

## Research Perspective

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## Microbial Diversity in Tea Fermentation: A Metagenomic Perspective

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**Abstract** Microbial diversity plays a crucial role in the fermentation of tea, affecting the flavor characteristics and health benefits of the final product. This study explores microbial diversity in tea fermentation from a metagenomic perspective, emphasizing how advanced metagenomic technologies have revolutionized our understanding of the microbial communities involved in tea processing. By examining the microbial profiles of different types of tea, such as green tea and black tea, and incorporating case studies like Pu-erh tea fermentation, the dynamic interactions and functional capabilities of these microbial communities are revealed. The study also discusses the impact of environmental factors, such as geographical location and fermentation conditions, on microbial diversity, and explores the application of microbial management to enhance tea quality. This comprehensive presentation of information highlights new opportunities and challenges in the field, proposing future directions for research and industrial applications to optimize the tea fermentation process. This study provides scientific basis and direction for continuous innovation and improvement in the tea industry.

**Keywords** Tea fermentation; Microbial diversity; Metagenomics; Microbial management; Fermentation process optimization

### 1 Introduction

Microbial diversity plays a pivotal role in the fermentation of various types of tea, such as Pu-erh, kombucha, and dark teas. The unique qualities of these teas are largely attributed to the specific microbial communities that dominate during fermentation. For instance, in Pu-erh tea, the presence of *Aspergillus* and other genera such as *Bacillus* and *Debaryomyces* are essential for the development of characteristic flavors and bioactive compounds (Zhao et al., 2015; Li et al., 2018). Similarly, the microbial interactions in kombucha tea, particularly between *Komagataeibacter rhaeticus* and *Brettanomyces bruxellensis*, are crucial for biofilm formation and fermentation quality (Landis et al., 2022). The microbial and chemical diversities in Chinese dark teas are influenced by geographical factors and manufacturing procedures, highlighting the importance of microbial diversity in determining tea quality (Kong et al., 2022).

Metagenomics has emerged as a powerful tool for studying the complex microbial communities involved in tea fermentation. This approach allows for the comprehensive analysis of microbial DNA directly from environmental samples, providing insights into the taxonomic and functional diversity of microbial populations. For example, shotgun metagenomic sequencing has been used to reveal the microbial composition and functional genes in Pu-erh tea fermentation, identifying key microorganisms and their roles in flavor production (Li et al., 2018). Similarly, metagenomic and metaproteomic analyses have been employed to investigate the microbial communities and enzymes involved in the solid-state fermentation of Pu-erh tea, advancing our understanding of the fermentation mechanisms (Zhao et al., 2015). These studies demonstrate the potential of metagenomics to uncover the intricate microbial interactions and metabolic pathways that drive tea fermentation.

This study provides a comprehensive overview of the microbial diversity involved in tea fermentation from a metagenomic perspective, summarizing current knowledge of microbial communities associated with different types of fermented tea. It emphasizes the importance of microbial diversity in influencing the quality and characteristics of fermented tea and discusses the application of metagenomic techniques in studying microbial

communities and their functional roles in tea fermentation. By integrating results from various studies, this study enhances the understanding of microbial dynamics in tea fermentation and offers insights for improving tea yield and quality.

## 2 Metagenomic Techniques

### 2.1 Evolution of metagenomic methods

The field of metagenomics has evolved significantly over the past few decades, transitioning from traditional culture-based methods to advanced sequencing technologies. Initially, the study of microbial communities relied heavily on the isolation and cultivation of individual species, which was time-consuming and often biased towards easily cultivable organisms. The advent of high-throughput sequencing technologies, such as pyrosequencing and shotgun metagenomics, has revolutionized our understanding of microbial diversity by allowing the comprehensive analysis of microbial communities directly from environmental samples without the need for cultivation (Lyu et al., 2013; Zhao et al., 2015).

