

RESEARCH ARTICLE

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Microbiome-Based Characterization of Microbial Community Structure and Diversity in White Tea (*Camellia sinensis*)

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ABSTRACT

Introduction: Aging storage plays a crucial role in enhancing both the flavor and health benefits of white tea. However, the microbial mechanisms underlying this process remain poorly understood, particularly regarding intervarietal differences in microbial succession.

Methods: We investigated bacterial and fungal communities in two white tea cultivars—Shoumei and Baihao Yinzhen—aged for five years, employing amplicon sequencing (16S rDNA and ITS), co-occurrence network analysis, and functional prediction using PICRUSt2.

Results: Bacterial abundance exceeded fungal abundance in aged white tea, based on detected amplicon sequence variants (ASVs) and species richness. Baihao Yinzhen exhibited higher bacterial richness but lower diversity than Shoumei. No significant differences were observed in fungal richness or diversity between the two cultivars. Shared dominant taxa included *Methylobacterium–Methylobacterium* and *Sphingomonas* (bacteria), as well as *Ascomycota*-unclassified and *Pleosporales*-unclassified (fungi). Network analysis identified *Bosea* (bacteria) and *Erythrobasidium* (fungi) as keystone taxa, while functional profiling linked microbial activity primarily to amino acid metabolism.

Conclusion: Our findings reveal cultivar-specific microbiome dynamics during white tea aging and their potential role in flavor modulation, providing a scientific foundation for optimizing fermentation protocols and quality control in tea production.

1 | Introduction

Tea is one of the world's three major beverages, with China leading global production, accounting for 35% of cultivated tea areas and 40% of total tea output [1]. White tea (*Camellia sinensis*), originating from and primarily produced in Fujian, China, is unique among the six major tea categories due to its minimal processing, with natural withering as its core technique. This limited fermentation process preserves its distinctive sensory properties and numerous health benefits [2, 3]. White tea is

characterized by an elongated appearance, gray–green coloration, a refreshing downy aroma, a sweet and mellow taste, a light yellow infusion, and soft, uniform leaves [4]. Research has highlighted its wide-ranging health benefits, including antifatigue, immune modulation, antioxidant, antihypertensive, lipid-lowering, hypoglycemic, and metabolism-boosting effects [5–10].

White tea is classified into four categories based on leaf tenderness: Baihao Yinzhen (BHYZ), White Peony, Gongmei, and Shoumei (SM). BHYZ is produced from single buds or tender buds with

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a single leaf and stem, while SM, the most widely produced variety, consists of tender shoots with one to three leaves and a dormant bud or, in some cases, leaves alone. Its processing involves withering, drying, and sorting [11]. Freshly produced white tea typically has a mild flavor and lower medicinal value, requiring prolonged storage to enhance its bioactive properties. This aligns with the traditional saying: “One-year tea, three-year medicine, 7-year treasure” [12].

Micro-organisms play a crucial role in tea cultivation, processing, and storage, influencing chemical composition and flavor [13]. Research on microbial activity in tea has predominantly focused on dark tea, where microbial fermentation during piling and storage shapes its unique characteristics. Micro-organisms alter key compounds, including tea polyphenols, catechins, flavonoids, amino acids, and caffeine, through enzymatic metabolism [14]. In Pu'er tea, dominant microbes such as *Aspergillus* and *Saccharomyces cerevisiae* contribute to alcohol and ester production. *Aspergillus niger* hydrolyzes proteins, modifying amino acid content, while *Saccharomyces cerevisiae* increase tea polyphenols and amino acids while reducing flavonoids, catechins, and thearubigins, compounds that can negatively impact tea quality [15]. Similarly, in Fu brick tea, microbial communities dominated by *Eurotium cristatum*, *A. niger*, *Mucoraceae*, *Penicillium*, *A. shevayii*, and *A. cristatus* contribute to its characteristic fungal aroma, with *E. cristatum* playing a central role [16].

Despite its distinct processing method, research on the microbial communities in white tea remains limited. In particular, how microbial diversity and structure differ among white tea varieties during storage is poorly understood. The advent of 16S rDNA and ITS amplicon sequencing provides powerful tools for exploring tea-associated microbiomes. In this study, we analyzed microbial diversity in SM and BHYZ white tea after five years of storage (2018–2023), using high-throughput sequencing to elucidate shifts in bacterial and fungal communities. Our findings offer insights into microbial contributions to tea quality, informing strategies for improving microbial safety, functional research, and quality control in aged white tea.

2 | Materials and Methods

2.1 | Sample Collection

White tea samples stored for five years (2018–2023) were collected from Shunmingdao White Tea Manor, located in Houjing Village, Dian Tou Town, Fu Ding City, Ningde City, Fujian Province, China (120°4′59.9988″E, 27°10′0.0120″N). The samples were harvested in spring (March–April), with BHYZ consisting of single buds and SM comprising one bud with two fresh leaves. Multiple batches were collected over a month to ensure biological replicates. The samples were processed by Shunmingdao Tea Co., Ltd., Fujian Province. All samples were stored under controlled conditions (temperature fluctuating between 20 and 32°C, relative humidity maintained at 55%, in darkness, and with storage containers placed off the ground and away from walls) to ensure consistency across storage durations. Six biological replicates of each variety were selected for amplicon sequencing to determine bacterial and fungal community composition.

2.2 | DNA Extraction

Genomic DNA was extracted using the CTAB method following the manufacturer's instructions (CTAB reagent, Sigma-Aldrich,

St. Louis, MO, USA). This reagent effectively isolates DNA from trace amounts of sample material, enabling efficient extraction from bacterial cells. A nuclease-free water blank was used as a negative control. The extracted DNA was eluted in 50 µL of elution buffer and stored at –80°C until PCR amplification, which was performed by LC-Bio Technology Co., Ltd., Hangzhou, Zhejiang Province, China.

2.3 | PCR Amplification and 16S/ITS Sequencing

Bacterial 16S rRNA gene amplification targeted the V3–V4 hypervariable region using primers 341F (5′-CCTACGGGNGGCW GCAG-3′) and 805R (5′-GACTACHVGGGTATCTAATCC-3′) [17]. The fungal ITS2 region was amplified using primers ITS1FI2 (5′-GTGARTCATCGAATCTTTG-3′) and ITS2 (5′-GTGART-CATCGAATCTTTG-3′) [18].

Each PCR reaction (25 µL) contained 25 ng of template DNA, 12.5 µL of PCR premix, 2.5 µL of each primer, and PCR-grade water. The thermocycling protocol was as follows: initial denaturation at 98°C for 30 s; 32 cycles of denaturation at 98°C for 10 seconds, annealing at 54°C for 30 seconds, and extension at 72°C for 45 s; followed by a final extension at 72°C for 10 min.

PCR products were confirmed via 2% agarose gel electrophoresis and purified using AMPure XT beads (Beckman Coulter Genomics, Danvers, MA, USA). DNA concentrations were quantified using a Qubit fluorometer (Invitrogen, USA). The amplicon libraries were prepared and evaluated for size and concentration using an Agilent 2100 Bioanalyzer (Agilent, USA) and the Library Quantification Kit for Illumina (Kapa Biosciences, Woburn, MA, USA). Sequencing was conducted on the NovaSeq PE250 platform.

2.4 | Data Analysis

Sequencing was performed on an Illumina NovaSeq platform following the manufacturer's protocol at LC-Bio. Paired-end reads were assigned to samples based on unique barcodes, with barcodes and primers trimmed. Merging of paired-end reads was conducted using FLASH, followed by quality filtering under defined thresholds using fqtrim (v0.94) to obtain high-quality clean reads. Chimeric sequences were removed using VSEARCH (v2.3.4).

Following dereplication via DADA2, a feature table and representative feature sequences were generated. Alpha diversity (Chao1, observed species, goods coverage, Shannon, and Simpson indices) and beta-diversity were calculated using QIIME2. Feature abundance normalization was performed with the SILVA database (Release 138). Beta-diversity metrics were computed in QIIME2, with graphical visualizations produced in R (v3.5.2). Sequence alignment was performed using BLAST, and feature sequences were annotated against the SILVA database. The processed and quality-filtered microbiome sequencing data have been deposited in the Sequence Read Archive (SRA) database hosted on the NCBI platform, with the Project Accession Numbers PRJNA1241493 (16S rRNA gene amplicon sequencing) and PRJNA1241506 (ITS region sequencing) assigned to the respective datasets.

2.5 | Microbial Correlation Analysis

The top 30 most abundant bacterial and fungal species were, respectively, subjected to Spearman correlation analysis to assess

TABLE 1 | Statistical analysis of 16S sample sequencing data.

Sample	Raw_tags	Raw_bases	Valid_tags	Valid_bases	Valid (%)	Q20 (%)	Q30 (%)	GC (%)
SM2018_1	84716	42.36M	81380	32.91M	96.06	98.19	94.31	55.11
SM2018_2	81000	40.50M	77761	31.45M	96.00	97.74	92.87	55.11
SM2018_3	81402	40.70M	77990	31.56M	95.81	97.03	90.84	55.07
SM2018_4	83012	41.51M	79619	32.20M	95.91	98.17	94.32	55.09
SM2018_5	82112	41.06M	78772	31.86M	95.93	98.35	94.74	55.08
SM2018_6	81481	40.74M	78296	31.68M	96.09	97.26	91.49	55.08
BHYZ2018_1	82850	41.42M	79007	32.09M	95.36	98.21	94.43	54.61
BHYZ2018_2	81020	40.51M	77085	31.43M	95.14	97.78	93.07	54.16
BHYZ2018_3	82082	41.04M	78007	31.83M	95.04	98.04	93.85	54.09
BHYZ2018_4	82633	41.32M	78592	32.04M	95.11	98.27	94.66	54.16
BHYZ2018_5	80444	40.22M	76547	31.22M	95.16	98.12	94.12	54.17
BHYZ2018_6	82747	41.37M	78999	32.18M	95.47	97.31	91.70	54.31

interspecies relationships and statistical significance (p values). Correlation networks were generated using OmicStudio tools (<https://www.omicstudio.cn/tool.Spearman>).

