.2. Changes of Soil Bacterial Community

Among the top 20 genera in relative abundance, *Acidothermus*, *Roseiarcus*, and *Variibacter* in *C. pingbianense* forest soil were higher than those in broad-leaved forest soil. *Acidothermus* belongs to *Actinobacteria*, which can degrade cellulose [32]. *Roseiarcus* and *Variibacter* are two genera of *Rhizobiales*. *Roseiarcus* can fix nitrogen and is significantly positively correlated with the nitrogen content of plant leaves [33]. *Variibacter* is the dominant group in many subtropical forest soils [34,35], and its relative abundance increases with the increase of soil C/N [34]. Furthermore, at the phylum level, the relative abundance of *Actinobacteria* in the *C. pingbianense* forest soil was more than 15%, much higher than that of broad-leaved forest soil. *Actinobacteria* are generally considered probiotics to promote plant growth. The previous studies on the bacterial community in woody bamboo forests, e.g., *Phyllostachys edulis* (Carrière) J. Houz, 1906 and *Dendrocalamus giganteus* (Wall.) Munro, 1868, also found that *Actinobacteria* was the dominant bacterial taxa in soil [25,36]. On the other hand, in the *C. kerrii* forest soil, the relative abundance of *Chloroflexi* and *Nitrospira* was significantly higher than that of the remaining four sites. *Chloroflexi* can produce energy through photosynthesis and prefer a low nutrient environment [37]. Compared with other nitrifying microbes, *Nitrospira*, an oligotrophic microbe with a slow growth rate, can perform nitrification independently [38,39]. In terms of soil bacterial diversity, no significant difference was detected among the remaining sites except for *C. kerrii* forest. Moreover, no obvious trend was found in soil bacterial diversity along the elevation gradient, indicating that altitude had little effect on soil bacterial diversity.

Based on the prediction of the ecological function for the soil bacterial community, the relative abundance of heterotrophy bacteria in the soil of *C. pingbianense* forest was significantly higher than that of the outside range, which implied that heterotrophic bacteria played an important role in the endemism of *C. pingbianense*. Woody bamboos have a strong capability for capturing and reserving soil N and P, which may reduce the cycling rate of soil nutrients in a bamboo forest and lead to soil degradation [40]. Fortunately, most heterotrophic bacteria have a complete coding system of carbohydrate-active enzymes, the main driving force involved in carbohydrate degradation [41]. Since *C. pingbianense* can produce bamboo shoots all year round and need enough long-term nutrient supply from the soil [3], abundant heterotrophic bacteria in *C. pingbianense* forest soil can accelerate the soil nutrient cycle rate and meet the nutrient demands of *C. pingbianense* forest. On the other hand, the bacterial community associated with nitrification and aerobic nitrite oxidation was lower in *C. pingbianense* forest soil than in broad-leaved forest soil. The ammonium nitrogen is generally preferentially absorbed at the early stage of plant growth [42]. A probable reason for the low nitrification bacterial community in *C. pingbianense* forest soil is that a vast amount of young bamboos absorb a large amount of ammonium nitrogen all year round, resulting in inhibited nitrification in *C. pingbianense* forest soil. Similarly, the expansion of *Phyllostachys edulis* to the evergreen broad-leaved forest would weaken soil nitrification in the previous broad-leaved forest [43].

Why does the microbial community change according to the host plants' distribution? It was believed to be determined by plant biological characteristics or genotype [44]. The central-marginal hypothesis deems that populations at the central range grow better than those at the range boundaries. The ecological environment at establishment sites might reflect the genetic diversity, which has been supported by several studies [45,46]. So, the symbiotic bacterial community is often affected by the distribution of host plants. In the current paper, we saw no significant difference in the soil bacterial community between the range center and margins of *C. pingbianense* forest, but the relative abundance of

heterotrophy bacteria in the soil of *C. pingbianense* forest was significantly higher than in that of neighboring broad-leaved forests. It may reflect the biological characteristics of *C. pingbianense* and is consistent with the central-marginal hypothesis.

4.3. Effects of Soil Chemical Properties and Altitude on Soil Bacterial Community

Results of correlation analysis indicated that soil pH was a major factor affecting the soil bacterial community structure, while no significant correlation between altitude and soil bacterial community was detected. A previous study on global topsoil microbiome also revealed that environmental factors, especially soil pH, had a stronger impact on the soil bacterial community than geographical distance [47]. Soil pH can be regarded as a key variable integrating many other environmental factors [48]. Globally, environmental factors such as temperature and precipitation affect microbial alpha diversity by regulating soil pH [49]. In the present paper, the relative abundance of some key chemoautotrophic bacteria, such as *Nitrospira*, H16, and *Pedomicrobium* [39,50,51], was positively correlated with soil pH values; while heterotrophic bacteria, e.g., *Acidothermus* and *Roseiarcus*, were negatively correlated with soil pH values. Therefore, adaptability to different soil pH values can be an indicator for distinguishing between autotrophic and heterotrophic bacteria. *Acidobacteria* is considered an oligotrophic bacteria often found in soil with deficient organic matter, but in this study, three representative genera of *Acidobacteria*, namely *Granulicella*, *Bryobacter*, and *Acidobacterium*, were significantly positively correlated with soil organic matter. This was probably because autotrophic bacterial groups weakened the differences in environmental preference between eutrophic and oligotrophic bacteria. Furthermore, among the top 20 abundant bacterial genera, *Gemmatimonas* metabolized phosphate and hypophosphoric acid, and it was significantly positively correlated with available phosphorus accordingly [52].

4.4. Endemism of C. pingbianense and Implication on Forest Management

Documented as only one species that produces edible shoots in all four seasons in natural conditions [1–3], *C. pingbianense* is of great value in germplasm conservation and utilization, and in understanding the shooting mechanism diversity in woody bamboos. *C. pingbianense* is endemic to the Dawei Mountain in tropical monsoon forests, and the soil bacterial community is characterized by a high relative abundance of heterotrophy bacteria, such as *Variibacter* and *Acidothermus*. More abundant heterotrophy bacteria may lead to a higher soil organic carbon mineralization rate and is compatible with the attribute of full-year shooting in *C. pingbianense.* Abundant heterotrophy bacteria in forest soil may be linked to the endemism of this distinctive woody bamboo. *C. pingbianense*, as yet, is not successfully ex situ introduced and cultivated in other areas of Yunnan. In addition to biological characteristics, we may also ignore the function and characteristics of the soil microbial community, especially the bacterial community, in *C. pingbianense* forests. Therefore, in order to facilitate asexual reproduction (namely producing shoots) and growth of *C. pingbianense*, we should concern the changes of the heterotrophic bacterial community in its forest soil management [26,36,43].

5. Conclusions

Our results revealed for the first time the characteristics of soil bacterial community and changes along the distribution range in *C. pingbianense* forests. Compared with the outside ranges, *C. pingbianense* forest soils possessed a significantly higher relative abundance of heterotrophy bacteria, implying that heterotrophy bacteria play an important role in the endemism of *C. pingbianense.* Therefore, in future germplasm conservation and introduction of *C. pingbianense*, in addition to its biological characteristics, more attention should be paid to the changes of the soil in the heterotrophic bacterial community in long-term forest management. In addition, the bacterial community structure and diversity will evolve with time and space. Strengthening studies on variation characteristics of bacterial community

at a temporal and spatial level along plant distribution range can better reveal the response of soil bacteria to plant distribution.

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