The forgotten wine: understanding the fermentation and composition of palm wine

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Abstract

Palm wine is an alcoholic beverage that has existed for centuries and has important economic and socio-culture values in many tropical and sub-tropical countries. Palm wine is made by spontaneous fermentation of palm sap by naturally occurring microbial communities, which determine product quality. Defining the core microbial communities driving the fermentation process is pivotal for the distinctive of palm wine characteristics; however, it is also challenging due to micro and macro-ecological factors, which contribute to geographic specificity. A dynamic consortium of microbial species occupies every stage of palm wine fermentation and consequently releasing metabolites to trigger growth of other associated species. Studies have been conducted to investigate palm wine composition and microbial diversity but these studies and have not been extrapolated to understand the function of microbial communities and metabolite diversity. In this review, we gather information of microbial communities and metabolite profiles from 47 published studies, covering a wide range of methodologies and regions to better understand the causal links between the principal microbial species and the metabolites of palm wine. We address palm wine quality across production regions to provide specific regional information to elevate our knowledge of this fermented beverage. This understanding will help to manage the causal effects of palm wine fermentation and define the regional signature of palm wine to help with the challenge of ensuring product quality in this unique, yet overlooked, fermented beverage.

Keywords: fermentation, metabolite signature, microbial community, palm wine, wine specificity

1. Introduction

Microbial communities are the main factor to reveal fermented beverage characteristics, attributed to chemical release as a results of ecological interactions (1–3). Other contributing factors to the determination of beverage sensory characteristics are regional variations of plant species and cultivar, genetic diversity of plant and microbe, which are expressed by the metabolic profile of the end product (4,5). We know that there are dynamic complex interactions, which impact upon the product quality and have been a major challenge for product development (6). Setting a biogeographical approach to understand and define the distinctiveness of fermented beverages will preserve the sensory diversity and increase the product value (4). This is an important concern to protect designations of origins (PDOs) and geographical indication (GIs) of fermented beverages, that have a significant impact in economic aspect of the product (7,8).

Palm wine is less acknowledged compared to the better-known fermented beverages made from grapes and rice. Palm wine is extremely important in many tropical countries as a traditional alcoholic beverage, contributing to local economy and with distinctive impacts upon social culture (9–12). Palm wine production is performed as a traditional practice and is treated differently based on its origin, which leads to distinctive regional variation. The production of palm wine relies on native microbial communities, which are likely have

adapted to local biogeographical constraints to conduct the fermentation (13). Some microbial species (including yeasts) have evolved to occupy a niche to engage with a wider range of ecological interactions (14). However, biotic and abiotic factors can specifically modify microbial community structure (15), and drive the differentiation of evolutionary traits and chemical release of the principal fermentative species, *Saccharomyces cerevisiae* (16). Understanding biogeographical ranges of microbial communities will contribute to the comparison of global populations, especially on domestication trajectory of palm wine's principal species (17–19) and gain cultural traction by being associated with the regionality of palm wine from topical countries.

Spontaneous fermentation of palm wine demonstrates dynamic nature and changing occurrence of fermentative and non-fermentative microbes, which can lead to flavour formation. Studying microbial ecology is important to conceptualize a fermentation model for developing a consistent beverage product (20). However, reports of palm wine ecology, especially on comprehensive microbial and metabolite profiles covering biogeographical perspective are limited. Compared to wines made from grapes and rice, the microbial ecology of palm wine study has not been intensively conducted to examine regional typicity. This scant information results in gaps for data comparison and general strategies for palm wine fermentation linked to the natural environment. Gathering and compiling recent studies can construct a general pattern of palm wine fermentation. For example, comprehensive studies of microbial communities and regional characteristics of grape wine have helped understanding of how the fermentation technique and ecological factors influencing product specificity (4,16). Examining palm wine microbial ecology across tropical areas will give new insights into the range, activity and formation of yeast and bacterial communities in sap from palm trees.

The important links of compromised microbial composition and metabolic properties to develop and preserve traditional fermented product are essential to better understand palm wine. This review focuses on the principal microbial communities and chemical compounds, that represent the characteristics of palm wine linked to ecology and geography, that influence the specific profiles for wine. We begin by discussing the distinctive composition of palm wine and the biogeographical areas of palm wine production. We explain the contribution of ecological factors on the fermentation process and how they affect palm wine sensory by collating the information present in published studies and examining them together. We conclude by examining the influence of local cultural practices on palm wine, followed by suggestions for directions in product development.