2.6 | Functional Prediction of Microbial Communities

Functional prediction was performed based on 16S rDNA and ITS sequencing data using PICRUSt2 via OmicStudio (<https://www.omicstudio.cn/analysis/>). Functional pathway enrichment was analyzed using STAMP, with statistical significance determined at $p < 0.05$ (95% confidence interval). Functional pathway predictions were annotated using the KEGG database.

3 | Results

3.1 | Bacterial Diversity Analysis

The sequencing results of 16S rDNA are summarized in Table 1. The raw dataset contained 985,499 sequences, of which 942,055 high-quality sequences (95.6%) were retained after quality filtering, demonstrating a high proportion of effective reads. The GC content ranged from 54.09% to 55.11%, with no significant GC bias. Sequencing quality was high, as indicated by Q20 values $\geq 97.03\%$ and Q30 values $\geq 90.84\%$, ensuring reliable downstream analyses.

Following DADA2 denoising and the removal of mitochondrial and chloroplast sequences, 2251 ASVs were identified for further analysis. A Venn diagram illustrated ASV distribution across samples, revealing 191 core bacterial ASVs shared between SM and BHYZ (Figure 1(a)). Notably, SM harbored 258 unique ASVs, whereas BHYZ had 490, suggesting greater bacterial richness in BHYZ. Rarefaction and rank-abundance curves confirmed that sequencing depth was sufficient, with adequate species representation (Figures 1(b) and 1(c)).

Alpha diversity analysis, based on six indices (observed_species, Shannon, Simpson, Chao1, Goods_coverage, and Pielou_e), highlighted significant differences between tea cultivars (Figure 2(a)). BHYZ exhibited higher species richness (observed_species, $p = 0.128$, and Chao1, $p = 0.004$), whereas SM

displayed greater species diversity and evenness (Shannon, Simpson, and Pielou_e, $p < 0.01$). Goods_coverage values approached 1 across all samples, indicating comprehensive microbial community coverage. Principal coordinates analysis (PCoA) using the weighted UniFrac distance matrix and non-metric multidimensional scaling (NMDS) based on the unweighted UniFrac distance matrix further demonstrated distinct microbial compositions in SM and BHYZ after 5 years of storage (Figures 2(b) and 2(c)).

3.2 | Bacterial Community Composition

During storage, bacterial community succession was evident, with 29 phyla, 65 classes, 134 orders, 235 families, 511 genera, and 744 species identified. In both tea samples, Proteobacteria emerged as the dominant phylum, exhibiting relative abundances of 65.16% (SM) and 68.59% (BHYZ). Bacteroidota was also a predominant phylum, accounting for 15.30% and 26.69% in SM and BHYZ, respectively (Figure 3(a)). However, Firmicutes (13.86%) were abundant in SM but nearly absent in BHYZ (1.38%). At the genus level, both samples shared similar structural compositions but differed significantly in abundance (Figure 3(b)). *Methylobacterium*–*Methylorubrum* and *Sphingomonas* were predominant in both tea cultivars. *Methylobacterium*–*Methylorubrum* accounted for 12.58% in SM and 25.13% in BHYZ, while *Sphingomonas* accounted for 16.12% in SM and 21.77% in BHYZ. Other notable genera included *Ligilactobacillus*, *Chryseobacterium*, and *Aureimonas* in SM, while *Pedobacter*, *Betaproteobacteria_unclassified*, and *Chryseobacterium* were more abundant in BHYZ. A heatmap highlighted these compositional differences at the genus level (Figure 3(c)).

LEfSe analysis (Kruskal–Wallis and Wilcoxon rank-sum tests, $p < 0.05$, LDA score > 4) identified significant biomarkers distinguishing the two tea cultivars (Figures 4(a) and 4(b)). Firmicutes and genera such as *Methylobacterium*–*Methylorubrum*, *Ligilactobacillus*, *Pseudoalteromonas*, and *Vibrio* were enriched in SM. In contrast, BHYZ was characterized by Bacteroidota, along with genera such as *Chryseobacterium*, *Bosea*, *Allorhizobium*–*Neorhizobium*–*Pararhizobium*–*Rhizobium*, *Sphingomonas*, *Betaproteobacteria_unclassified*, and *Pedobacter*.

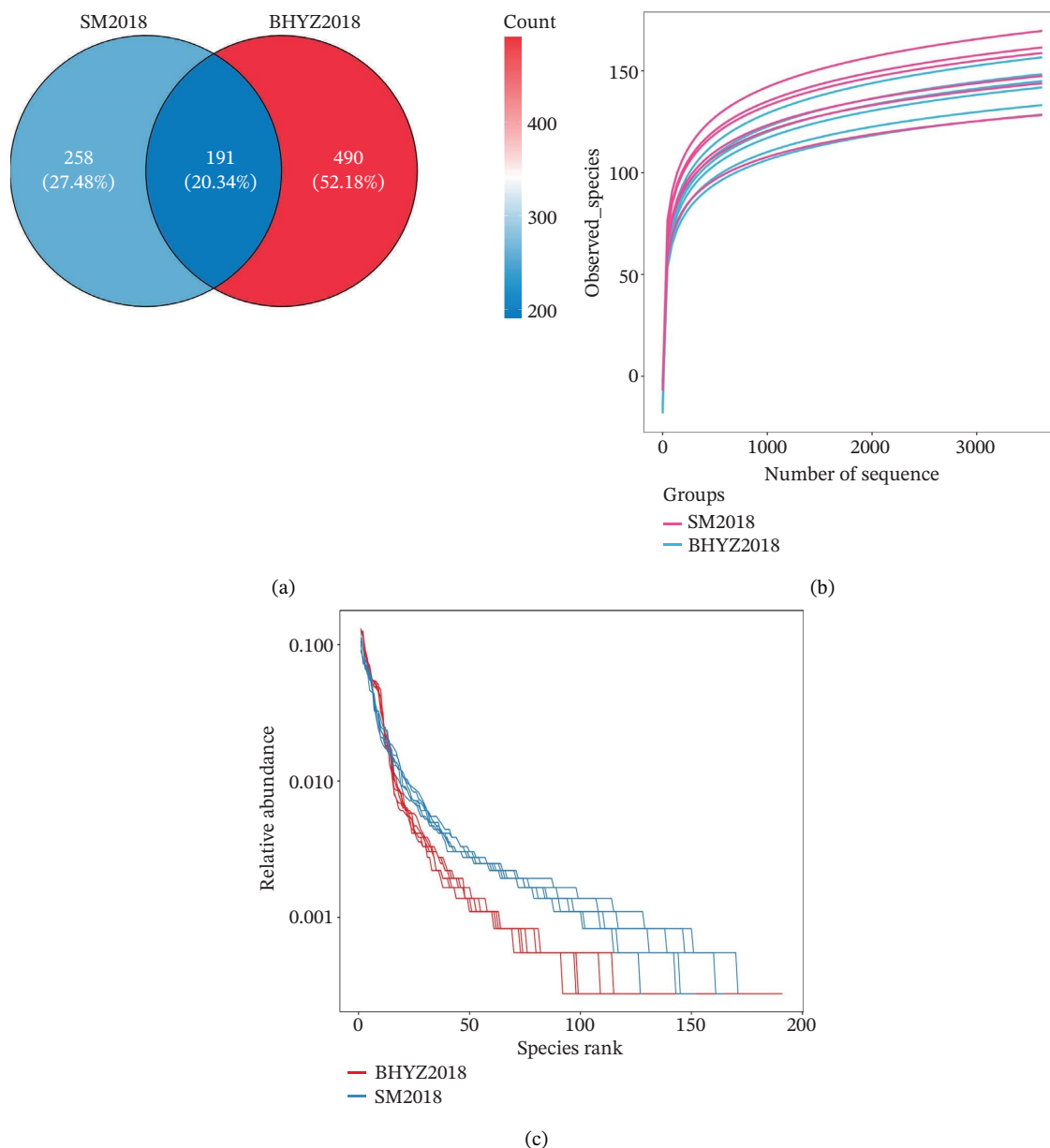


FIGURE 1 | ASV-based detection of bacterial communities. (a) Venn diagram illustrating shared and unique bacterial ASVs between SM and BHYZ. (b) Rarefaction curve of observed species richness. (c) Relative abundance distribution curve of bacterial communities.

Barplot analysis identified the five most abundant genera with significant differences ($p < 0.05$) (Figure 4(c)). *Sphingomonas*, *Pedobacter*, *Chryseobacterium*, and *Betaproteobacteria_unclassified* were more abundant in BHYZ, with *Pedobacter* and *Betaproteobacteria_unclassified* showing the greatest differences. Conversely, *Methylobacterium*–*Methylobacterium* was significantly more prevalent in SM.

3.3 | Fungal Diversity Analysis

ITS sequencing results are shown in Table 2. The raw dataset contained 1,002,984 sequences, of which 954,301 high-quality sequences (95.1%) were retained after filtering. The GC content ranged from 52.26% to 65.6%, with no significant GC bias. Sequencing quality was high, with Q20 values $\geq 96.94\%$ and Q30 values $\geq 92.73\%$, ensuring robust downstream analyses.

Following DADA2 denoising and removal of nontarget sequences, 1948 ASVs were identified. The Venn diagram showed 122 core fungal ASVs shared between SM and BHYZ, while SM had 288 unique ASVs and BHYZ had 242, indicating higher fungal richness in SM (Figure 5(a)). Rarefaction and rank-abundance curves confirmed that sequencing depth was sufficient for comprehensive fungal community analysis (Figures 5(b) and 5(c)).

Alpha diversity analysis showed no significant differences between tea cultivars across most indices ($p > 0.05$), except for the Simpson index ($p = 0.02$) (Figure 6(a)). Goods_coverage values were equal to 1 across all samples, indicating comprehensive community representation. PCoA and NMDS based on the weighted UniFrac distance matrix confirmed distinct fungal community structures between SM and BHYZ after 5 years of storage (Figures 6(b) and 6(c)).

