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# Fermentation microbiome and metabolic profiles of Indian palm wine

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ABSTRACT

Fermented food and beverages provide huge benefits to humans. The nutritionally rich palm wine (toddy) is a popular fermented beverage in India. The present study reveals the bacterial diversity and metabolic profile of Indian palm wine using next-generation sequencing of the V3-V4 regions of the 16S rRNA gene. The metagenomic sequencing reveals the dominance of the phyla *Proteobacteria*, *Firmicutes*, and *Tenericutes* in the Indian palm wine. Bacteria such as *Acetobacter*, *Lactobacillus*, *Candidatus phytoplasma*, and *Gluconobacter* were abundant in palm wine. The sequence-based metagenomics approach revealed that *Acetobacter* sp. and *Lactobacilli* sp., which are beneficial bacteria, were the most predominant microbial populations in the Indian palm wine. The metabolic functional profile of the palm wine microbiome was studied based on gene ontology terms to identify industrial by-products and bio-prospecting genes. Metabolic profiling revealed that a major microbial population was involved in ammonia oxidation, sulfate reduction, nitrite reduction, atrazine metabolization, and acid production. The results can aid in developing probiotics from palm wine for human consumption with a multitude of health benefits.

## 1. Introduction

Fermentation is one of the oldest practices, as old as humanity itself, which dates back to the Neolithic period (Motlhanka et al., 2018). Fermented foods and beverages are known to be a microbial community hub, which can improve intestinal permeability, help maintain a balanced gut microbiota, and ultimately improve the consumer's brain health (Navarro et al., 2016; Hiippala et al., 2018; Bell et al., 2018). Fermented food and beverages are the results of microbial fermentation, which convert the raw food both biochemically as well as organoleptically into an improved and healthier product containing aromatics, organic acids, alcohols, and many other compounds which provides nutritional benefits to the consumer (Campbell-Platt, 1994; Steinkraus, 1997; Tamang et al., 2016; Motlhanka et al., 2018). Fermentation lowers the number of toxic compounds such as phytic acids, tannins, etc. and also improves the shelf-life of the food (Sharma et al., 2020). According to recent studies, the ecological aspects of the microbial community influence its metabolic activities and, ultimately, the composition of the fermented product (Escalante et al., 2015; Astudillo-Melgar et al., 2019).

Palm wine is a popular traditional alcoholic beverage consumed throughout the world, particularly in Asia, Africa, the Caribbean, and South America (Herzog et al., 1995; Amoikon et al., 2020). Palm wine is known by various names all over the world, such as "Toddy" in India, "*kallu*" in South India. In India, Palmyra palm wine, Silver date palm wine, and Coconut palm wine are widely consumed (Akinrotoye and Kehinde, 2014; Astudillo-melgar et al., 2019; Chandrasekhar et al., 2012). Palm wine is rich in nutrients like vitamins which improve eyesight, gastrointestinal tract health. In addition, it has been used in various social and religious ceremonies and prayers (Chandrasekhar et al., 2012). Palm wine is produced from the fermented sap of palm trees, the most common is the coconut palm (*Cocus nucifera*). It is produced by two different processes, either from the young inflorescence by tapping (making an incision on the bark about 15 cm of the trunk's apex) the live standing tree and inserting a tube to collect the sap or by chopping the tree before tapping (Chandrasekhar et al., 2012). Palm wine is made from sap, which is a clear, colourless, and delicious liquid. Upon fermentation, the sap becomes milky white and effervescent, whereby the sugar content gets reduced into alcohol and other metabolites which make up the palm wine (Chandrasekhar et al., 2012;

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Karamoko et al., 2016; Obire, 2005).

As soon as the sap is collected from the plant, the fermentation in palm sap begins, within an hour, the alcohol content shoots up to 4%, making it an estimable substrate for microbial growth (Chandrasekhar et al., 2012). The presence of acetic acid bacteria (AAB), yeasts, and lactic acid bacteria (LAB) such as *Zymomonas* and *Leuconostoc* causes lactic, alcoholic, and acetic acid fermentation in palm sap (Alcántara-Hernández et al., 2010). *Leuconostoc mesenteroides*, *Lactobacillus plantarum* (Amoa-Awua et al., 2007), *Lactobacillus nagelii*, and *Lactobacillus sucicola* were the most prevalent LABs found in palm wine (Alcántara-Hernández et al., 2010). The aroma of palm wine is caused by *Saccharomyces* sp., naturally occurring yeast found in fermented palm sap (Aidoo et al., 2006; Uzochukwu et al., 1999). Moreover, the inclusion of different volatile chemicals such as alcohols, esters, organic acids, aldehydes, and ketones gives palm wine its distinct aroma (Santiago-Urbina and Ruíz-Terań, 2014).