### 2.2 Current tools and technologies in metagenomics

Modern metagenomic studies employ a variety of advanced tools and technologies to analyze microbial communities. Shotgun metagenomic sequencing, for instance, enables the sequencing of all genetic material in a sample, providing insights into the taxonomic composition and functional potential of the microbiota (Li et al., 2018; Landis et al., 2022). Additionally, metaproteomics, which involves the large-scale study of proteins expressed by microbial communities, complements metagenomic data by offering a functional perspective on microbial activity (Xie et al., 2019). Techniques such as 16S rRNA sequencing are also commonly used to identify and classify bacteria within complex communities (Wu et al., 2022).

### 2.3 Challenges in metagenomic analysis

Despite the advancements in metagenomic techniques, several challenges remain. One major issue is the complexity of data analysis, as metagenomic datasets are often large and require sophisticated bioinformatics tools for processing and interpretation. Another challenge is the accurate assembly of metagenomic sequences, which can be hindered by the presence of highly similar sequences from different organisms (Landis et al., 2022). Additionally, the functional annotation of metagenomic data is complicated by the vast diversity of microbial genes, many of which have unknown functions (Xie et al., 2019). The integration of metagenomic data with other omics approaches, such as metaproteomics and metabolomics, requires careful consideration to ensure comprehensive and accurate interpretations.

## 3 Microbial Profiles in Different Tea Types

### 3.1 Microbial composition in green tea fermentation

Green tea fermentation involves a diverse microbial community, primarily dominated by lactic acid bacteria (LAB) and yeasts. In the fermentation of Miang, a traditional fermented tea from northern Thailand, LAB such as *Lactobacillus* and *Acetobacter* were found to be the predominant bacterial genera, while *Candida* and *Pichia* were the main fungal genera (Unban et al., 2020). Similarly, in industrial-scale green tea kombucha fermentations, the bacterial community was dominated by *Acetobacteraceae*, with *Oenococcus oeni* being strongly associated with green tea fermentations (Coton et al., 2017). These microbial communities play crucial roles in the biochemical properties of the tea, contributing to its flavor and health benefits.

### 3.2 Microbial dynamics in black tea fermentation

Black tea fermentation, particularly in kombucha, is characterized by a dynamic microbial community that includes both bacteria and yeasts. Studies have shown that the bacterial genus *Komagataeibacter* and the yeast *Brettanomyces bruxellensis* are the most common microbes in kombucha communities (Landis et al., 2022). The microbial diversity in black tea kombucha is influenced by the fermentation process, with significant shifts in the yeast community from *Candida* to *Lachancea* during the fermentation period (Chakravorty et al., 2016). Additionally, the presence of *Gluconacetobacter europaeus* and *Acetobacter peroxydans* has been noted as dominant species in black tea fermentations (Coton et al., 2017).

### 3.3 Comparative analysis of microbial diversity in other tea types

Other types of fermented teas, such as Pu-erh and Fuzhuan brick tea, exhibit unique microbial profiles. In Pu-erh tea, the dominant bacteria are *Proteobacteria*, while *Aspergillus* is the predominant fungus (Zhao et al., 2015). The microbial community in Fuzhuan brick tea is characterized by a higher abundance and diversity of bacterial communities (Figure 1), with *Lactococcus* and *Bacillus* being the main bacteria, and *Eurotium* as the predominant fungus (Xia et al., 2012). The microbial composition in these teas is crucial for the development of their unique flavors and bioactive compounds. For instance, in Sichuan South-road Dark Tea, *Aspergillus niger* plays a significant role in enhancing the tea's organoleptic qualities by producing enzymes such as  $\beta$ -glucosidase and pectinase, which contribute to the tea's sweet and mellow taste (Zou et al., 2022).