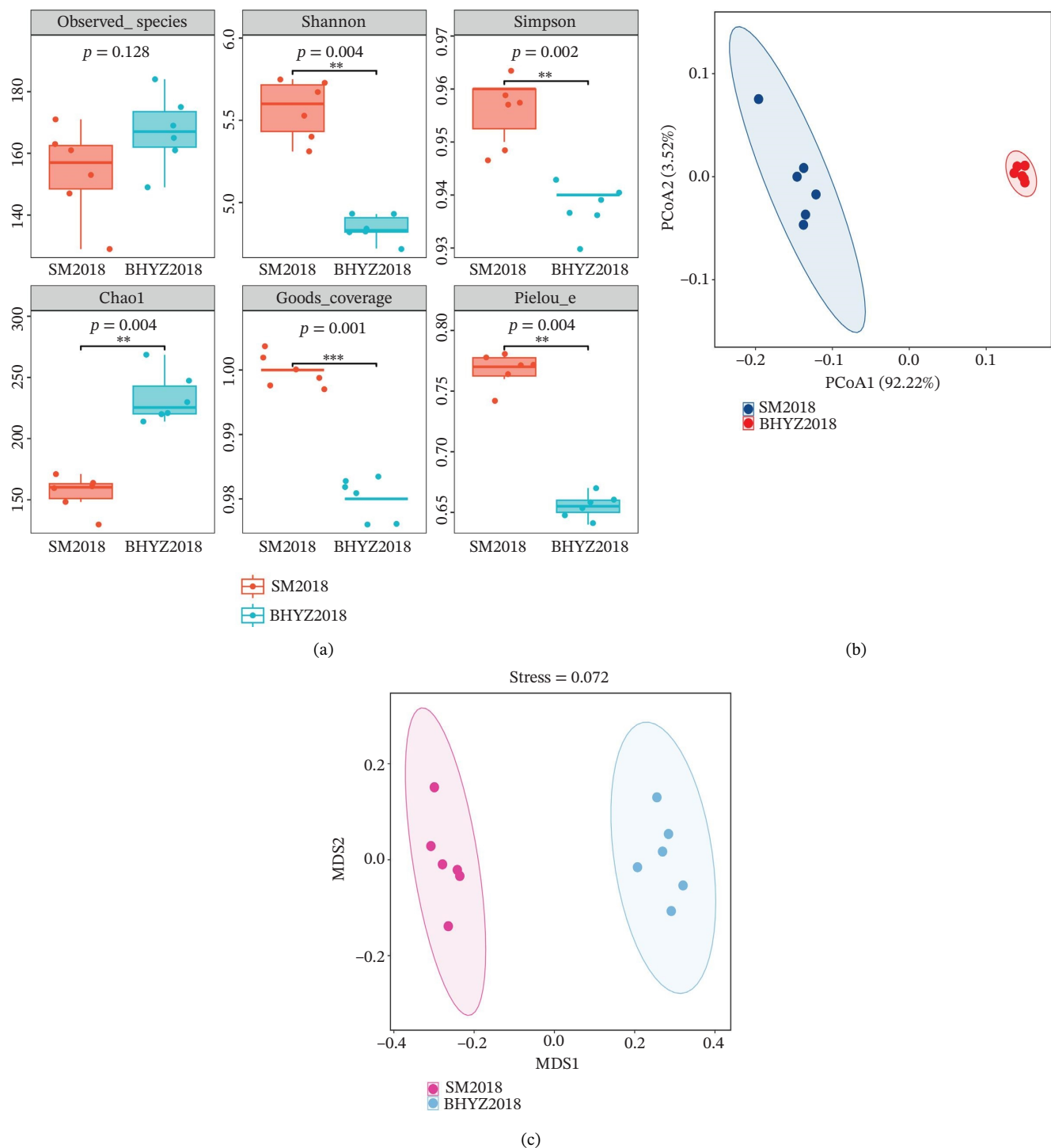


FIGURE 2 | Bacterial diversity analysis. (a) Alpha diversity box plots ($n = 6$) showing observed species, Shannon, Simpson, Chao1, goods_coverage, and Pielou_e indices between SM2018 and BHYZ2018 groups. The Kruskal–Wallis test with Dunn’s post hoc was used (*, $p < 0.05$; **, $p < 0.01$; ***, $p < 0.001$). (b) PCoA based on weighted UniFrac distances. (c) NMDS based on unweighted UniFrac distances.

3.4 | Fungal Community Composition

Fungal community succession during storage was characterized by identifying four phyla, 23 classes, 63 orders, 131 families, 248 genera, and 381 species. The fungal community was dominated by Ascomycota, which reached a higher relative abundance in BHYZ (95.25%) than in SM (86.67%). Basidiomycota also showed a higher abundance in BHYZ (12.38%) compared to SM (Figure 7(a)). At the

genus level, a significant portion of the fungal community remained unclassified (Figure 7(b)). Two unclassified taxa were predominant and shared between both tea cultivars. *Ascomycota_unclassified* accounted for 24.25% in SM and 61.63% in BHYZ, while *Pleosporales_unclassified* accounted for 30.23% in SM and 44.69% in BHYZ. *Dothideomycetes_unclassified* (13.11%) was notably more abundant in BHYZ than in SM (1.39%). A heatmap visualization of genus-level abundance patterns revealed

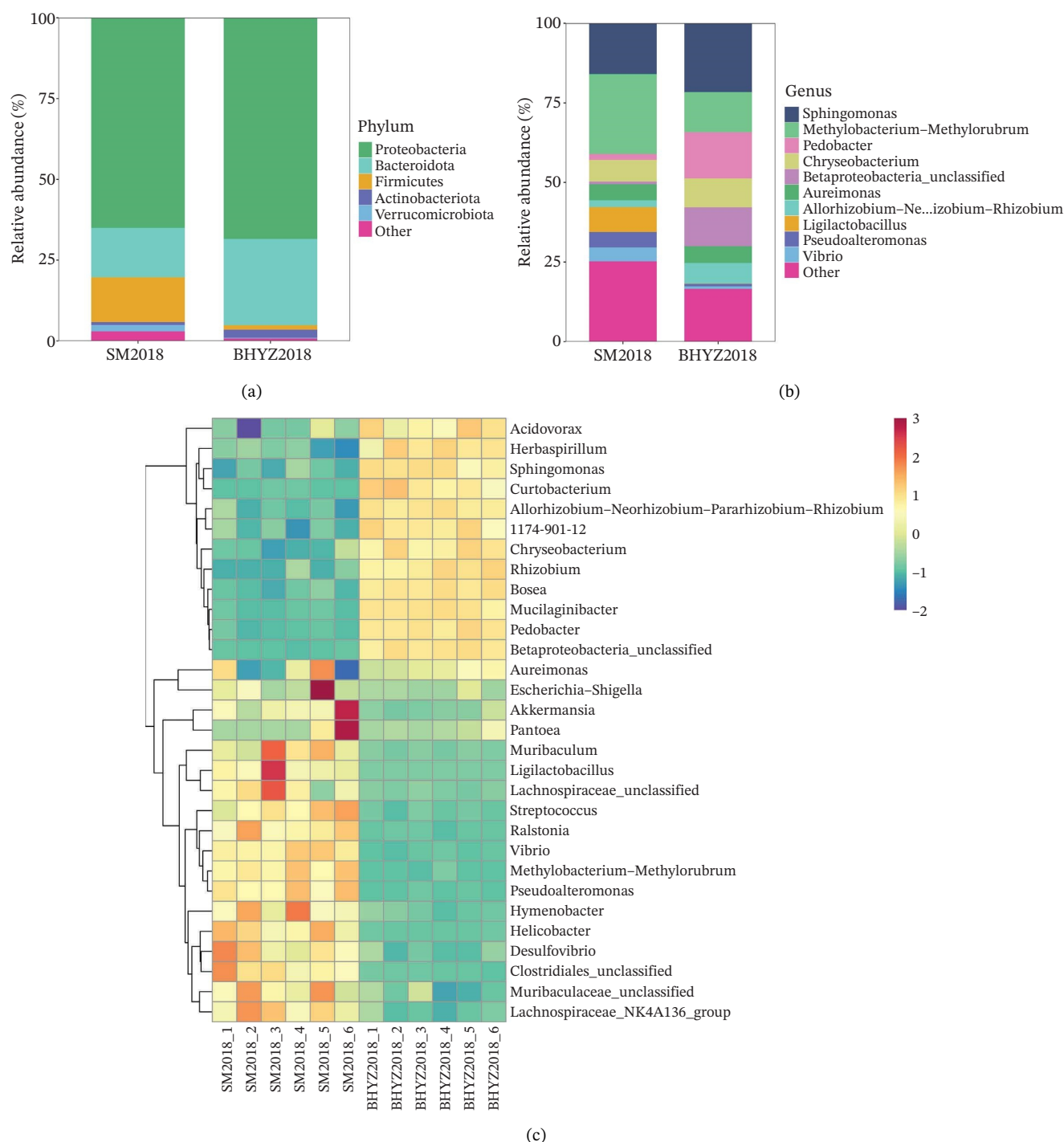


FIGURE 3 | Bacterial community composition analysis. (a) Stacked bar plot of bacterial composition at the phylum level (top five phyla). (b) Stacked bar plot of bacterial composition at the genus level (top ten genera). (c) Cluster heatmap displaying the relative abundance of the top 30 bacterial genera.

variability among replicates within the same tea type, indicating potential intragroup heterogeneity (Figure 7(c)).

LEfSe analysis ($p < 0.05$, LDA score > 4) identified key biomarkers distinguishing SM from BHYZ (Figures 8(a) and 8(b)). In SM, the dominant biomarkers were the phyla Ascomycota and Fungi_unclassified, with corresponding enrichment at the genus level. Conversely, in BHYZ, Basidiomycota emerged as the biomarker phylum, with

Cryptococcus, *Dothideomycetes_unclassified*, and *Pleosporales_unclassified* identified as key genera. Barplot analysis of the five most abundant fungal genera with significant differences ($p < 0.05$) showed that while *Ascomycota_unclassified* was more prevalent in SM, BHYZ exhibited higher abundances of *Pleosporales_unclassified*, *Dothideomycetes_unclassified*, *Cryptococcus*, and *Fungi_unclassified*, with *Dothideomycetes_unclassified* and *Cryptococcus* displaying the most pronounced differences (Figure 8(c)).