Since the fermentation of various food and beverages is a complicated phenomenon that involves a huge population of microbial consortia, it is crucial to study the microbiota of the fermented products (De Filippis et al., 2017). Palm wine offers an array of health benefits, making it an interesting and considerable beverage whose microbiota is worth studying. Previous studies have utilized microbiological techniques to investigate the microorganisms found in palm wine and have found that it has antibacterial properties against a few infections (Ojo and Agboola, 2019). Culture-based techniques cannot reliably identify the sequence-structure-evolutionary mechanism of unknown species. Therefore, the metagenomic approach is an advanced tool that can be used to understand the microbial community's evolutionary footprint present in the environmental samples. Thus, the current study reveals the microbiome profile of *Borassus flabellifer* palm wine derived from Puducherry, India's southernmost state, using both culture-dependent and culture-independent approaches.

## 2. Materials and methods

### 2.1. Sample collection

The fermented palm wine samples were collected in sterile bottles in the early morning on December 28, 2018, from three visibly healthy coconut palms located (Latitude and Longitude: 11.9416′N, 79.8083′E) in the outskirts of Puducherry, India, based on the accessibility of production sites. Three palm wine samples were collected directly from the producers and stored in ice and transported to the laboratory in the cold chain for analysis. For culture-independent analysis, each sample was centrifuged for 50 ml at 12,000 ×*g*, and the pellets were washed thrice with phosphate buffer saline (PBS) under pH 6.4 and stored in −80 °C.

### 2.2. Isolation and biochemical characterization of bacteria from palm wine

The palm wine samples were serially diluted to $10^6$ and plated on Luria-Bertani agar (Himedia) and incubated at 37 °C overnight. After incubation, the total colony forming units (CFU/ml) were calculated using the plate count technique, and colonies showing visibly dissimilar morphologies were sub-cultured and maintained in Luria-Bertani agar (Himedia) for further studies. The isolates were also streaked on TCBS agar to detect the presence of *Vibrio* sp. Biochemical assays were performed based on Bergey's manual of systematic bacteriology (Bergey and Holt, 1994). The isolates were tested for Gram's staining, and biochemical tests such as IMViC, mannitol motility, triple sugar iron, and catalase test were also performed (Tang and Stratton, 2006; Winn et al., 2006).

### 2.3. Antibiotic sensitivity assay

The antibiotic sensitivity patterns of the isolates were examined using the Kirby-Bauer disc diffusion assay. The isolates were incubated in nutrient broth overnight at 37 °C and 100 μl of culture was swabbed on the Mueller-Hinton agar (Sigma, Switzerland) and antibiotic discs (Himedia) were positioned on the agar surface. The antibiotic discs included Ampicillin (10 μg), Tetracycline (30 μg), Erythromycin (15 μg), Ceftriaxone (30 μg), Penicillin G (10 U), Chloramphenicol (30 μg), Gentamicin (10 μg), Cefpodoxime (10 μg), Vancomycin (30 μg), Norfloxacin (10 μg), Nalidixic acid (30 μg), Polymyxin B (300 μg), and Ceftazidime (30 μg). The plates were then incubated at 37 °C for 24 h, and the diameter of the zones of inhibition around each disc was measured, and the results were interpreted based on CLSI guidelines (Wayne, 2006).

### 2.4. Metagenomic DNA isolation and 16S rRNA gene amplification

The ZR Soil Microbe DNA kit was used to extract DNA from all three samples according to the manufacturer's instructions. Briefly, 200 μl of the pellet was re-suspended in PBS, 650 μl of lysis solution, and 2% *v*/v of proteinase K solution was added to the ZR Bashing beads and incubated for 30 min. This setup was secured in a bead beater fitted with a 2 ml tube holder assembly and processed at maximum speed for 10 s, followed by centrifugation at 10,000 ×*g* for 1 min. 400 μl of the supernatant was transferred into another tube and centrifuged at 8000 ×*g* for 1 min, into which 1200 μl of DNA binding buffer was added. 800 μl of the mixture was then transferred into another tube and centrifuged at 10,000 ×*g* for 1 min. The DNA was then eluted and used for further analysis. The quantity and purity of the isolated DNA were analyzed using a NanoDrop at A 260/280, (NanoDrop ND-1000, USA), and the DNA integrity was confirmed by 1% agarose gel electrophoresis (AGE). The DNA was stored at −20 °C until further processing. 40 ng of extracted DNA was used for PCR amplification of the V3-V4 16S rRNA ribosomal gene (Supplementary Table S1). PCR was done using 2 μl genomic template DNA; 0.5 mM of each deoxynucleotide, 5 μl 10× PCR buffer, 3.2 mM $MgCl_2$, 10 pM of primer, 1 U Taq DNA Polymerase and 37.1 μl autoclaved distilled water (all the reagents were purchased from Invitrogen Corporation, Carlsbad, CA, USA). The mixture was then subjected to initial denaturation at 95 °C for 3 min followed by 25 cycles of denaturation at 94 °C for 15 s, annealing at 60 °C for 15 s and elongation at 72 °C for 2 min and a final extension at 72 °C for 10 min and kept at 4 °C. The purity and quantity of the PCR products were analyzed with a NanoDrop at A 260/280, (NanoDrop ND-1000, USA) and separated by AGE. Finally, all the libraries were subjected to sequencing by Illumina MiSeq.