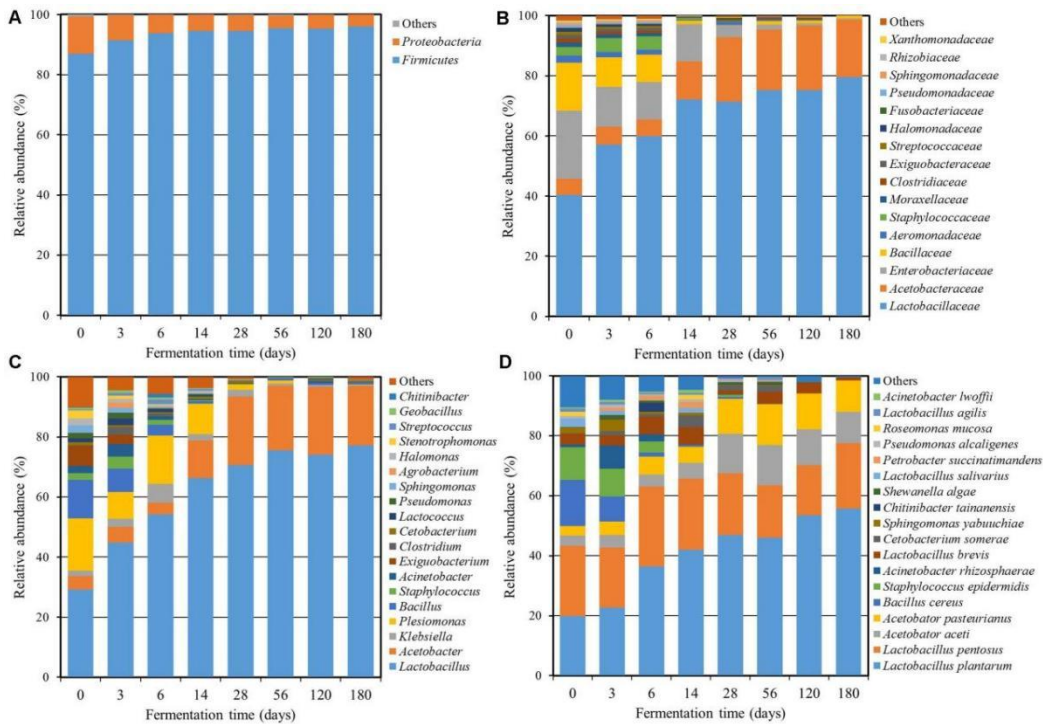


Figure 1 Relative abundance of the bacterial community at the phylum (A), family (B), genus (C), and species (D) levels throughout the fermentation period (Adopted from Unban et al., 2020)

Unban et al. (2020) demonstrated the relative abundance changes of bacterial communities at the four levels of phylum, family, genus, and species during the fermentation process. From the graph, it can be seen that during fermentation, *Proteobacteria* and *Firmicutes* are the main bacterial phyla, with relatively stable abundance. The diversity changes from family to species level indicate that certain genera and species in families such as *Lactobacillaceae* and *Streptococcaceae* become more prominent during the fermentation process. These changes may be related to environmental factors, selectivity of fermentation substrates, and interactions between microorganisms, reflecting the dynamic balance of microbial community structure and its adaptability to the fermentation environment.

## 4 Case Studies in Tea Fermentation

### 4.1 Case study: metagenomic insights from Pu'er tea fermentation

Pu'er tea fermentation is a complex process involving a diverse microbial community that significantly influences the tea's quality and flavor (Figure 2). Shotgun metagenomic and metabolomic analyses have revealed substantial variations in the composition of microbiota, functional genes, and flavor compounds during the solid-state fermentation (SSF) process. Key microorganisms such as *Aspergillus*, *Bacillus*, *Rasamsonia*, *Lichtheimia*, and *Debaryomyces* play crucial roles at different stages of fermentation, contributing to the production of dominant flavors like theabrownin and methoxy-phenolic compounds (Kong et al., 2022). Additionally, integrated metagenomics and metaproteomics approaches have identified *Proteobacteria* and *Aspergillus* as dominant taxa,

with enzymes involved in plant cell wall degradation and catechin oxidation being crucial for the fermentation process (Li et al., 2018). These insights bridge the gap between microbiota and tea quality, offering pathways for optimizing production efficiency and product quality.