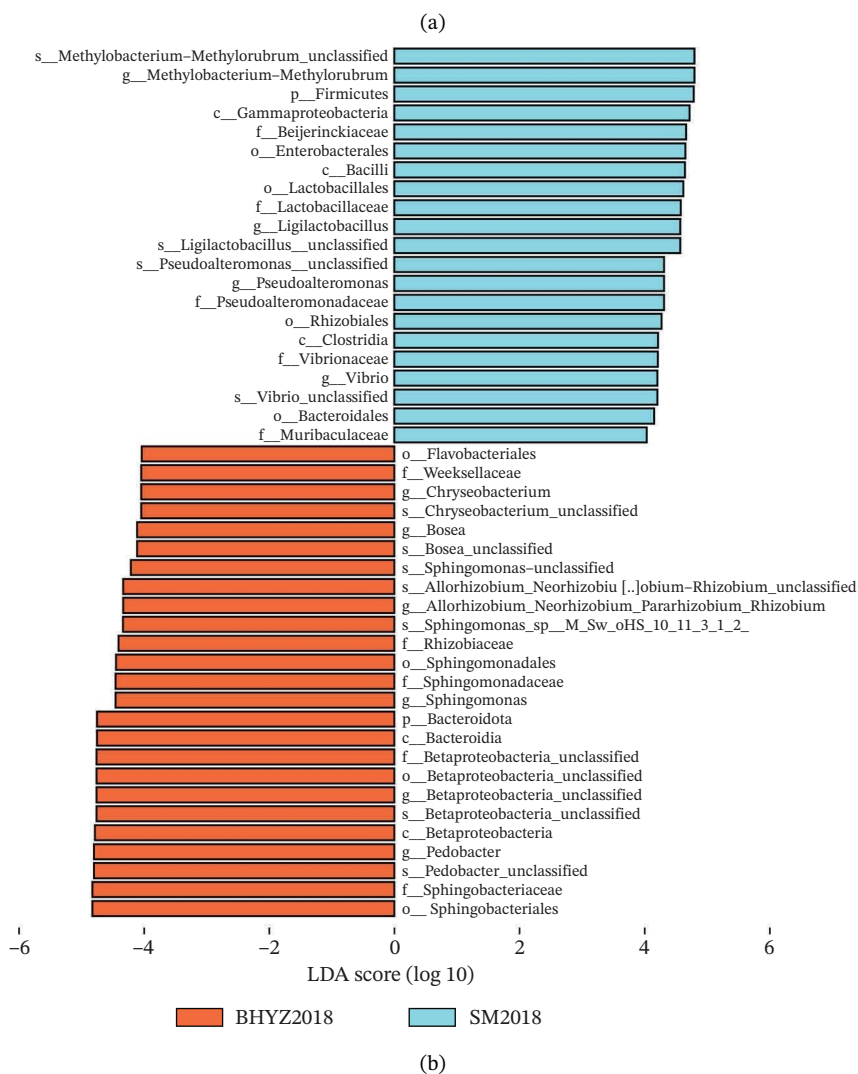
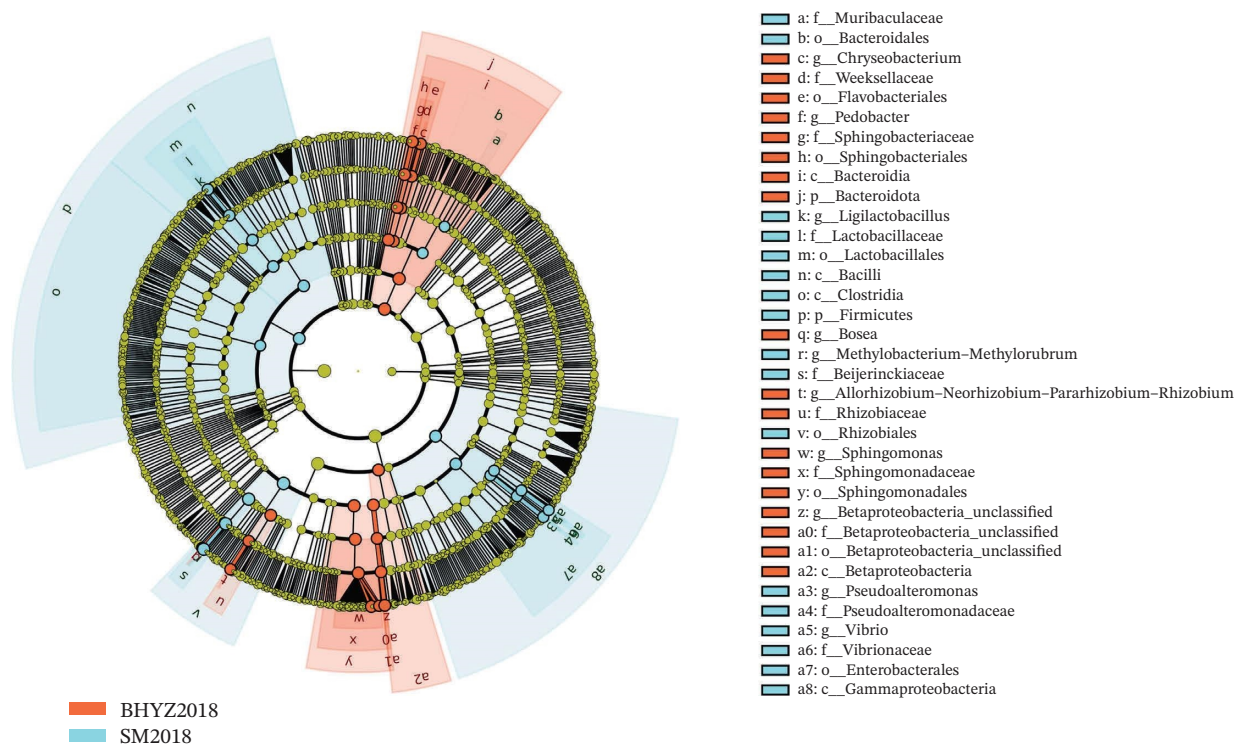


FIGURE 4 | (Continued)

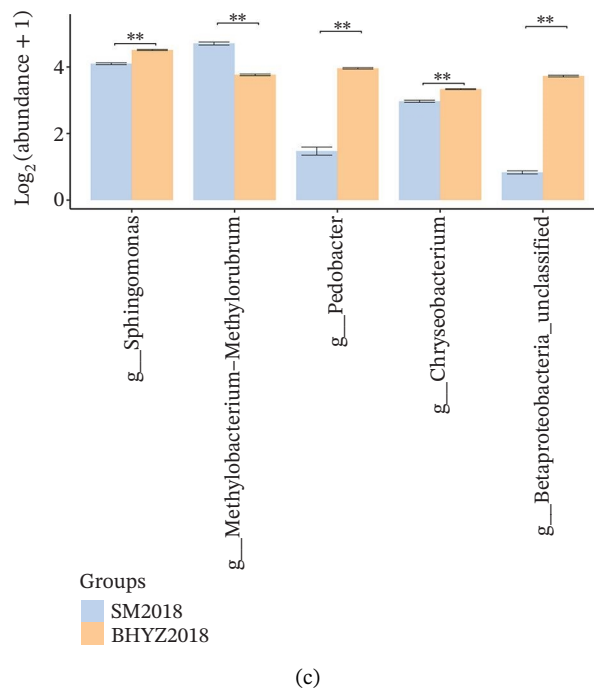


FIGURE 4 | LEfSe differential analysis of bacterial communities. (a) Cladogram depicting taxonomic differences across bacterial communities. (b) Distribution bar chart highlighting significantly enriched taxa. (c) Bar plot showing the top five differentially abundant genera (statistical significance of differences for each genus was determined using the Mann–Whitney U test [$p < 0.05$]).

3.5 | Species Composition Analysis

To explore microbial interactions, the top 30 most abundant bacterial and fungal genera were selected for Spearman correlation network analysis (Figure 9). In the network, nodes represent the dominant genera, with colors indicating their respective phyla. Edges between nodes denote the correlations, with their thickness proportional to correlation strength. The solid and dashed lines represent the positive and negative correlations, respectively. Node size reflects connectivity, with larger nodes indicating genera with more associations.

In the bacterial network, relationships with $|r| > 0.8$ were visualized, identifying *Bosea* (phylum Proteobacteria) as the core

genus, with 12 direct associations. Positively correlated genera included *Sphingomonas*, *Herbaspirillum*, *Mucilaginibacter*, and *Rhizobium*, while negatively correlated genera included *Ligilactobacillus*, *Pseudoalteromonas*, *Lachnospiraceae_NK4A136_group*, *Ralstonia*, *Streptococcus*, *Muribaculum*, *Pseudomonas*, and *Allorhizobium-Neorhizobium-Pararhizobium-Rhizobium*. Other highly interconnected bacterial genera included *Sphingomonas*, *Hymenobacter*, *Ligilactobacillus*, *Mucilaginibacter*, and *Desulfovibrio*.

In the fungal network, the genus *Erythrobasidium* (phylum Basidiomycota) had the highest number of associations with other species (13 types). Genera that exhibited positive correlations with *Erythrobasidium* included *Pestalotiopsis*, *Rhodotorula*, *Kabatiella*,

TABLE 2 | Statistical analysis of ITS sample sequencing data.