### 2.5. Metagenomic analysis

The next-generation sequencing analysis of V3-V4 regions of the 16S rRNA gene was carried out using GAIA 2.0. This analytical method allows to execute genus and species-level identification. The study is proposed by comparing sequence similarity search of the 16 s RNA gene against Green genes (DeSantis et al., 2006) and SILVA (SSU) V138 databases (Yilmaz et al., 2014). We predicted the genus-phylum based classification of the selected three toddy microbiome sample (TodMic1, TodMic2, and TodMic3) referred to as the accession (PRJNA602592, PRJNA603438, and PRJNA603440). Alpha and Beta diversity index were calculated using various methods (Itskovich et al., 2021; Prathiviraj et al., 2021). The operational taxonomic unit (OTUs) was predicted among three TodMic samples based on genus-level. Metabolic profiles of each sample were predicted using Gene Ontology (GO) terms, which were then contrasted for an improved understanding of the microbial community.

## 3. Results

### 3.1. Isolation and biochemical characterization of bacteria from palm wine

The palm wine samples plated after serial dilution showed 26 colonies with different morphology on incubation at 37 °C. Most of the isolates showed circular, entire margins with different shades of white color (Supplementary Fig. S1). Of the 26 isolates, 22 were Gram-positive, 4 were Gram-negative, and most of the isolates were rod-shaped (Supplementary Table S2-S5). The biochemical test and other assays indicated the presence and abundance of *Acetobacter* sp. Also, most isolates were sensitive to antibiotics tests that showed the absence of pathogenic strains and proved the sterile collection method.

### 3.2. Analysis of basic properties

The microbiome of the fermented palm saps were analyzed and sequenced by Sanger Illumina 1.9. The result reveals that a total of 25,880, 21,704, 29,704 untrimmed reads with sequence lengths ranging from 8 to 21,304, 8–17,460, 1–17,460 for TodMic1, TodMic2, and TodMic3, respectively. Whereas 23,060, 18,206, 19,625 trimmed residues with sequence lengths ranging from 501 to 19,672, 501–14,205, 503–14,205 were present for TodMic1, TodMic2, and TodMic3, respectively (Table 1; Supplementary Fig. S2). Overall, 54% of guanine and cytosine was found in all three samples, which determine the convergence of nucleotide base (Itskovich et al., 2021; Prathiviraj et al., 2021).

### 3.3. Analysis of diversity and disparity index

The analysis of microbial species richness was analyzed using Simpson, Shannon, and Chao1 value index, which reflect the alpha diversity in microbial communities (Itskovich et al., 2021; Prathiviraj et al., 2021), displayed significant variances between all three palm wine samples (Table 2). TodMic2 and TodMic3 had similar species richness, whereas, TodMic1 exhibited the least diversity with the least observed OTUs. TodMic3 displayed the highest evenness among species. The beta diversity analysis showed significant between TodMic1 and TodMic2 and moderate diversity between TodMic1 and TodMic3, whereas the least differences in the diversity between TodMic2 and TodMic3. Whereas, the genomic correlation of beta genetic diversity among three samples showed that, TodMic1 has comparatively diverged with TodMic2 and TodMic3. The correlation diversity value occurred in the range between 0.061 and 0.078. TodMic2 and TodMic3 were closely related, and the correlation between these two samples occurs in 0.078 (Table 3). The overall base-pair quality of the sequences occurred in the lengths ranging from 8 to 19 and further, the standard deviation bar graph of individual samples reveals that base pair quality may be extended up to 3–28 (Supplementary Fig. S3).

We found three major distributions of sequence base-pair length (A, T, G, C) in the position of 100–550 bp, 1000–2000 bp, and 2500–3500 bp (Supplementary Fig. S4). This distribution in subsequences occurs due to the overlapping capability in the samples (Gentleman and Mullin, 1989). It states that some sequence fluctuation may occur in those positions, and it transmits one species to another during evolution in the diverse environmental niche. A solid small RNA adapter was used to sequence from the fragmented DNA. The adapter is a short set of DNA fragments that helps identify the adapter content in each genome to make the process easier by sequencing the sample named "tagmentation" (Turner, 2014). Once the genomes were sequenced the adapter was trimmed off. In all three samples, the sequence length distribution of adapter content is roughly 1000 base pairs, while their concentration in terms of sequence length varies between 0.017 and 0.023 (Supplementary Fig. S5).