Figure 2 Taxonomic diversity of 23 kombucha microbiomes (Adopted from Landis et al., 2022)

Image caption: (A) Kombucha fermentation, showing floating biofilm and liquid tea; (B) Assignment of order-level taxonomy to unassembled reads using the Kaiju and NCBI BLASTnr+euk databases; (c) obtain the assignment of genus classification in the same manner; (D) At the different species level (Adopted from Landis et al., 2022)

The Figure 2 presents a metagenomic analysis of the fermentation microbiome of 23 Pu'er teas, in which the taxonomic diversity of bacteria and yeast is detailed through advanced database tools. At the level of phylum and genus, there are significant differences in the main classifications such as *Enterobacteriales* and *Lactobacillales*, which reflect the unique fermentation environment of Pu'er tea. In particular, *Komagataeibacter rhaeticus* is marked as the most common and abundant bacterial species in Figure 2D, while *Brettanomyces bruxellensis* is the main yeast species. These findings not only reveal the structure of the microbial community in Pu'er tea, but also emphasize the potential role of certain key species in the fermentation process.

#### 4.2 Case study: Impact of microbial diversity on tea flavor

The microbial diversity in tea fermentation significantly impacts the flavor profile of the final product. In Pu'er tea, the dynamic changes in microbial communities, including bacteria and fungi, during fermentation stages are

closely linked to the development of unique flavors. For instance, the presence of *Aspergillus* in the early stages and other genera like *Bacillus* and *Rasamsonia* in later stages contribute to the formation of key flavor compounds. Similarly, in kombucha tea, the interaction between bacteria such as *Komagataeibacter rhaeticus* and yeast like *Brettanomyces bruxellensis* is crucial for biofilm production and flavor development. The metabolic activities of these microbes, including the fermentation of sucrose and production of key metabolites, shape the sensory characteristics of kombucha (Landis et al., 2022). These findings underscore the importance of microbial diversity in determining the flavor attributes of fermented teas (Zhao et al., 2019).

#### 4.3 Case study: Health implications of microbial interactions

The health benefits of fermented teas are closely linked to the interactions within their microbial communities. For example, Pu'er tea has been shown to alter the gut microbiota composition and function in diet-induced obese rats, promoting microbial diversity and beneficial metabolic processes. The administration of Pu'er tea extracts increased the relative abundances of *Firmicutes* and decreased *Bacteroidetes*, enhancing community metabolic processes such as sucrose metabolism and glycolysis (Xia et al., 2019). These changes are associated with the prebiotic effects of Pu'er tea, potentially promoting the growth of beneficial bacteria like *Akkermansia muciniphila*. Additionally, the microbial interactions in kombucha tea, particularly between bacteria and yeast, contribute to the production of bioactive compounds that may have health-promoting properties. These studies highlight the potential health benefits of microbial interactions in fermented teas.

### 5 Functional Analysis of Microbial Communities

#### 5.1 Functional roles of dominant microbes

The functional roles of dominant microbes in tea fermentation are diverse and critical for the development of the unique flavors and qualities of fermented teas. In Pu-erh tea fermentation, *Aspergillus* species are identified as the primary flavor-producing microorganisms during the early stages of solid-state fermentation (SSF), contributing to the formation of key flavor compounds such as theabrownin and methoxy-phenolic compounds (Li et al., 2018). Similarly, in the SSF of Pu-erh tea, *Aspergillus* is the dominant fungus and a major host of identified proteins, including enzymes involved in the degradation of plant cell walls and the oxidation of catechins (Zhao et al., 2015). In Fuzhuan brick tea, bacterial communities, particularly *Lactococcus* and *Bacillus*, play significant roles in the metabolic processes, correlating with the production of various metabolites (Xia et al., 2021). Additionally, in kombucha tea, the bacterium *Komagataeibacter rhaeticus* and the yeast *Brettanomyces bruxellensis* are the most common microbes, with *B. bruxellensis* enhancing biofilm formation and fermentation qualities (Landis et al., 2022).