Sample	Raw_tags	Raw_bases	Valid_tags	Valid_bases	Valid (%)	Q20 (%)	Q30 (%)	GC (%)
SM2018_1	81888	40.94M	78820	23.19M	96.25	98.23	95.99	64.27
SM2018_2	80997	40.50M	77153	21.79M	95.25	97.93	94.87	61.71
SM2018_3	81980	40.99M	76647	22.43M	93.49	96.94	92.73	64.12
SM2018_4	81358	40.68M	77307	22.39M	95.02	97.33	93.44	63.61
SM2018_5	86013	43.01M	83455	24.98M	97.03	97.88	94.74	65.60
SM2018_6	86726	43.36M	83486	24.37M	96.26	98.45	96.50	63.85
BHYZ2018_1	87760	43.88M	83386	22.24M	95.02	99.29	98.23	55.85
BHYZ2018_2	82350	41.17M	78895	20.34M	95.80	99.54	98.58	52.26
BHYZ2018_3	81413	40.71M	71560	18.84M	87.90	99.16	97.83	54.53
BHYZ2018_4	81635	40.82M	78235	20.27M	95.84	99.38	98.12	52.78
BHYZ2018_5	83222	41.61M	80721	21.34M	96.99	99.41	98.47	54.67
BHYZ2018_6	87642	43.82M	84636	22.68M	96.57	99.24	98.16	56.13

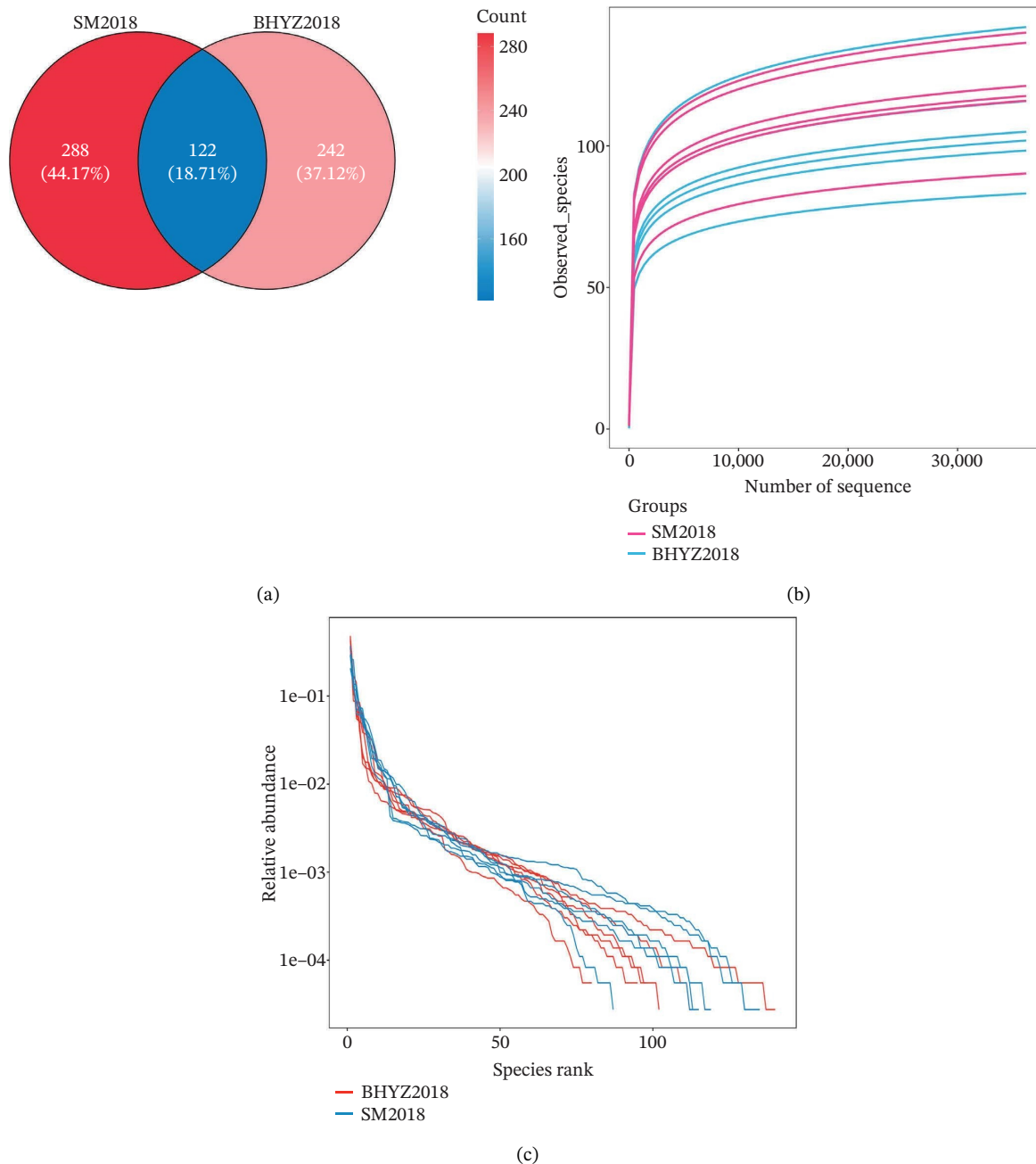


FIGURE 5 | ASV-based detection of fungal communities. (a) Venn diagram showing shared and unique fungal ASVs between SM and BHYZ. (b) Rarefaction curve of observed species richness. (c) Relative abundance distribution curve of fungal communities.

Sporobolomyces, *Strelitziana*, *Eurotium*, *Ophiosphaerella*, and *Rhodospiridium*, while genera that exhibited negative correlations included *Cryptococcus*, *Alternaria*, *Bullera*, and *Elsinoe Botryosphaeria*. Other fungal genera with a relatively high number of associations, aside from *Erythrobasidium*, included *Rhodotorula*, *Kabatiella*, *Sporobolomyces*, *Alternaria*, and *Strelitziana*.

3.6 | Microbial Community Function Prediction

The functional potential of microbial communities in SM and BHYZ after 5 years of storage was predicted using PICRUSt2, which infers gene functional profiles from 16S rRNA and ITS sequences.

KEGG Level 1 pathway analysis indicated that most predicted functions were related to metabolic pathways in both bacteria and fungi (Figure S1). At Level 2, the most abundant bacterial functions included membrane transport, amino acid metabolism, and replication and repair (Figure 10(a)). In fungi, the predominant functions were amino acid metabolism, translation, and poorly characterized pathways (Figure 10(b)). Notably, amino acid metabolism was a common feature in both bacterial and fungal communities, with a slightly higher relative abundance in BHYZ than in SM. Since amino acids are key contributors to tea flavor, these findings suggest that microbial activity during storage may influence white tea's

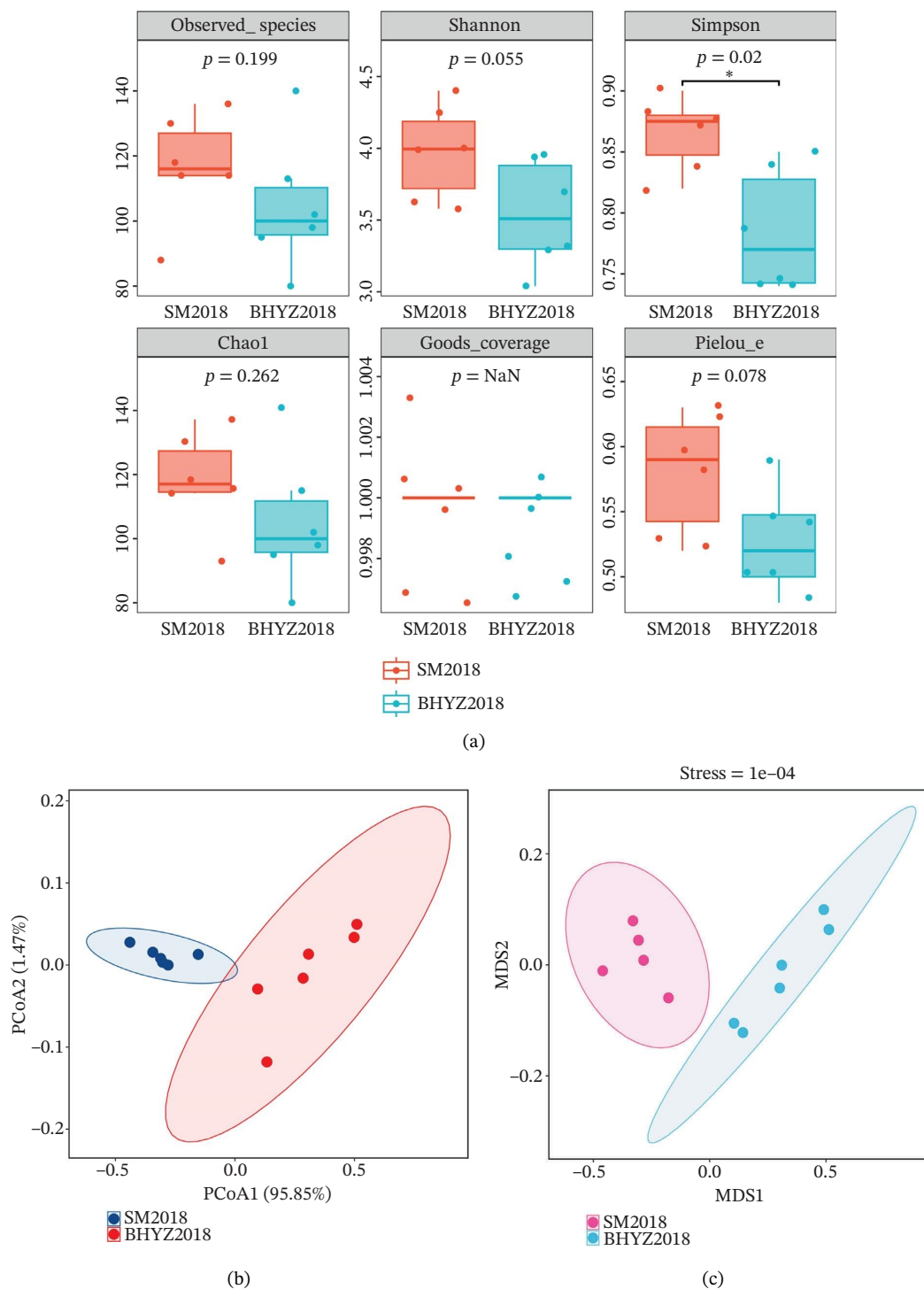


FIGURE 6 | Fungal diversity analysis. (a) Alpha diversity box plots ($n = 6$) showing observed species, Shannon, Simpson, Chao1, goods_coverage, and Pielou_e indices between SM2018 and BHYZ2018 groups. The Kruskal–Wallis test with Dunn’s post hoc was used (*, $p < 0.05$). (b) PCoA based on weighted UniFrac distances. (c) NMDS based on unweighted UniFrac distances.

sensory properties by modulating amino acid metabolism in leaf tissues.