2. The distinctive composition and flavour of palm wine

Grapes and rice wines are the most known types of fermented beverages across the world and play an important part in social and economic development of many countries (4,21). Meanwhile, palm wine from topical countries is largely unknown. Palm wine is a traditional alcoholic beverage in Africa, south Asia, southeast Asia, and central America (11). Palm wine is derived from palm sap, which is tapped form the blossom or apical structure of palm tree (10,22). The fresh sap drips from the cutting part with slightly white turbid colour and moderate sweetness (23), containing sugars (predominantly sucrose) (24,25). In grapes, fructose and glucose predominate (26) and a crushing step is needed to release these sugars from the grapes to initiate the fermentation process. Rice requires extensive processing before starch conversion is ready to ferment (27). In contrast, palm sap can be directly fermented after tapping without any pre-processing steps.

Palm sap is a versatile commodity from palm trees, that can be transformed into further derivative products (**Fig. 1**). The fresh sap can be directly consumed and has various beneficial metabolites, including organic acids (24,28–30), vitamins (31,32), proteins (30),

phenolics (33), and minerals (31). A shift from sugar fermentation to acidic fermentation generates a variety of derivative products, such as palm sugar, alcoholic beverages, and palm vinegar (25,32,34,35). The fresh sap can be refined to obtain palm sugar and left naturally at room temperature to produce palm wine. Palm wine typically has shelf life only for 2-3 days of fermentation with alcohol content similar to beer (up to 6% v/v ethanol). Before a subsequent acidic fermentation, palm wine can be distilled to produce spirits, which has more than 40% ethanol (v/v) (36). A longer fermentation generates organic acids as a source to produce a palm vinegar. In all cases, the typical fermentation is conducted by palm's natural microbial community without addition of cultured microbes and in general swift and dynamic fermentation process occur (9,10).

3. Biogeographical perspectives of palm wine

Palm tree distribution across the sub and tropical countries is related to palm wine making practice. The utilization of specific palm species for palm wine making and the ecological factors exposure can mediate microbial ecology, which determines the distinctiveness of palm wine sensory attributes. Limited studies have been performed to establish and define palm wine regional typicity and so we have compiled recent studies to construct a clear picture of palm wine practices. Here, we have collated data from 47 studies, specifically focused on microbial and biochemical diversity topics within various approaches (**Supplementary Fig. S1**). Based on our compiled studies, palm wine has been studied across three continents over 14 tropical and subtropical countries (**Fig. 2A**). More than half of the studies was conducted in Africa, with the most studies in India. Each continent has specific palm species, utilized for palm wine making; *Nypha* sp. in Asia, *Acrocomia* sp. in Central America, *Elaesis* spp. and *Raphia* spp. in Africa. Of the studies collated, 17 focussed on description of the microbes present, 7 on the small molecules, which are microbially derived and likely to be sensorially active and 23 studies combined these approaches (**Fig.2B**).

Palm species can contribute to the regionality of palm wine characters, which are also attributed into a traditional name. In Burkina Faso and Cote d'Ivoire, palm wine is widely known as *Bandji* (37,38); *Mimbo* in Cameroon (20,39); *Akpeteshie* in Ghana (40); *Toddy* in India (41); *Tuak* in Indonesia (12,42); *Taberna* or *Tavern* in Mexico (11,43); *Ogogoro* in Nigeria (44); *Lambanog* in Philippines (45); *Ra* in Sri lanka (20); *Songkhla* in Thailand (24); *Lagmi* in Tunisia (46).

3.1 Macro-ecology affects palm wine signatures

Environmental variables have a significant role on palm sap production and characteristics (47). Although it may be less appreciated, environmental factors contribute to the palm physiology, which can directly affect the sap yield and physicochemical characters, inducing the microbial communities, and alter the fermentation process. Astudillo-Melgar et al. (13). believed that microbial diversity is correlated to biogeographical factors from where palm wine is produced and adapted with specific ecological variables. Factors such as climate, weather, palm species, microbial vector, and tapping process may not work independently to alter the microbial composition, but often exert an integrated effect. Therefore, impacts will be discussed as an important aspect to taking further action on expected mitigation for product development.

3.1.1 Biogeographical locality

Although palm is mostly observed in coastal area of tropical and sub-tropical countries (48), the variety of local factors could also impact the diversity of microbial community. Barata et al. (49) emphasised that microbial diversity is relied on climatic condition, temperature, sunlight exposure, wind, and rainfall where the plant origin, indicating the sign of terroir.