#### 5.2 Metabolic pathways involved in tea fermentation

The metabolic pathways involved in tea fermentation are complex and involve various microbial interactions. In Pu-erh tea, the formation pathways of dominant flavors such as theabrownin, methoxy-phenolic compounds, alcohol, and carvone have been proposed, highlighting the intricate metabolic processes driven by microbial communities (Hu et al., 2020). The integration of metagenomics and metaproteomics in Pu-erh tea fermentation has revealed enzymes associated with the degradation of plant cell walls and the oxidation of catechins, further elucidating the metabolic pathways involved. In Fuzhuan brick tea, predictive metabolic functions indicate pathways related to cellular growth, environmental information processing, genetics, and material metabolism, with significant correlations between bacterial populations and metabolites. Additionally, in kombucha tea, the enhanced ability of *B. bruxellensis* to ferment and produce key metabolites in sucrose-sweetened tea is linked to its role in stimulating biofilm formation (Landis et al., 2022).

#### 5.3 Bioinformatics tools for functional prediction

Bioinformatics tools play a crucial role in predicting the functional properties of microbial communities in tea fermentation. Shotgun metagenomic sequencing and metabolomic analysis are employed to reveal the composition and functional genes of microbiota in Pu-erh tea fermentation, providing insights into the association between microbiota and tea quality. Metaproteomics analysis, combined with metagenomics, is used to identify

and classify proteins into biological processes and molecular function categories, advancing the understanding of SSF mechanisms in Pu-erh tea (Illegheems et al., 2015). High-throughput sequencing and Liquid Chromatography-Mass Spectrometry (LC-MS) are utilized to profile the microbial community and metabolites in Fuzhuan brick tea, revealing essential correlations between bacterial populations and metabolites (Fu et al., 2021). Additionally, metagenomic pyrosequencing is applied to delineate the microbial taxonomy and functional ontologies of microbial genes in Pu-erh tea pile fermentation, providing a comprehensive overview of the microbial community (Lyu et al., 2013).

## 6 Influence of Environmental Factors

### 6.1 Effect of geographic location on microbial diversity

Geographic location significantly influences the microbial diversity in tea fermentation. For instance, the microbial and chemical diversities of Chinese dark teas (CDTs) are notably affected by latitude and pile fermentation processes. These factors determine the microbial  $\beta$  diversity and the nonvolatile chemical  $\alpha$  and  $\beta$  diversities, which are crucial for the nutritional and flavor profiles of the tea (Kong et al., 2022). Additionally, the microbial community dynamics in traditional fermented teas like Miang from northern Thailand are shaped by the local environmental conditions, with *Firmicutes* and *Proteobacteria* being the dominant bacterial phyla, and *Ascomycota* the main fungal phylum (Unban et al., 2020).

### 6.2 Influence of fermentation conditions on microbial profiles

Fermentation conditions, including the type of fermentation and the specific methods used, play a critical role in shaping the microbial profiles of tea. In the fermentation of Pu-erh tea, for example, the microbial community undergoes significant changes, with *Aspergillus* being the dominant fungus in the early stages and other genera like *Bacillus* and *Debaryomyces* becoming more prominent later (Zhao et al., 2015). Similarly, the fermentation process of Kombucha tea involves dynamic shifts in microbial communities, with *Komagataeibacter* and *Brettanomyces bruxellensis* being the most common microbes, and the microbial interactions within biofilms significantly influencing the fermentation qualities (Chakravorty et al., 2016).

### 6.3 Adaptation and resilience of microbial communities

Microbial communities in tea fermentation exhibit remarkable adaptation and resilience to varying environmental conditions and fermentation processes. In the case of Fuzhuan brick tea, bacterial communities such as *Lactococcus* and *Bacillus*, along with the fungus *Eurotium*, adapt to the fermentation environment, contributing to the metabolomic profile of the tea (Xia et al., 2021). The microbial communities in Kombucha tea also demonstrate resilience, with specific bacteria and yeasts maintaining their presence and functional roles throughout the fermentation process, despite changes in environmental conditions (Landis et al., 2022). This adaptability is crucial for maintaining the quality and consistency of fermented tea products.