### 3.4. Taxonomic classification

The difference in microbial composition between the three palm wine samples was also analyzed by comparing the microbial abundance and predominance at genus and phylum taxonomic levels (Fig. 1a). The overall predominant bacterial phyla present in all the palm wine samples were *Proteobacteria* (91.6%), *Firmicutes* (5.6%) and *Tenericutes* (2.6%). Whereas the genus level classification shows *Acetobacter* (~90%), are found to be abundance in all the three samples (Fig. 1b).

### 3.5. Analysis of relative abundance from OTUs

The most richness of OTUs in three samples was grouped and clustered using the heat map to identify the overriding bacterial species (Fig. 2). TodMic1 cluster showed the highest relative abundance by *Gemmatirosa*, *Erythrobacter*, *Bacillus*, *Aciditerrimonas*, *Arcobacter*, *Gaiella*, etc. Whereas, TodMic2 cluster was abundant in *Halophaga*, *Candidatus*, *Acidobacterium*, *Gluconacetobacter*, etc. TodMic3 cluster mainly comprises *Dechloromonas*, *Desulfuromonas*, *Hydrogenophaga*, *Burkholderia*, *Acinetobacter*, *Gemmatimonas*, *Conexibacter*, *Acidovorax*, *Citrobacter*, *Enterobacter*, etc. The results indicated that the palm wine microbiota comprises potential probiotic strains. We further classified the top 10 best enriched OTUs found between TodMic1, TodMic2, and TodMic3 samples based on their metabolic features (Fig. 3; Supplementary Fig. S6). We found that *Acetobacter* was predominant (90%) in the samples. Whereas, remaining 10% of enriched OTUs were *Lactobacillus*, *Candidatus*, *Gluconobacter*, *Burkholderia*, *Clustoridium*, *Oenococcus*, *Zymomonas*, *and Enterobacter* species. These probiotic bacteria can act as beneficial partners in human gut ecosystems, hence boosting the overall health and immunity of the host.

### 3.6. Analysis of metabolic features

The functional metabolic features in the microbial community of palm wine were predicted using GO terms (Fig. 4). The most abundant microbes were ammonia oxidizers (89.8%), followed by sulfate reducer (85.4%), nitrite reducer (84.2%), nitrogen fixers (82.6%), atrazine metabolizing organism (82%) and acid producers (81.9%). The metabolic profiling of individual samples was represented in (Supplementary Fig. S7).

## 4. Discussion

Palm wine is a naturally fermented beverage consumed by various people globally (Amoikon et al., 2019). Palm wine is one of the most popular alcoholic beverages among lower socioeconomic groups in various countries, and it also has a place in folklore medicine. Since it is consumed without further treatments, it becomes quite important to

**Table 1**
Predicted basic features amplicon region among selected three different toddy microbiome samples TodMic1, TodMic2 and TodMic3.

| Samples | SRA Accession No. | Untrimmed | | Trimmed | | Mean GC | Encoding |
|---|---|---|---|---|---|---|---|
| | | Total # of residues | Sequence range | Total # of residues | Sequence range | | |
| TodMic1 | PRJNA602592 | 25,880 | 8–21,304 | 23,060 | 501–19,672 | 54 | Sanger/Illumina 1.9 |
| TodMic2 | PRJNA603438 | 21,704 | 8–17,460 | 18,206 | 501–14,205 | | |
| TodMic3 | PRJNA603440 | 29,704 | 1–17,460 | 19,625 | 503–14,205 | | |

**Table 2**
Predicted α-diversity index among selected three different toddy microbiome samples TodMic1, TodMic2 and TodMic3.

| Samples | Observed | Chao1 | Se. Chao1 | Shannon | Simpson | Fisher |
|---|---|---|---|---|---|---|
| TodMic1 | 102 | 102 | 0 | 0.81431 | 0.27908 | 13.73453 |
| TodMic2 | 110 | 110.2308 | 0.58765 | 0.89022 | 0.30487 | 15.56962 |
| TodMic3 | 110 | 110 | 0 | 1.10752 | 0.3945 | 15.37968 |

**Table 3**
Predicted β-diversity index among selected three different toddy microbiome samples TodMic1, TodMic2 and TodMic3.

| Samples | TodMic1 | TodMic2 | TodMic3 |
|---|---|---|---|
| TodMic1 | 0 | 0.078 | 0.061 |
| TodMic2 | 0.078 | 0 | 0.018 |
| TodMic3 | 0.061 | 0.018 | 0 |

know the microbial composition and diversity along with the metabolic profile of the existing microbiota for the safety of the consumers and the quality of the beverage (Djeni et al., 2020). Even though the culture-dependent technique provides cultivable microbes for further analysis, it is a quite tedious and laborious technique and also has a demerit of inability to obtain the data regarding the uncultivable microbes. However, the culture-independent technique uses high-throughput technology to analyze the entire microbial population and abundance of each species in the consortium. The metagenomic approach is user friendly and less laborious technique that enables the study of uncultivable organisms and their metabolic profile in a time-saving manner.