Environmental factors have been observed on their influence for plant and soil-microbes association (15); however, there is a lack information on arboreal microbes, correlated to palm sap tapping. A study by Ziadi et al. (47) reported that sap production and physicochemical characters are significantly influenced by tapping season. Higher sugar content and less acidic are characterized from palm sap in warmer seasons, which have more sunlight exposure to increase palm photosynthesis and thus sugar content. Microbial counts are slightly higher, which is less affected by the warmer temperature. The fluctuation of microbial occurrence in a specific region is altered by rainfall although a consistent pattern are not shown (49). The variety of regional factors and microbial characteristics determine how a microbial species might adapt to those specific niches. In conjunction to the local climate and specific biogeographical factors, there are very limited studies which might help to determine the regional typicity of palm wine. It is likely that these factors are important as the interplay among environment, plant species, and winemaking practice impacts the microbial populations and their metabolism and contributes to formation of the final product characteristics, reflecting a fermented beverage product's origin and terroir (2,4,16).

3.1.2 Palm diversity

Palm species are a critical aspect that contribute to the differences of palm sap characteristics and thus flavour. There are more than 10 species of palm trees, that have utilized for making palm wine (22). As showed in **Fig. 2C**, palm species are established and well-adapted to local biogeographical characteristics. For example, *Elaensis* and *Raphia* palm species are used in Africa but unrecorded in both Asia and America. Palm tree specificity can be considered using chemical analysis of the sap where each palm species likely has different composition and quantity of macro and micronutrient, contributing to the growth of microbial communities (31,50). This concords to a unique microbial composition in each palm species (10,25,29), which depends upon geographical location (9,10,19,25). Although a general pattern might be showed by each palm species, that generally the fermentative species, *S. cerevisiae*, conquers to all palm sap niches. The diversity differentiation likely occurs in non-*Saccharomyces*, determining the flavour complexity. This variation indicates that palm species genetic diversity and the influence of geographical locality are the significant factors to determine palm wine specificity. These processes and the collated data from our survey are explained in the following sections.

3.2 Introduction of microbes into palm sap

Palm sap is believed in a sterile condition upon collection and microbial communities are inoculated through insect visitation and the tapping process (24,51,10). Insects and microbes have an intimate relationship with plants, signalling symbiotic associations to help them detecting nutrient, protecting from pathogens, and as parasites (52,53). Insects find sugar source through the detection of released volatile compounds by plants (52,54). Palm sap is rich in sugars, which attract bees and other insects to the collected sap and can be observed floating in the liquid and visiting the collection vessels. Honeybees seek sugary elements of plants, and then acts as pollinator while vectoring microbes (55). Wasps and vinegar flies are often observed in sugar-rich environments in other fermentations (56,57). The close relationships of palm sap and insects reflect the vital role of microbial vectors to contribute to the palm wine flavour characteristics. On the other hands, artisanal processes can also contribute to the introduction of microbial communities. Since the tapping process is carried out with a traditional way, and without deliberates sanitation, the possibility of microbe introduction is inevitable and may be from the collection container, human hands, and cutting equipment such as knives. Microbial loads in palm sap can be influenced by a perpetual tapping practice, which can reduce up to 25% (47). Factor of slicing stress during the tapping process is likely related to the decrease of palm sap nutritive value after 10 weeks consecutive tapping and impacts to microbial load. The decrease of microbial loads directly impacts to the fermentation process, affecting the quality and stability of final

product. It is likely that the tapping process is a crucial management for product hygiene and sap production sustainability.

4 How does the nature of palm wine fermentation contribute to the construction of wine flavour?

The nature of palm wine fermentation is extremely fast and complex, involving sugars accessibility (10,58). Spontaneous fermentations allow all natural microorganisms to compete organic resources without deliberate addition of selected yeast strains. The limitation of the fermentation environment is one of significant factor to alter microbial interactions and ecological dynamics (59,60). As a result, a change in microbial structure is often observed along the fermentation process. Here, to see microbial diversity and dynamic along the fermentation process, we reanalysed next generation sequencing (NGS) data of 7 abstracted studies with further data from Sumerta et al. (61); (**Supplementary Table S4**). We subsequently selected several studies by inclusion criteria, representing a vast diversity change in 24 hours fermentation (**Fig. 3A & 3B)**.

Comparison within country or region, type of sample, and some time frames are less informative because of the limitation in comparable parameters, such as research focus, methodology, and data distribution. Since palm wine fermentation is swift, the species loss of fermenting microbial communities is seen within 24 hours (**Fig. 3A)**; demonstrated by the decrease in Shannon index during fermentation (0, 12, and 24 hours of fermentation). Higher diversity is observed in early stage of the fermentation and decrease to the following process (62). Nwachukwu et al. (63) used isolation methods and found a diversity loss because of succession of some microbial species. Djeni et al. (50) reiterated that microbial diversity loss was due to a unique inhabitant species in every stage of palm wine fermentation, that dominant growth.