## 7 Applications in Industry

### 7.1 Enhancing tea quality through microbial management

The quality of tea, particularly fermented varieties like Pu-erh and dark teas, is significantly influenced by the microbial communities involved in the fermentation process. Studies have shown that specific microbes, such as *Aspergillus*, *Bacillus*, and *Rasamsonia*, play crucial roles in the development of flavor compounds and overall tea quality (Zou et al., 2022). For instance, the presence of *Aspergillus niger* M10 in Sichuan South-road Dark Tea (SSDT) has been linked to enhanced sweetness and improved color attributes. Similarly, the microbial diversity in Pu-erh tea fermentation, dominated by *Proteobacteria* and *Aspergillus*, contributes to the degradation of plant cell walls and oxidation of catechins, which are essential for the tea's unique taste and aroma (Zhao et al., 2015). By understanding and managing these microbial communities, producers can optimize fermentation conditions to enhance tea quality.

### 7.2 Innovative fermentation techniques in tea production

Innovative fermentation techniques, such as the use of synthetic microbial pairs and integrated meta-omics approaches, are being explored to improve tea production. In kombucha tea, the manipulation of microbial

communities, particularly the interaction between *Komagataeibacter rhaeticus* and *Brettanomyces bruxellensis*, has been shown to influence biofilm production and fermentation qualities. Additionally, the application of enzymatic fermented soybean as a fertilizer in tea plantations has been found to regulate soil microbial communities and positively affect lipid metabolites in tea shoots, leading to higher quality tea (Zhang et al., 2022). These innovative techniques highlight the potential for controlled microbial fermentation to produce consistent and high-quality tea products.

### 7.3 Safety considerations in microbial fermentation

Safety is a critical consideration in microbial fermentation, especially in the production of fermented foods and beverages. The microbiome in tea fermentation not only impacts quality but also safety. For example, the integrated meta-omics approach used in Pu-erh tea fermentation has provided insights into the microbial communities and their metabolic activities (Figure 3), which are essential for ensuring the safety of the final product. Similarly, understanding the microbial dynamics in traditional fermented teas like Miang and Fuzhuan Brick Tea can help identify potential pathogenic microbes and ensure safe fermentation practices (Unban et al., 2020). By monitoring and controlling the microbial communities involved in tea fermentation, producers can mitigate risks and ensure the safety of their products.