4 | Discussion

The dynamic evolution of microbial communities during tea processing and storage is of both theoretical and practical significance, offering insights into optimizing storage

conditions and elucidating flavor formation mechanisms. Traditional research has relied on techniques such as quantitative real-time PCR (qPCR), PCR-DGGE, and clone libraries. However, advancements in molecular biology have led to the widespread adoption of high-throughput sequencing technologies, including metagenomics and amplicon sequencing (16S/ITS/18S), for studying tea microbiomes. Notably, most studies have focused on postfermented and fully fermented teas, such

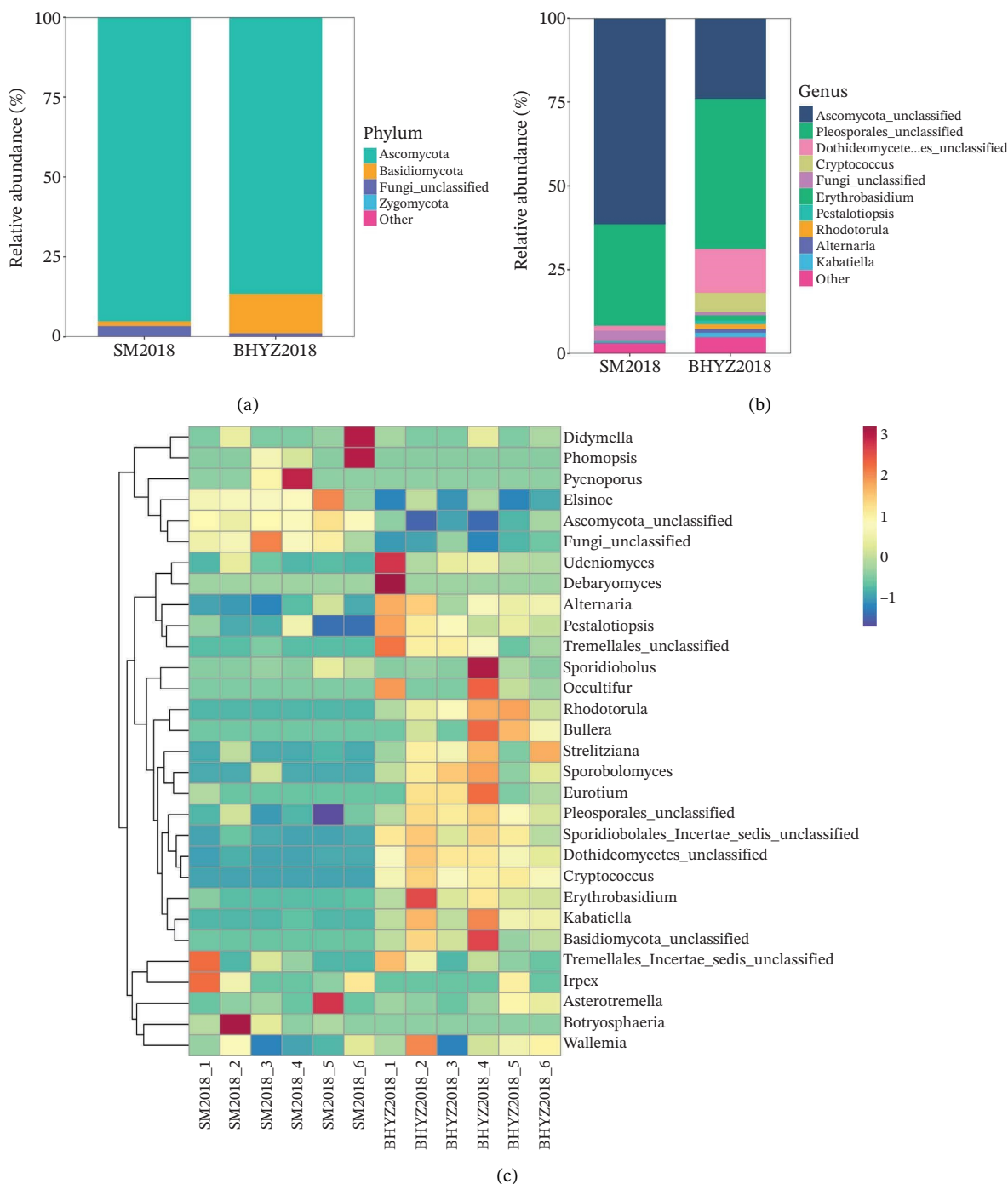


FIGURE 7 | Fungal community composition analysis. (a) Stacked bar plot of fungal composition at the phylum level (top five phyla). (b) Stacked bar plot of fungal composition at the genus level (top ten genera). (c) Cluster heatmap displaying the relative abundance of the top 30 fungal genera.

as Pu-erh and black tea, while the microbial ecology of white tea, a minimally fermented category, remains largely unexplored [19]. This study employed dual-target amplicon sequencing of the 16S rRNA gene and ITS region to characterize bacterial and fungal community shifts in white tea during storage. By systematically elucidating microbial diversity patterns over time, this research provides critical evidence for understanding the molecular mechanisms underlying microbial participation in the aging and transformation of white tea, thereby contributing to the refinement of white tea quality control strategies.

Analysis of ASVs and species richness revealed that bacterial diversity was slightly higher than fungal diversity in both SM and BHYZ samples after 5 years of storage, suggesting that bacteria exhibit greater activity during white tea aging. In bacterial communities, BHYZ exhibited higher species richness than SM but lower diversity. It is worth further investigating whether it is caused by the physical barriers in BHYZ that are unsuitable for certain microbial colonization, as well as the presence of some nutrients that may attract specific types of microbes. While the overall bacterial composition was similar between the two tea varieties, their relative abundances varied. The dominant genera

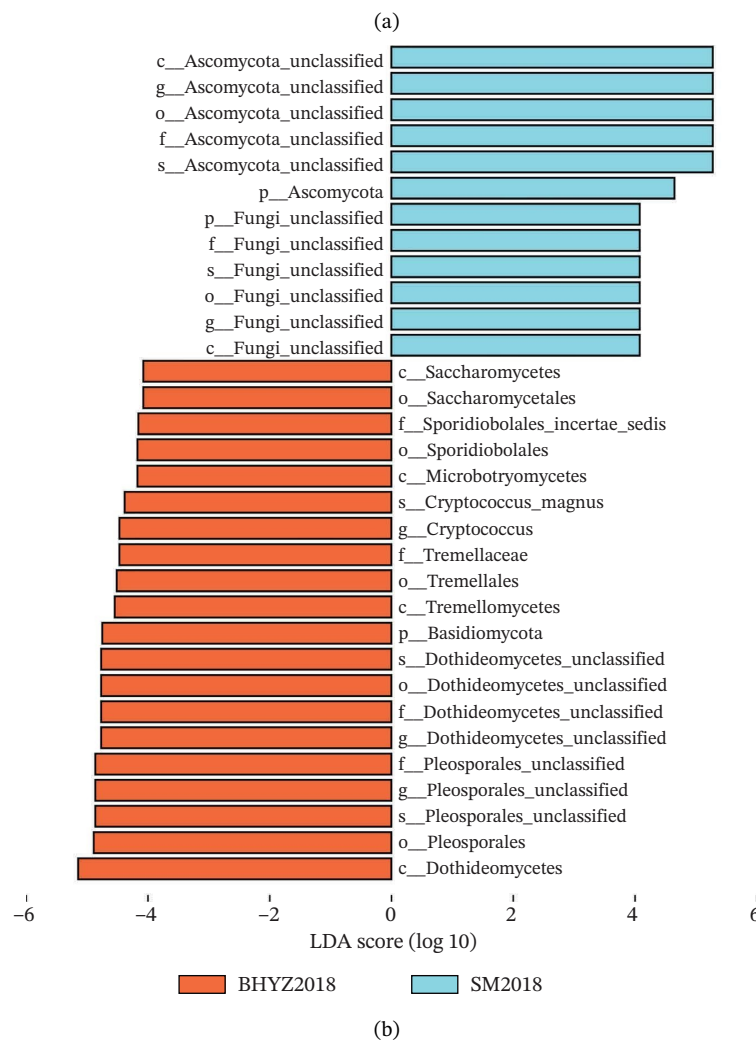
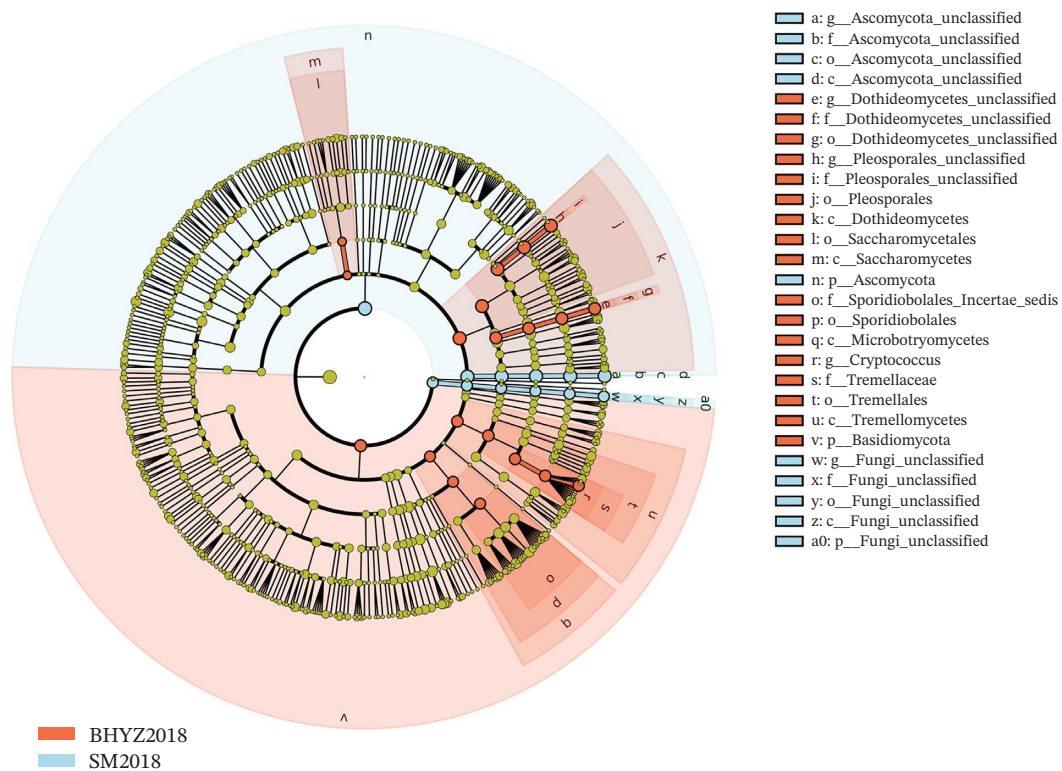