The relative abundance of bacterial and fungal amplicons from next generation sequencing and collated demonstrate that while the initial microbial populations may be maintained for 12 hours, the dominance of *Lactococcus* and *Saccharomyces* is evident (**Fig. 3B**). There are 10 studies that describe a collapse of one microbial group in every stage of palm wine fermentation (**Supplementary Table S6**). Microbial species fluctuate over 24 hours fermentation of palm wine (**Fig. 3B**). The decrease of *Leuconostoc* and the growth of *Lactococcus* present in early stage, with a concurrent drop in *Hanseniaspora* species occurrence and the increase of *Saccharomyces* species. A shift between *Saccharomyces* and non-*Saccharomyces* is inevitable in every stage of the fermentation (50,58,63,64). This succession of microbial composition over the fermentation process is identified as a key feature to determining palm wine characteristics (50).

4.1 *Saccharomyces cerevisiae* is prominent in palm wine fermentations

In a natural fermentation, the complex microbial interactions may result in the dominance of certain species. We sought to find the microbial species most regularly associated with palm fermentation Through the comparison of a conventional microbial isolation and species inferred from amplicon barcodes, we selected data of top 10 abundance of culturable species (CD) (**Supplementary Table S1)** and NGS profiling (CI) (**Supplementary Table S4)**. We found the general pattern of microbial composition in palm wine with the presence of both principal yeast species and principal bacterial genera, which are *S. cerevisiae* and *Leuconostoc*, respectively (**Fig.3C**). Both of methods confirm that the role of *S. cerevisiae* and *Leuconostoc* and this contributes to more than 40% of the total microbial abundance. Some species that do not present in one of those methods may relate to the limitation of each method. Meanwhile, as described in previous studies, *S. cerevisiae* is dominant in all fermentation stages while *Leuconostoc* fluctuates during the final stage (9,50). The principal species may dominant for the primary product, but non-fermentative or non-*Saccharomyces* species enriches the sensory outputs for fermented beverages more broadly (65,66).

4.1.1 What circumstances allow for dominance of microbes?

The role of the key yeast species on producing ethanol as the primary product is pivotal in palm wine fermentation. Some bacterial species are reported to produce ethanol, such as *Zymomonas* spp. (62), but production is less effective than *S. cerevisiae.* The fermentation process is driven by *S. cerevisiae* in the production of many beverages, as this yeast is able to readily transport sugars, other carbohydrates are hydrolysed and various compound are produced and released. Some of the produced compounds can inhibit other species and the others yet may display e synergistic actions to adapt with the change of ecological factors during the fermentation process (67,68). This often leads to the dominance of certain species in a complex spontaneous fermentation of alcoholic beverages of which *S. cerevisiae* in the prime example (66,69,70).

S. cerevisiae is widely regarded as the most tolerance species to ethanol, acidity, and physical interactions (71–74). Perrone et al. (69) suggested that its dominancy is triggered by the occurrence of other species, driving various mechanisms to suppress non-*Saccharomyces*. A regulatory mechanism of its alcohol dehydrogenases (*ADH*) genes controls the ethanol production and at the same time can recover energy when the ethanol excess (75). *ADH1* gene regulates the fermentation process to produce ethanol, while *ADH2* gene is responsible to transferring energy from ethanol conversion. Non-*Saccharomyces* species are relatively vulnerable and non-competitive to the alcohol and other environmental factors (74). *S. cerevisiae* may secrete compounds, such fungicide like mycosin and perform cell-contact abundance and triggering to the death of other species in mixed culture fermentation (76,77). Albergaria et al. (78) found that the 2-10 kDa size of peptides secreted by *S. cerevisiae* can inhibit the growth of *Kluyveromyces marxianus, Kluyveromyces thermotolerans, Torulaspora delbrueckii* and *Hanseniaspora guilliermondii*. The type of cell-to-cell contact and antibiotic production mechanism can also result in the death of certain species (76). Meanwhile, cell-to-cell contact induces the metabolites properties of the species and affect cell viability in late stage of the fermentation (66,77). However, physical contact is not the major factor to decrease the presence of non-*Saccharomyces* and confirmed that the metabolites produced by *S. cerevisiae* mostly sharps the non-*Saccharomyces* population (77). With the efficiency of energy use, less osmotic stress, high ethanol production, tolerant to lower pH, and enable to inhibit other species, *S. cerevisiae* often survives until the final stage of fermentation (19). It is likely that many of these characteristics are also true of *S. cerevisiae* found in palm wine environments, but they have not been directly shown.