Here we have studied the composition and diversity of the microbiome of naturally fermented alcoholic beverage palm wine collected from the outskirts of Puducherry, India. The culture-based method revealed the presence of 26 colonies with different morphology and

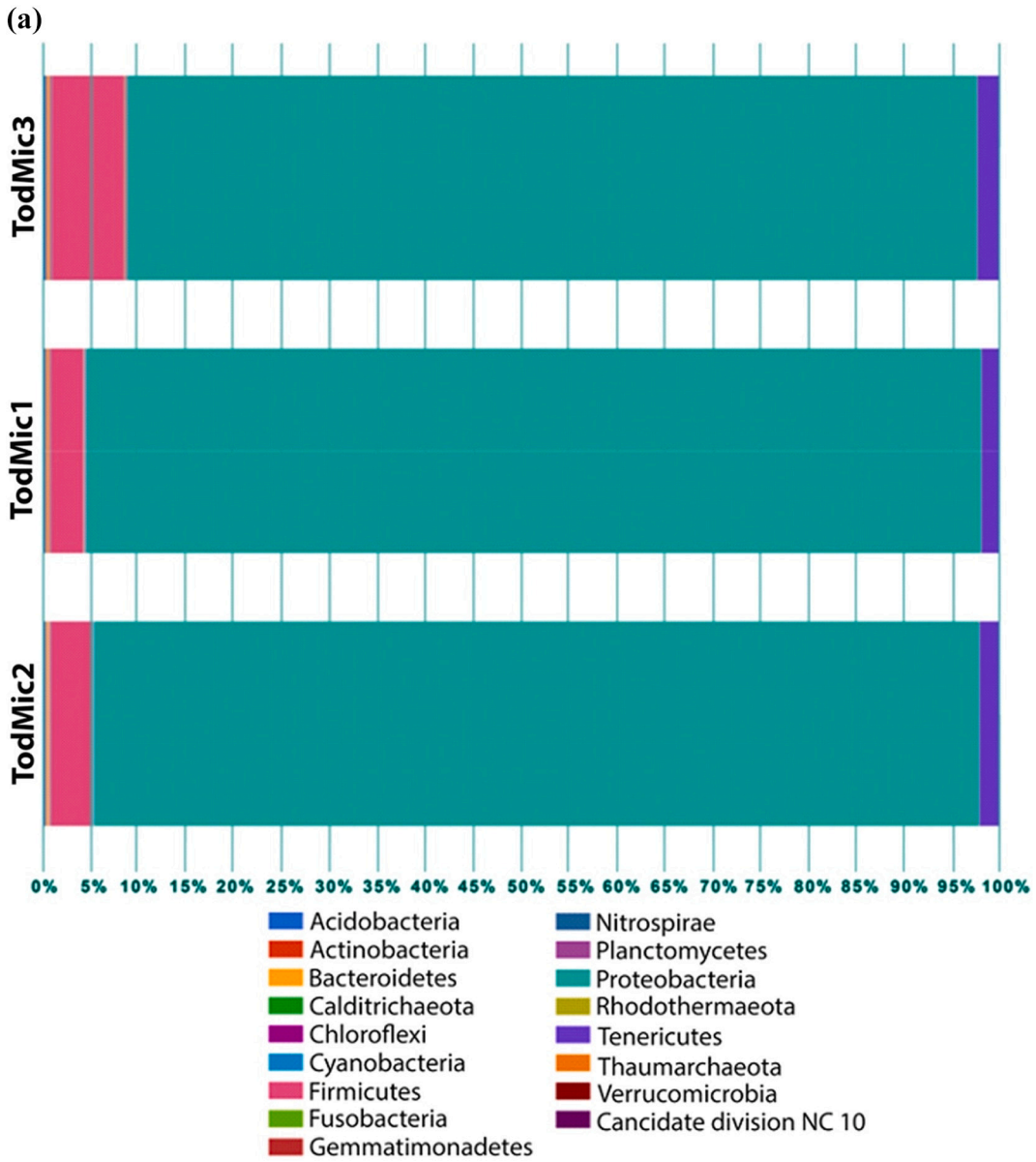


**Fig. 1.** Construction of taxonomic plot analysis phylum (a) and genus level (b) upon TodMic1, TodMic2 and TodMic3 samples.