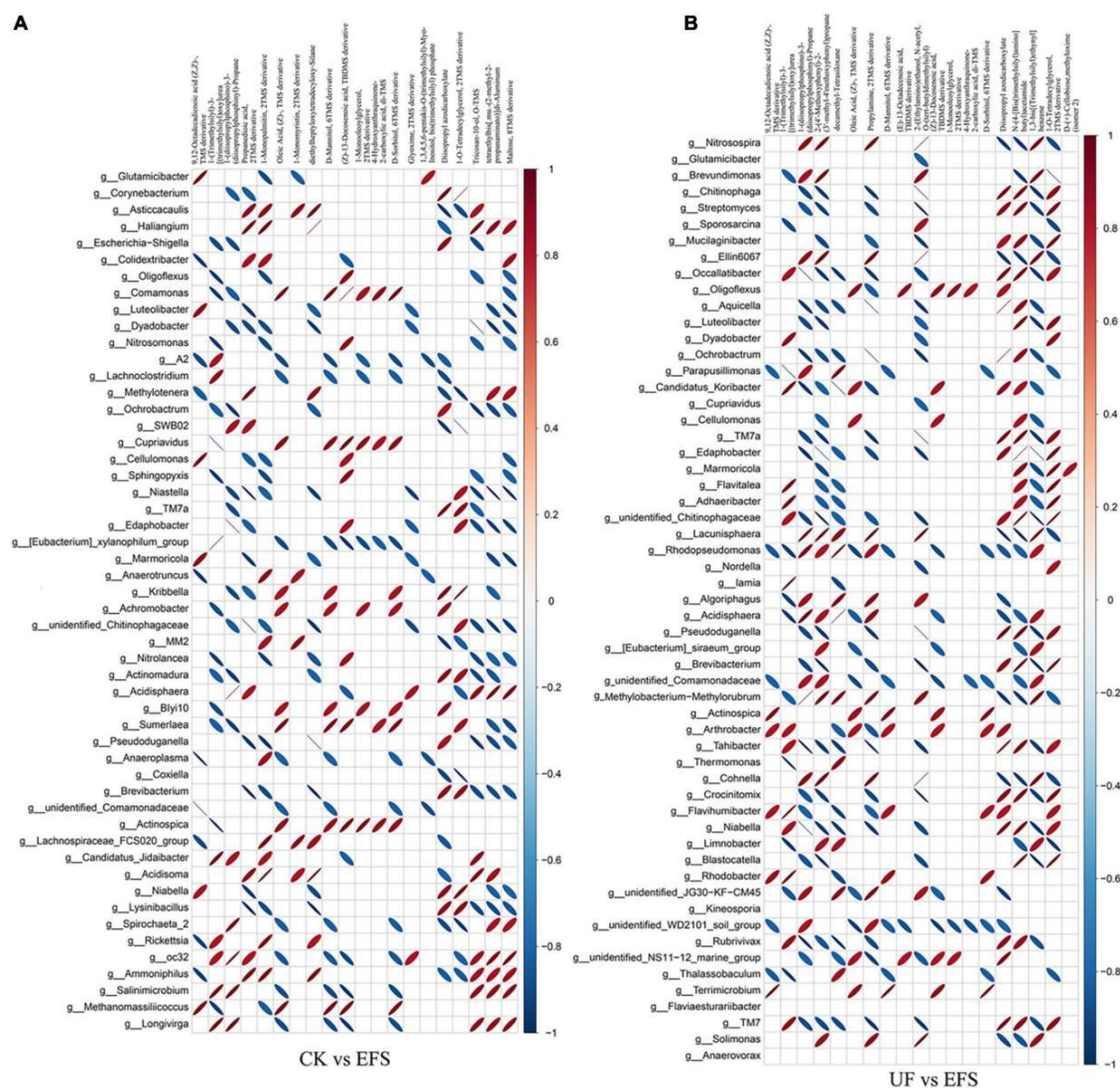


Figure 3 The ellipse heatmap of relationships between soil bacterial communities and soil metabolites (Adopted from Zhang et al., 2022)  
 Image caption: (A) The relationship of soil bacterial communities and soil metabolites in CK vs EFS group. (B) The relationship of soil bacterial communities and soil metabolites in UF vs EFS group (Adopted from Zhang et al., 2022)

The study by Zhang et al. (2022) showed the relationship between soil bacterial communities and soil metabolites. The comparison of two different treatment groups (CK vs EFS and UF vs EFS) can be seen through an elliptical heatmap, reflecting the impact of different soil treatments on the structure and function of microbial communities. This further relates to the safety considerations of microbial fermentation. During microbial fermentation, it is important to ensure that the selected microbial community is not only environmentally friendly, but also aware of the potential health risks associated with its metabolites. Some microbial metabolites may be beneficial to soil, but they may also pose a potential threat to human or animal health. Therefore, detailed analysis of microorganisms and metabolites is essential before commercial fermentation applications.

## 8 Future Prospects and Challenges

### 8.1 Emerging trends in metagenomic research

Metagenomic research in tea fermentation is rapidly evolving, with integrated approaches such as metagenomics and metaproteomics providing deeper insights into microbial communities and their functional roles. For instance, studies on Pu-erh tea have utilized these techniques to identify dominant microbial taxa and their associated enzymes, which play crucial roles in the fermentation process. Similarly, the microbial diversity in kombucha tea has been explored using metagenomics, revealing the interactions between bacteria and yeast that influence fermentation qualities and biofilm production (Coton et al., 2017). These advancements highlight the potential of metagenomic research to uncover complex microbial interactions and their impact on tea fermentation.