FIGURE 8 | (Continued)

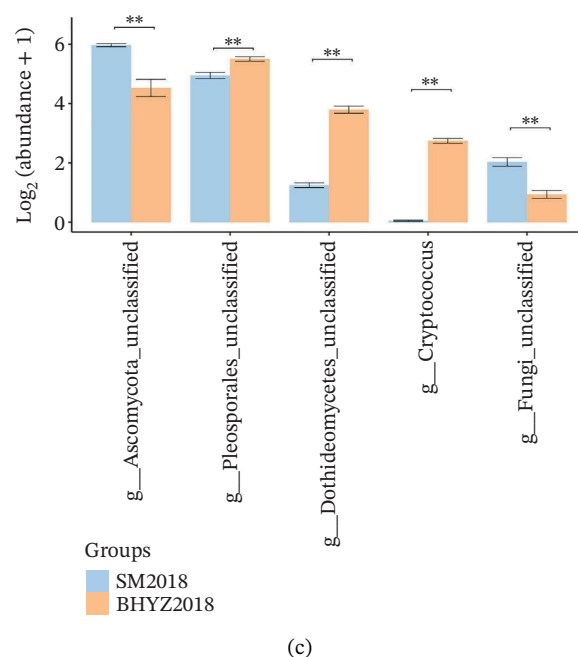


FIGURE 8 | LEfSe differential analysis of fungal communities. (a) Cladogram illustrating taxonomic differences across fungal communities. (b) Distribution bar chart highlighting significantly enriched taxa. (c) Bar plot showing the top five differentially abundant genera (statistical significance of differences for each genus was determined using the Mann–Whitney U test ($p < 0.05$)).

common to both samples were *Methylobacterium*–*Methylorubrum* and *Sphingomonas*, with *Sphingomonas* being more abundant in BHYZ and *Methylobacterium*–*Methylorubrum* more prevalent in SM. These genera are widely distributed in the plant phyllosphere, rhizosphere, and soil environments. Studies indicate that *Sphingomonas* predominantly colonizes the rhizosphere, while *Methylobacterium* is concentrated in the phyllosphere, demonstrating spatial niche specificity [20]. Both genera have been implicated in plant disease resistance and stress tolerance [21, 22]. During tea processing, Liu et al. reported that *Methylobacterium* and *Sphingomonas* jointly dominate the fermentation of Liupao tea, influencing metabolite dynamics, particularly flavonoid glycosides and terpenes [23]. Additionally, in fermented teas such as black and dark teas, *Sphingomonas* has been linked to aromatic compound degradation, while *Methylobacterium* contributes to the biosynthesis of key flavor compounds, including thearubigins [24].

Chryseobacterium, a minor dominant genus in both white tea samples, has been identified as a key bacterial taxon in fresh tea leaves through high-throughput sequencing [25]. However, its abundance declines in aged leaves, likely due to shifts in metabolite composition during maturation [24]. Beyond these shared genera, SM and BHYZ harbored distinct dominant bacterial taxa. *Ligilactobacillus* was significantly more abundant in SM than in BHYZ and, like other lactic acid bacteria, may contribute to tea fermentation, enhancing flavor complexity [26]. Conversely, *Pedobacter* was more abundant in BHYZ. This genus, commonly found in soil, is notably abundant in unfermented Pu-erh tea, but its relative abundance declines after inoculation with *Bacillus licheniformis* for enhanced fermentation [27]. LEfSe and barplot analyses further highlighted the compositional differences between SM and BHYZ microbial communities. Whether these variations in the bacterial community structure influence

metabolic pathways and, consequently, the distinct flavor profiles of these teas warrants further investigation.

No significant differences in fungal richness or diversity were observed between the two white tea varieties. Ascomycota was the dominant fungal phylum in both, consistent with previous studies showing that it is the most abundant fungal phylum in tea garden soils, where its relative abundance is closely linked to soil nutrient conditions [28]. Within this phylum, *Eurotium* is a well-documented genus known for its crucial role in the fermentation of brick tea. The amylases and oxidases secreted by *Eurotium* catalyze starch hydrolysis into monosaccharides, enhancing the color and taste of tea liquor and serving as key markers of tea quality [29]. However, in this study, the dominant fungal taxa at the genus level were predominantly unclassified, likely due to limitations in the ITS database, incomplete sequence annotation, or insufficient research on the target fungal groups. Future validation using multi-omics approaches is necessary. Among the dominant fungal taxa, *Ascomycota_unclassified* and *Pleosporales_unclassified* were common in both SM and BHYZ. Additionally, *Dothideomycetes_unclassified* and *Cryptococcus* were more abundant in BHYZ than in SM. Nonpathogenic *Cryptococcus* species are commonly found on soil and plant surfaces, while fungi belonging to Dothideomycetes are major endophytes in tea leaves [30, 31]. However, the roles of these fungi in white tea growth and storage remain largely unexplored.

In addition to the dominant genera, we have identified several taxa that are not typical constituents of the phyllosphere or soil microbiota, such as the bacterial genera *Vibrio*, *Escherichia*–*Shigella*, *Aeromonas*, and *Helicobacter*. Their presence likely indicates specific, postharvest sources of contamination (e.g., water and human handling). Furthermore, we detected fungal genera such as *Aspergillus* and *Alternaria*, which, while common in the environment, are of particular concern in stored food

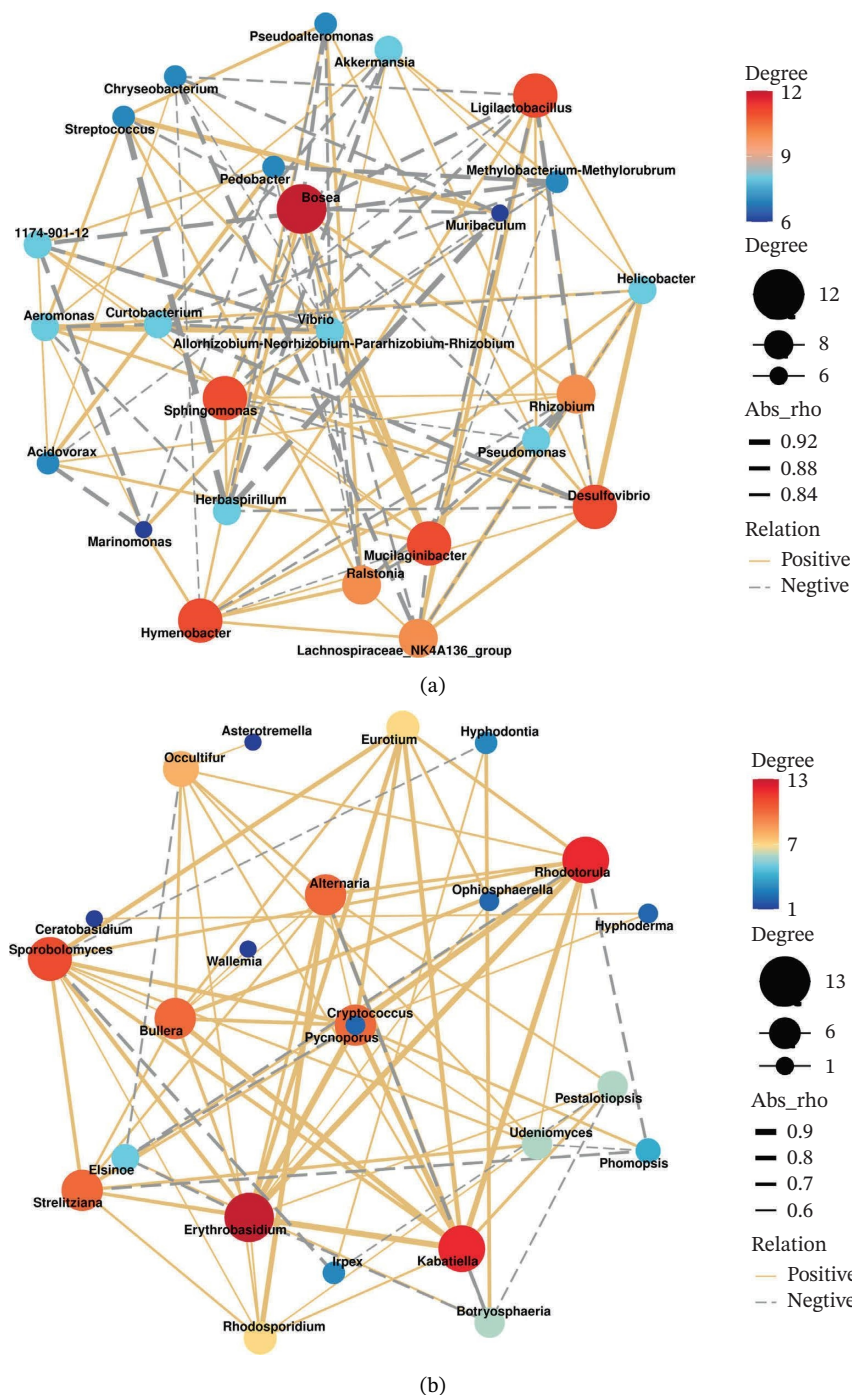


FIGURE 9 | Microbial co-occurrence network based on the spearman correlation analysis. (a) Bacterial co-occurrence network. (b) Fungal co-occurrence network.

products due to their known potential for spoilage and mycotoxin production [32]. Although they do not occupy a dominant position in the aging process of the two cultivars of white tea, we should be aware of the potential challenges they may pose to the quality and safety of tea.