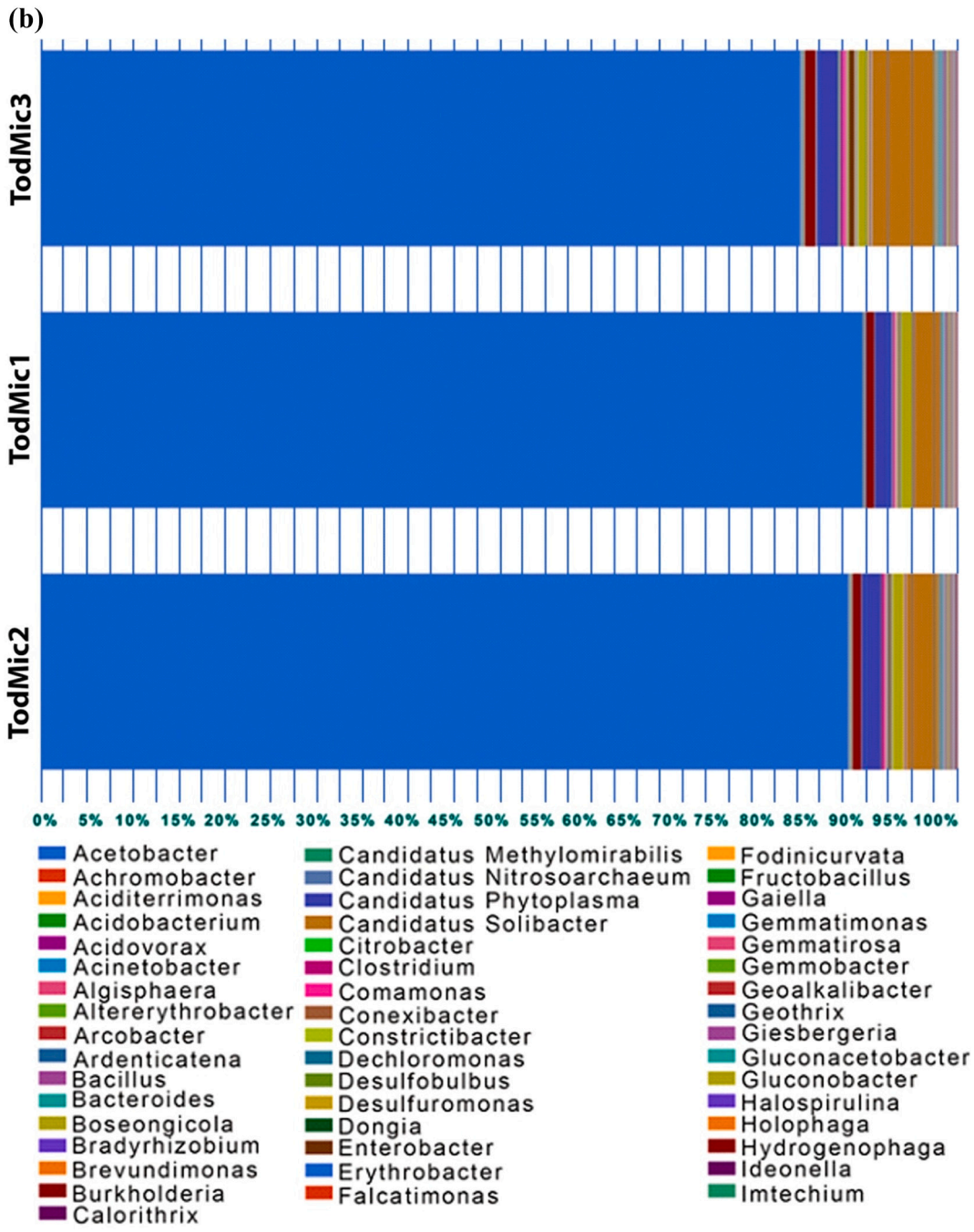


**Fig. 1.** (*continued*).

biochemical characteristics. Also, the results revealed the absence of any antibiotic-resistant strains in the palm wine, indicating the absence of any potent pathogens or contaminants in the sample. The high throughput next-generation sequencing showed that the overall predominant bacterial phyla present in the three types of palm wine were *Proteobacteria* (91.6%), *Firmicutes* (5.6%), and *Tenericutes* (2.6%), which is in agreement with the results reported by Djeni et al., 2020. In the study of microbial diversity in fermented palm saps from three different palm species (*Raphia hookeri*, *Elaeis guineensis*, *Borassus aethiopum*) in Côte d'Ivoire where the *Firmicutes* (68.8%) and *Proteobacteria* (32.6%) were abundant phyla (Djeni et al., 2020). In the present study, phyla *Proteobacteria* including *Acetobacter* (89.6%), *Gtuconobacter* (1%), *Burkholderia* (1%) and *Pelobacter* (0.3%), phylum Firmicutes represented mainly by *Lactobacillus* (4.6%), *Candidatus Phytoplasma* (1%) and *Clostridium* (1%) were abundant. Similar results were obtained by Astudillo-Melgar et al. (2019) during the study of bacterial diversity and dynamics during the production of Tuba palm wine in Guerrero Mexico. The results showed that the predominant bacterial population in tuba palm wine was LAB (*Fructobacillus*, *Leuconostoc*, and *Lactococcus*) and AAB (*Gluconacetobacter* and *Acetobacter*) and *Proteobacteria* (*Vibrio*) (Astudillo-melgar et al., 2019). The presence of LAB and AAB in fermented food and beverages prevent the spoilage of the food product and invasion of many foodborne pathogens due to the production of acid (Amoikon et al., 2019).