### 8.2 Potential discoveries in microbial ecology of tea

The microbial ecology of tea fermentation holds numerous opportunities for discovery. For example, the identification of specific microbial taxa and their metabolic pathways can lead to a better understanding of flavor formation and quality improvement in fermented teas (Li et al., 2018; Kong et al., 2022). In Fuzhuan brick tea, the correlation between bacterial populations and metabolites has been elucidated, providing insights into the role of bacteria in shaping the metabolomic profile of the tea. Additionally, the study of microbial communities in different types of tea, such as kombucha and Chinese dark teas, has revealed the influence of geographical and manufacturing factors on microbial and chemical diversities. These findings suggest that further exploration of microbial ecology in tea fermentation could lead to the discovery of novel microorganisms and metabolic pathways that enhance tea quality and health benefits.

### 8.3 Challenges in translating research to practice

Despite the promising advancements in metagenomic research, several challenges remain in translating these findings into practical applications. One major challenge is the complexity of microbial communities and their dynamic interactions during fermentation, which can be difficult to replicate and control in industrial settings (Lyu et al., 2013). Additionally, the variability in microbial composition and activity across different fermentation batches poses a challenge for standardizing production processes and ensuring consistent product quality (Chakravorty et al., 2016). Another challenge is the need for advanced bioinformatics tools and expertise to analyze and interpret metagenomic data, which can be resource-intensive and time-consuming (Fu et al., 2021). Addressing these challenges will require collaborative efforts between researchers, industry stakeholders, and policymakers to develop standardized protocols, improve data analysis methods, and implement findings in practical applications.

## 9 Concluding Remarks

The metagenomic perspective on microbial diversity in tea fermentation has unveiled significant insights into the complex microbial ecosystems involved in various types of fermented teas. Studies have shown that the microbial communities in tea fermentation are highly diverse and play crucial roles in determining the quality and characteristics of the final product. For instance, in Pu-erh tea, dominant microbial taxa such as *Proteobacteria* and *Aspergillus* have been identified, with specific enzymes linked to the degradation of plant cell walls and oxidation of catechins. Similarly, in kombucha tea, key microbial interactions between bacteria and yeast, such as *Komagataeibacter rhaeticus* and *Brettanomyces bruxellensis*, have been found to influence biofilm formation and



fermentation qualities. The microbial diversity in other fermented teas like Fuzhuan brick tea and Xiaguan Tuo tea also highlights the significant roles of bacteria and fungi in shaping the metabolomic profiles and enhancing the organoleptic qualities of the teas.

Future research should focus on a more detailed understanding of the functional roles of specific microbial taxa in tea fermentation. This includes exploring the metabolic pathways and interactions between different microbial species to better understand their contributions to flavor and quality. Advanced techniques such as integrated metagenomics and metabolomics should be employed to map out these interactions comprehensively. Additionally, there is a need for studies that investigate the impact of controlled microbial inoculation on fermentation outcomes, which could lead to more consistent and high-quality tea products. Research should also explore the potential health benefits of fermented teas, given their rich microbial and chemical profiles, to substantiate claims of their beneficial properties.

For tea industry stakeholders, these findings underscore the importance of microbial management in the fermentation process. By understanding the specific microbial communities and their roles, producers can optimize fermentation conditions to enhance the quality and consistency of their products. This could involve the use of targeted microbial inoculants to steer fermentation in desired directions, thereby improving flavor profiles and potentially adding health benefits. Additionally, the industry can benefit from adopting advanced analytical techniques to monitor and control the fermentation process more precisely, ensuring that the final product meets high standards of quality and safety. Overall, leveraging the insights from metagenomic studies can lead to innovations in tea production, offering new opportunities for product differentiation and market expansion.

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### Conflict of Interest Disclosure

The authors affirm that this research was conducted without any commercial or financial relationships that could be construed as a potential conflict of interest.

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