4.1.2 Diversity of *Saccharomyces* and the implications for palm wine fermentations

S. cerevisiae is a model species for genomics and plays a pivotal role in many food systems, having been selected, adapted, and well domesticated across human history (79–82). Peter et al. (83) described that the highest variation in *S. cerevisiae* genomes is correlated to the wider differences of phenotypic characters, and it is these characters that are responsible for the signature and originality of fermentation products. The evolutionary process of *S. cerevisiae* at genome level can be modified by human interferences, and the yeasts adapt to various growth conditions, alter phenotypes, and change reproductive mode (84,85). In natural conditions, the population structure of *S. cerevisiae* is primarily shaped by ecology (86). *S. cerevisiae* evolution can be triggered by its respond to ecological interactions in harsh fermentation environments (1).

Spontaneous fermentation on fermented beverage making has been reproducibly conducted and if it affects on microbial diversity loss, this potentially leads to a species domestication (87). Interaction with the natural environment is often possible, where new strains may contribute, and experience variable abiotic conditions (80,84). Legras et al. (88) stated that a rich environmental condition, geographical condition, and repetitive use in the same

condition results in gradual genotypes evolution, species distinction, and suggest local domestication pattern. However, spontaneous fermentation of palm wine is still argued to generate domestication and leaved as an open question (89). Some reports released that *S. cerevisiae* population of African palm wine is admixed compared to global references, showing a unique signature relatively to different continents, niches, and favour strain migration through human interference (18,19). Tra Bi et al. (19) showed that the genetic relationship of *S. cerevisiae* in palm wine is significantly related to ecological niches and sharing the similar geographical origin generates less genetic diversity. A local domestication may be attributed to *S. cerevisiae* from palm wine strains, which are observed as homozygous strains (18,90).

4.2 Interactions amongst microbes in fermentation

We conducted a network analysis of the co-occurrence of species groups from compiled studies which used culture-dependent methods to assess microbial diversity (**Fig. 4**). The contribution of *Saccharomyces* is dominant and acts as a central hub to other species group in palm wine fermentation. It also has a strong relationship to other yeast genera (*Hanseniaspora, Candida*, and *Pichia*) and the core bacteria in organic acids production, such as *Lactobacillus*, *Leuconostoc*, and acetic acid bacteria (AAB). These show a vital connection pattern of those microbial groups on constructing palm wine characters and suggest a fermentation model retrieved from multi-biogeographical studies. This pattern reveals a network of microbial ecology, and reveals potential microbial interactions which may be able to predict the occurrence of unwanted species (91).

In spontaneous fermentation, interactions have a significant role on driving the fermentation process, involving various microbial groups. Interactions among microbial species may deliver positive and negative impacts, which determine the product formation (92–95). In spontaneous fermentations, synergistic interactions among different species mediate tolerance to the robustness of dynamic condition in particular level. Mutualism and commensalism interaction are attributed to the synergistic interaction with cross-feeding mechanism or supporting certain metabolite producer (3). For instance, yeasts ferment the sugar into ethanol while acetic acid bacteria convert the ethanol into acetic acid which is not affect the yeast (96). Lactic acid bacteria and yeast sometimes support each other by exchanging some metabolites for their metabolism (3). Each group of microbial species has different way to develop its functionality by interacting with other species. Fleet (68) highlighted the interaction among yeast species contributes to the fermentation behaviour while yeast-bacteria interactions determine the ecological dynamic. This interesting feature of complex microbial communities interaction can be proposed as new model of the fermentation to create flavourful product (67). Specific interactions between microbes have not been described in a palm wine environment, but they are likely to occur.

4.3 The implications of metabolite release on fermentation dynamics

The associations of microbial communities and chemical release have a major contribution on constructing palm wine characteristics. A wide range of microbial groups occupies in every stage of the fermentation process but following the depletion of sugar in the fermentation process, microbial diversity decreases because of biochemicals alteration and ecological interactions. Here, we abstracted 10 studies (**Supplementary Table S6**), exploring both in microbial communities and chemical composition along the fermentation stages, representing palm wine fermentation dynamics and summarised in **Fig. 5**. The abundance of ethanol is likely attributed to the presence of *Saccharomyces* yeasts during fermentation. Lactic acid bacteria (LAB) and acetic acid bacteria (AAB) grow on palm wine fermentation related to the significant number of organic acids in final stages of fermentation (38,97–99). Total phenolics and flavonoids impact shifts in microbial community composition through the fermentation process (58). We presented the examples of chemical yield in the table, which represents the gradual change in line graph. It is important to note that chemical

content of palm wine ultimately depends on, geographical location, palm species, and the way analytical process and research design conducted, so the results vary among studies. By summarising related studies, the general pattern was demonstrated to provide a better understanding of palm wine fermentation.