Acetic acid bacteria isolated from Iranian traditional curd and yogurt was reported to have potential probiotic activity as well as anti-cancer effect (Haghshenas et al., 2015). *Lactobacillus*, *Acetobacter*, and *Gluconobacter* were predominant genera in this study were belong to potential

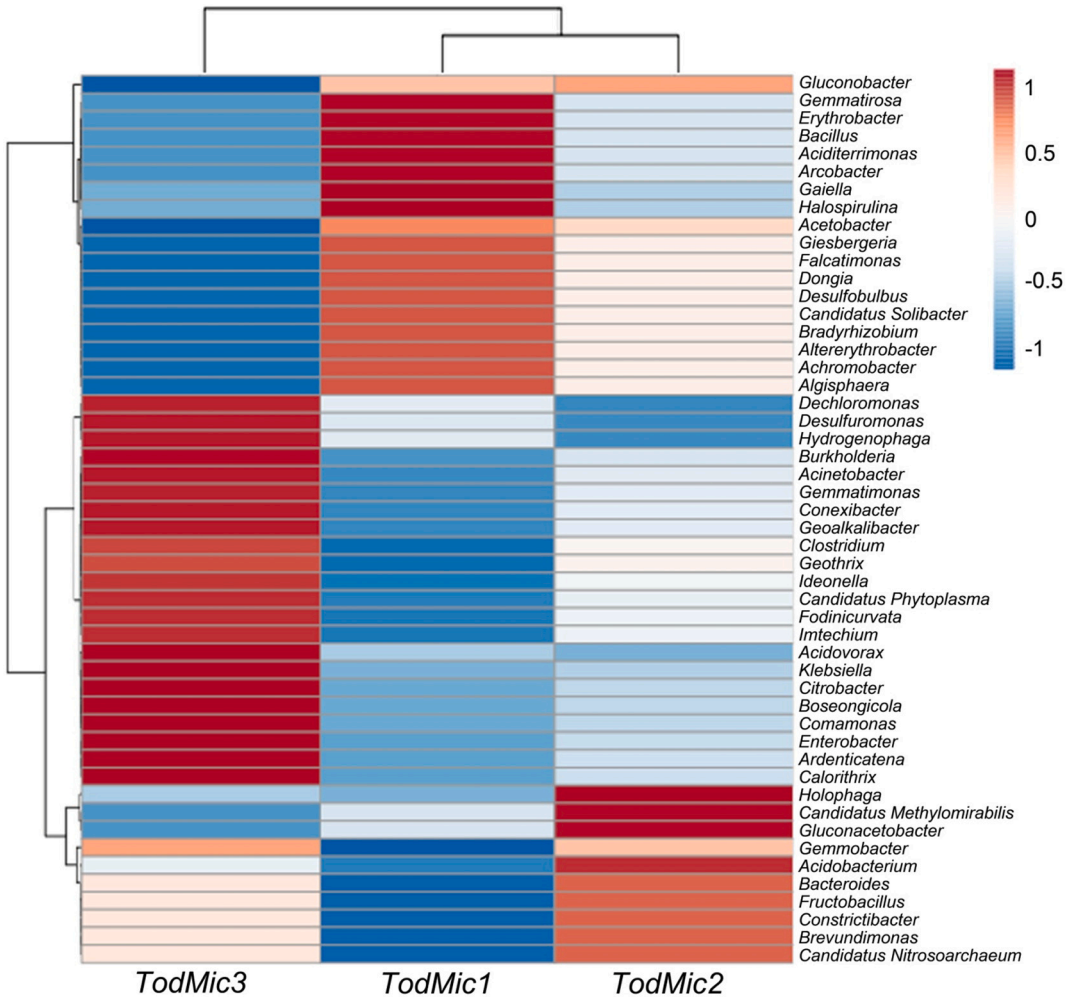


**Fig. 2.** Comparison of Heat map analysis for the involvement of the key species found between TodMic1, TodMic2 and TodMic3 samples.