Furthermore, the reasons for the differences in the microbial composition between SM and BHYZ were analyzed. In terms of raw material selection, BHYZ is composed of carefully selected plump single buds, with the buds covered in dense white downy hairs. This unique morphology and the hydrophobicity of the

white downy hairs may limit the attachment space for micro-organisms and inhibit the colonization of certain micro-organisms. In contrast, SM is made from a bud along with several mature leaves. The more spread-out structure in SM may provide a larger surface area for microbial adsorption and facilitate gas exchange. Moreover, BHYZ has higher contents of water-soluble substances, caffeine, and free amino acids, while SM contains a higher content of soluble sugar [33]. These differences in nutritional components may also affect the colonization preferences of micro-organisms. Owing to the different tenderness of the raw materials, during the processing, the

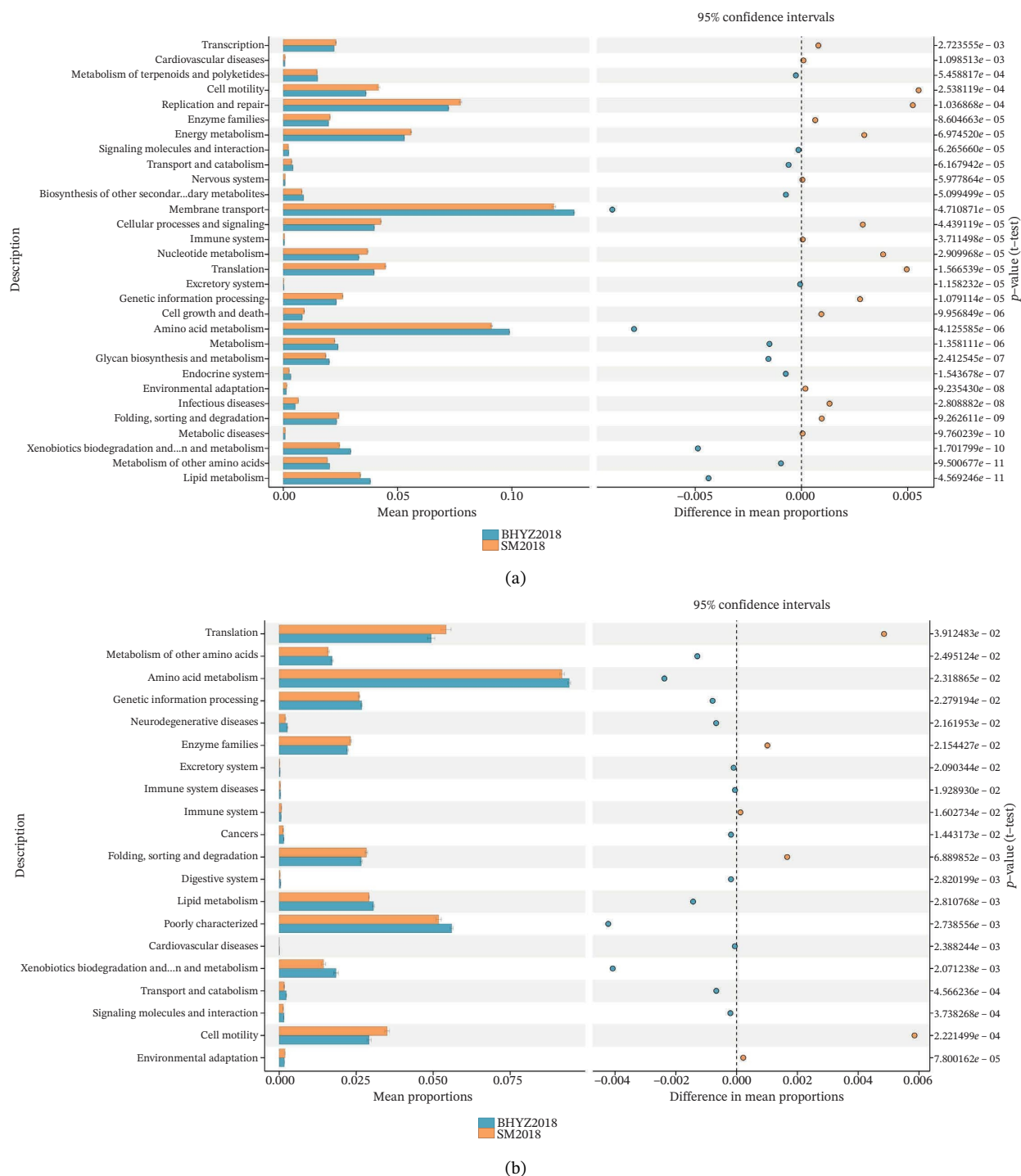


FIGURE 10 | Functional predictions of microbial communities using PICRUST2 (based on KEGG Pathway Level 2). (a) Functional prediction of bacterial communities. (b) Functional prediction of fungal communities.

control of temperature and humidity for BHYZ is usually stricter [34]. Therefore, the differences in the microbial composition between the two cultivars of white tea may be a result of the combined effects of variations in raw material characteristics, processing techniques, and storage environments.

Co-occurrence network analysis identified *Bosea* and *Erythrobasidium* as the core genera with the highest connectivity in bacterial and fungal networks, respectively. *Bosea* is known to

colonize the rhizosphere of tea plants, with its abundance increasing under drought conditions [35]. Wu et al. suggested that *Bosea* is a characteristic bacterium involved in flavor compound formation in Wuyi rock tea, although its specific role in tea quality remains unclear [36]. It is hypothesized that *Bosea* interacts with other dominant species to influence metabolic processes during white tea storage. *Erythrobasidium*, a common epiphytic yeast on plant leaves, has been associated with leaf health status [22]. In a study on jujube fruit storage,

Erythrobasidium abundance was positively correlated with fruit firmness and the sugar-to-acid ratio, potentially due to its ability to inhibit spoilage fungi such as *Penicillium*, thereby preserving fruit quality [37]. However, its function in tea remains unknown. Given these findings, we speculate that *Bosea* and *Erythrobasidium* may contribute to microbial homeostasis on tea leaves during storage, but further research is required to clarify their biological roles.

Predicted functional profiles of microbial communities during white tea storage, obtained using PICRUSt2, revealed that both bacterial and fungal communities were primarily associated with amino acid metabolism pathways. Amino acids are essential for tea flavor and aroma development, as their composition and interactions directly influence taste, scent, and color. Beyond their contribution to umami, amino acids and their derivatives offer health benefits, such as neurodegenerative disease prevention and fat metabolism regulation [38–40]. Compared to other tea types, white tea has a higher amino acid content, potentially due to the withering process, which promotes amino acid accumulation [41]. Previous research has shown that BHYZ contains higher levels of free amino acids compared to SM. These elevated amino acid levels are thought to effectively counteract the astringency of tea polyphenols, thereby enhancing the sweet aftertaste [42].

Overall, this study indicates that microbial activity plays a significant role in flavor modulation during the aging process. Future work could explore temperature and humidity conditions that are more suitable for the storage of BHYZ and SM, respectively, based on their distinct microbial community compositions. Additionally, to optimize microbial activity for enhanced flavor and bioactive properties, the incorporation of natural substrates that support the growth of beneficial microbes could be considered. In traditional market perception, the aged flavor quality of BHYZ is generally considered superior to that of SM. If a multidimensional interaction network of “microbial community–environmental factors–flavor compounds” could be constructed in the future, it might be possible to improve the quality of SM through the targeted regulation of the microbial structure. Furthermore, future studies could investigate the microbial succession dynamics in SM and BHYZ throughout the entire process from initial processing to long-term storage. This work would delineate the distinct aging trajectories of different white tea cultivars, thereby informing and optimizing their processing and storage protocols.

5 | Conclusion

This study employed microbiome amplicon sequencing to characterize the microbial community structure of two grades of white tea, SM and BHYZ, after 5 years of storage. The results revealed that while the overall microbial community composition was similar between the two teas, significant differences in relative abundance were observed. In bacterial communities, *Methylobacterium*–*Methylobacterium* and *Sphingomonas* were the dominant genera in both samples. However, *Ligilactobacillus*, *Chryseobacterium*, and *Aureimonas* were more abundant in SM, whereas *Pedobacter*, *Betaproteobacteria_unclassified*, and *Chryseobacterium* were enriched in BHYZ. LEfSe analysis identified Firmicutes as the signature phylum in SM, with *Methylobacterium*–*Methylobacterium*, *Ligilactobacillus*, *Pseudomonas*, and *Vibrio* as key genera. In contrast, BHYZ was

characterized by Bacteroidota, with *Chryseobacterium*, *Bosea*, *Allorhizobium*–*Neorhizobium*–*Pararhizobium*–*Rhizobium*, *Sphingomonas*, *Betaproteobacteria_unclassified*, and *Pedobacter* as signature genera.

For fungal communities, *Ascomycota_unclassified* and *Pleosporales_unclassified* were dominant in both tea samples, while *Dothideomycetes_unclassified* was more abundant in BHYZ. LEfSe analysis revealed that SM was characterized by *Ascomycota* and *Fungi_unclassified*, with *Ascomycota_unclassified* and *Fungi_unclassified* as signature genera. In BHYZ, Basidiomycota was the distinguishing phylum, with *Cryptococcus*, *Dothideomycetes_unclassified*, and *Pleosporales_unclassified* as signature genera.

Co-occurrence network analysis identified *Bosea* and *Erythrobasidium* as the core genera with the highest connectivity in bacterial and fungal networks, respectively, suggesting that these taxa may play crucial roles in maintaining microbial homeostasis during storage. Functional predictions indicated that most microbial communities were associated with amino acid metabolism pathways, which may contribute to flavor transformations in stored white tea. These findings provide a foundation for further elucidating microbial contributions to tea aging and offer valuable insights into microbial hygiene, flavor development, and poststorage quality evolution in white tea.

Author Contributions

S.X.: conceptualization, funding acquisition, investigation, formal analysis, and writing–original draft.

Z.C.: investigation, formal analysis, and writing–original draft.

C.Z.: supervision and writing–review and editing.

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Conflicts of Interest

The authors declare no conflicts of interest.

Data Availability Statement

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

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Supporting Information

Additional supporting information can be found online in the Supporting Information section. (*Supporting Information*)

Figure S1. PICRUST2 function prediction (taking KEGG Pathway Level 1 results as an example) (A) bacterial function prediction and (B) fungal function prediction.