We simulated the co-occurrence of microbial groups and compounds based on the correlation analysis of each microbial group follows the biochemical pattern (**Fig. 6**). Data was summarised from the frequency of microbial groups and metabolite components presented in each study. Lactic and acetic acid production in the final stage of palm wine fermentation positively corelate to the frequency of lactic acid and acetic acid bacteria group while *Saccharomyces* and *Candida* group may also have similar contribution. These compounds reduce the pH and alter the microbial diversity. Since pH decreasing, the evaporation of volatile fatty acids is possibly high (100). Meanwhile in alcohol production, non-*Saccharomyces* yeasts have a negative correlation compared to bacterial groups and *Saccharomyces*. This simulation provides the influence of metabolite components on the composition of microbial diversity, which can demonstrate the fermentation dynamics.

5 The intersection of culture on palm wine production

The process of palm wine making is still performed in traditional ways from tapping process to the fermentation. Depend on palm species, tapping process can be conducted through destructive and non-destructive methods (10). In West Africa, destructive tapping process is mostly observed by notching or perforating the apical meristem, often resulting in the death of the tree. The widely used method is non-destructive by cutting the inflorescence and the sap drips from cutting tip to the collection container (25). The collected palm sap is then processed into various products for daily consumption or sold. For some areas, this activity is the main job of local communities and maintains economic stability in many villages.

The use of palm sap and/or wine has an important role as part of culture and tradition (12). Palm spirits can be used as part of wedding ceremonies, event celebration, welcoming rituals, and religious rituals. In some tropical countries, palm sap products are also responsible for ethnomedicines. Anthropologists have acknowledged that palm wine is important as stimulant, depressant, and part of traditional medication, well-written in traditional transcripts (101). Recent scientific reports also suggested that palm sap/wine compounds have health benefits, related to the empirical thoughts of local people, such as decrease diabetes risk, antioxidant, antibiotics, anaemia treatment, and immunomodulators (22,31,102–105). Palm wine contains phenolic compounds that may contribute to antioxidant activity in the plasma (22,33) and modulate the growth of gut microbiota (106–108). A probiotic-type microbiome that benefits for digestive system is also found in fresh palm sap (64) and fermented sap showed bioactive chemical activities (109). Despite the significance of pharmacological and ethnomedicinal utilization, basic information on microbial community structure and dynamic of metabolite profile benefits to the traditional thoughts and practices that may evolve driving regional identity.

6 The future of palm wine and derivatives in modern food systems

Understanding microbial ecology and controlling microbial composition are a pivotal aspect to the beverage quality and a major challenge for future product development (6). A rough and inconsistent characteristic of beverages results from spontaneous fermentations and it is difficult to control the product quality and consistency. By the application of defined starter culture, more consistency, efficiency, and desire characters of the alcohol products are achieved; however, the product might lack complexity of organoleptic characteristics (82). The presence of spoilage bacteria is inevitable amid a spontaneous fermentation. Spoilage bacteria, for example lactic acid and acetic acid bacteria, can compete for nutrients and produce lactic and acetic acids which limit the ethanol production during the fermentation

process (110). Intervention at harvesting can obtain higher ethanol production before the spoilage bacteria rapidly conducts the acidic fermentation.

As palm wine is product of spontaneous fermentation and has demand in local communities, preserving the product and maintaining the product quality and stability are the major challenge to bring this beverage to a global market. Palm wine has a swift fermentation for alcohol and organic acids that the selection of fermentation time can help to obtain the best yield. However, many ecological factors in palm productivity, season, tapping process, and microbial composition may create unstable product quality and quantity. Defining processing solution and while maintaining palm wine regional distinction will stimulate local economies and support maintaining traditional practices.

Mimicking the natural fermentation in the laboratory from raw materials to environmental conditioning can support product quality and stability at an industrial scale. Indeed, alcoholic fermentation development begun from spontaneous fermentation, evolving to current commercial practices with selected yeast strains (82,111). Procedures could adapt by shifting the fermentation practices from natural fermentation to the use of defined starter to maintain the sensory characters by mixing microbes together in a starter culture. The mixed cultures can provide a broader profile of aroma and flavour than using single culture starter, at least in grape juice fermentations (112,113). Using non-*Saccharomyces* associated with *S. cerevisiae* is a growing trend in the fermented beverage industry (67). Non-*Saccharomyces* play a significant role on constructing the product value, acting as a co-culture to support the fermentation process (65) and their metabolic releases might be adjusted through the mixed fermentation (67). We recognise that there may be limitations have to further action as there is a need to retain and foster traditional food products, which may at odds with the use of commercial starter cultures.