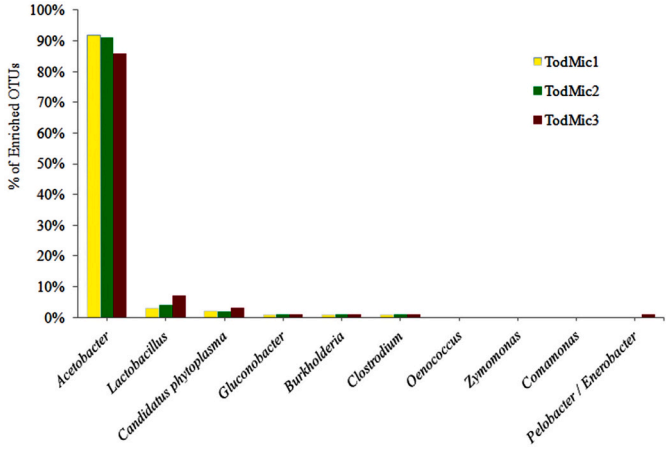


**Fig. 3.** Top hit enriched OTUs predicted from TodMic1, TodMic2 and TodMic3 samples based on its metabolic features.

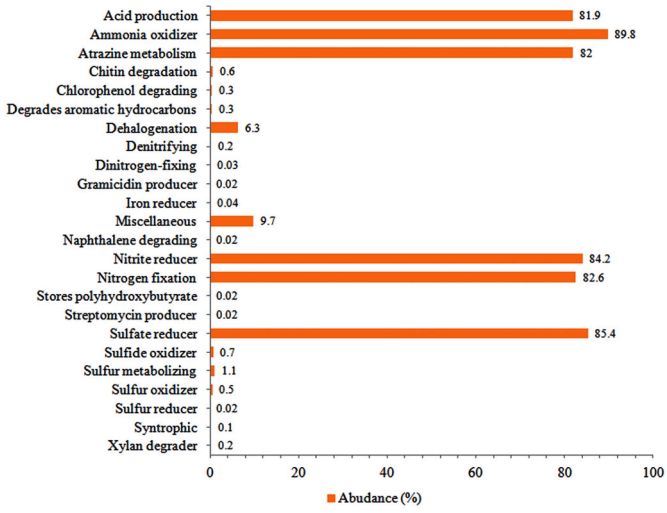


**Fig. 4.** Predicted metabolic features at pathway-level found between TodMic1, TodMic2 and TodMic3 samples.

probiotics in various other fermented food products like chhurpi, churkam, dahi and gheu/mar in the North-eastern part of India as well (Shangpliang et al., 2018). The global probiotics market potential showed a steady increase to 15 billion USD per year with an annual growth rate of 7% (Van den Nieuwboer et al., 2016). Probiotics like *L. bulgaricus*, *Lactobacillus delbrueckii* and *Streptococcus thermophiles* were known to reduce lactose intolerance in humans (Kechagia et al., 2013). Probiotics are capable of suppressing the proliferation of various disease-causing organisms. They can control pathogens by producing a variety of antimicrobial compounds like bacteriocins, lactic, and acetic

acid (Spinler et al., 2008). Probiotics are being innovated as therapeutic interventions and rebiosis of the healthy microbiome for humans (Aresti Sanz and El Aidy, 2019; Rajeev et al., 2021; Adithya et al., 2021). The microbiome-assisted design and development of probiotics would be a breakthrough in discovering interventional probiotics including probiotics in cognitive health (Mohammadi et al., 2016; Cheng et al., 2019). Metabolic profiling revealed that a major microbial population was involved in ammonia oxidation, sulfate reduction, nitrite reduction, atrazine metabolization, and acid production. The results can aid in developing probiotics from palm wine for human consumption with a multitude of health benefits.

## 5. Conclusion

A metagenomic study plays a major role in better understanding the species diversity among the microbial community present in the environmental samples. In this study, we have provided the first ever report on the microbial diversity and metabolite profile of naturally fermented palm wine from Puducherry, India. Here we studied the alpha and beta diversity of palm wine microbiota using a metagenomics approach using 16S amplicon sequencing to analyze the various microorganisms present and compared it with the culture-dependent approach. The knowledge of microbial composition and diversity helps in knowing the health benefits obtained by consuming palm wine and utilizing the microbes for the large-scale production of certain useful metabolites. Also, potential probiotic strains can be isolated from palm wine and used for therapeutic purposes, preventing harmful chemical drugs.

## CRediT authorship contribution statement

**R. Prathiviraj & Riya Rajeev**: Performed the analysis and preparation of the draft manuscript, **Chris Maria Jose**: Collected samples and performed experimental analysis, **Ajima Begum**: Investigation. **J. Selvin**: Supervision. **G. Seghal Kiran**: Conceptual, Writing- Reviewing and Editing.

## Declaration of competing interest

The authors declare that no competing interest in the present manuscript.

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## Appendix A. Supplementary data

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