7 Conclusions

Palm wine fermentation is challenged by many factors, which contribute to differences of product composition and distinction. The main actor is the microbial communities, which affect palm wine composition, metabolic release, and genetic diversity to drive the fermentation process and determine product characteristics. Environmental factors are an additional aspect of typical raw material, collection and tapping strategy, then biogeographical location leads to the product specificity. The interplay of those factors contributes to the construction of palm wine regional signature, fostering local product quality into a global economic quality. We support further actions to strengthen the fundamental understanding of palm wine production and here we have provided an overview of the challenges for sustainable product development and appreciating a local knowledges and traditions.

Supplementary materials

Supplementary Fig. S1 Literature searching and data variability of retrieved studies
Supplementary Table S1 Data of included studies in microbial diversity
Supplementary Table S2 Data of included studies in metabolite profile
Supplementary Table S3 Data of studies both in microbial diversity and metabolite profile
Supplementary Table S4 Abstracted studies conducting NGS method
Supplementary Table S5 Abstracted data of studies in frequency and occurrence of microbial groups
Supplementary Table S6 Abstracted studies representing fermentation stages

Conflict of Interest

Authors declare no conflict of interest

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Author contributions

INS: research design, data compilation and analysis, and writing the manuscript
XR: data analysis supervision and review the manuscript
KH: research design supervision, writing, and review the manuscript

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771

772

Figure legends

Fig. 1 Schematic to describe the processing of palm sap with its derivative products. Created with BioRender.com

Fig.2 A survey of palm wine studies which include measures of microbial ecology and metabolite profiling (n= 47), details are available on **Supplementary Table S1 & S2**. A) Country distribution of scientific studies in both microbes and metabolites across continents; B) The Venn diagram shows the focus of compiled scientific studies; C) Proportion of the studies of palm species for all compiled studies.

Fig 3. Microbial dynamics and community proportion of palm wine fermentation. Next generation sequencing (NGS) data of 7 abstracted studies with data from Sumerta et al. (2024); **Supplementary Table S4**) were analysed together. A) Microbial diversity loss (measured as Shannon index) over 24 hours palm wine fermentation (Wilcoxon test; p-value <0.05); B) Change in top 10 abundance of microbial species in 24 hours palm wine fermentation. C) The proportion of top 10 microbial species, obtained by CD (inner circle; n =33) compared to CI (outer circle; bacteria n=7-1, excluded due to technical limitation; fungi n = 5).

Fig 4. Network analysis of the relationship of microbial group in palm wine fermentation. The contribution of each group is represented as an edge. Different colour showing different microbial group (blue= yeasts, red= bacteria), then different size of font represents the abundance value. The data set used for this study consists of 23 studies based on the abundance and frequency each species group in **Supplementary Table S3**, omitting 7 studies of NGS, where data was abstracted in **Supplementary Table S5** and used R studio adopting the codes by Schweinberger (2024).

Fig. 5 Schematic of the process of palm wine fermentation which summarises the microbial and chemical composition, dynamics of microbial communities, raw materials, and metabolites over time. A gradual pattern of palm wine fermentation was reconstructed from compiled studies (n= 10, **Supplementary Table S6**) and table shows the examples of chemical yield during the fermentation process, created with BioRender.com.

Fig. 6 Correlation heatmap between microbial and metabolite groups (n= 23-3, studies which used amplicon sequencing were disregarded). The frequency of microbial and metabolite groups were abstracted from **Supplementary Table S3** and analysed with Spearman correlations (p value > 0.05).

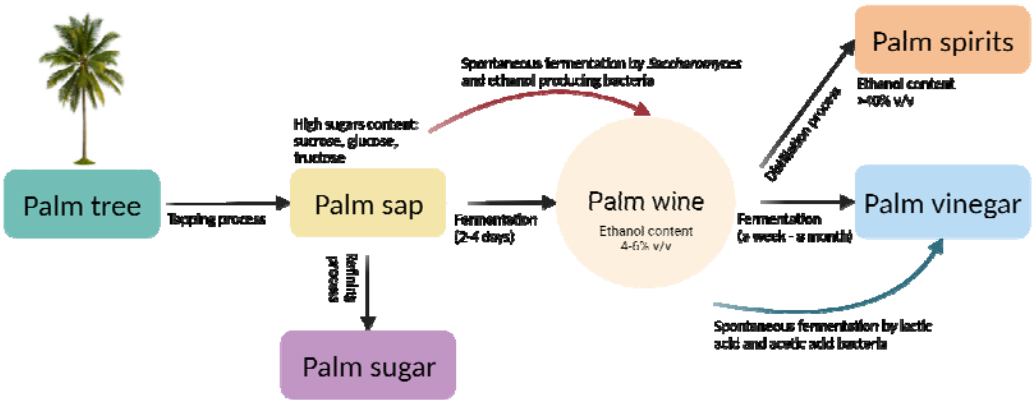


Figure 1

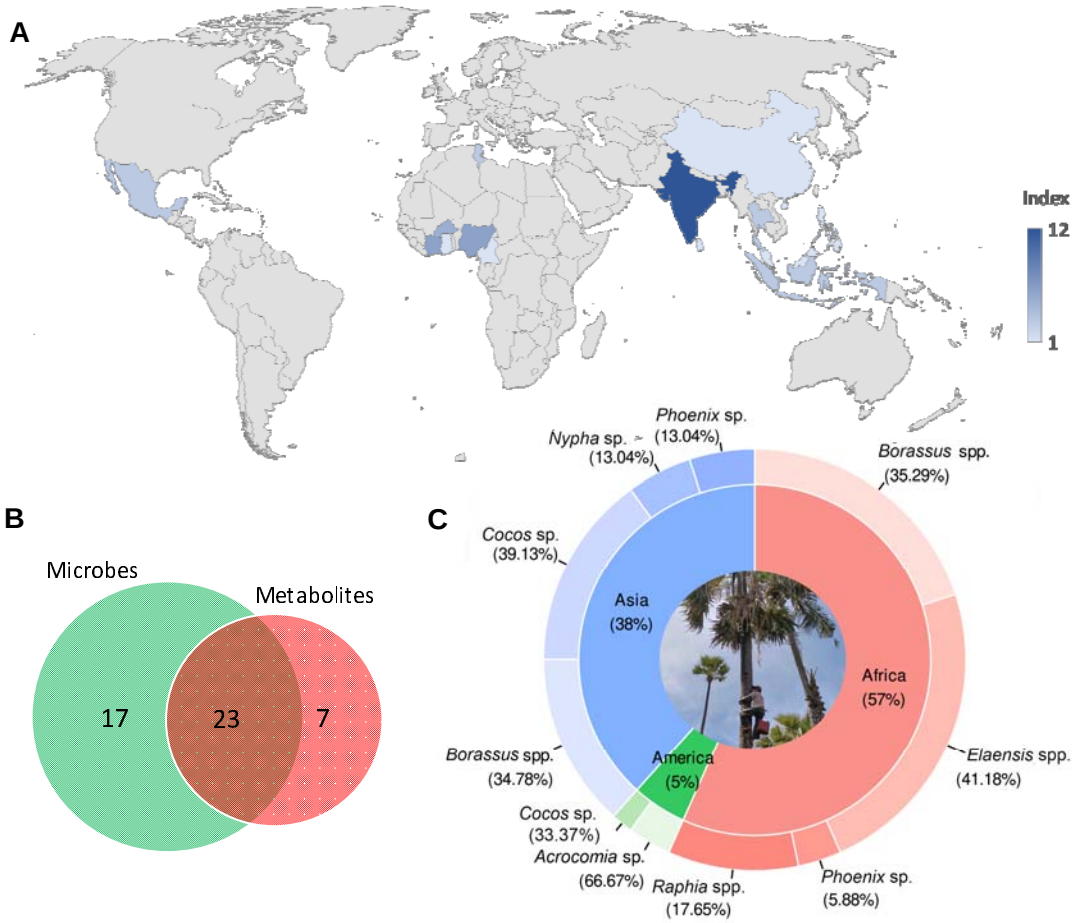

A
Index
12
1
B
Microbes
Metabolites
17
23
7
C
Phoenix sp.
(13.04%)
Nypha sp.
(13.04%)
Borassus spp.
(35.29%)
Cocos sp.
(39.13%)
Asia
(38%)
Africa
(57%)
Borassus spp.
(34.78%)
America
(5%)
Elaensis spp.
(41.18%)
Cocos sp.
(33.37%)
Acrocomia sp.
(66.67%)
Raphia spp.
(17.65%)
Phoenix sp.
(5.88%)

Figure 2

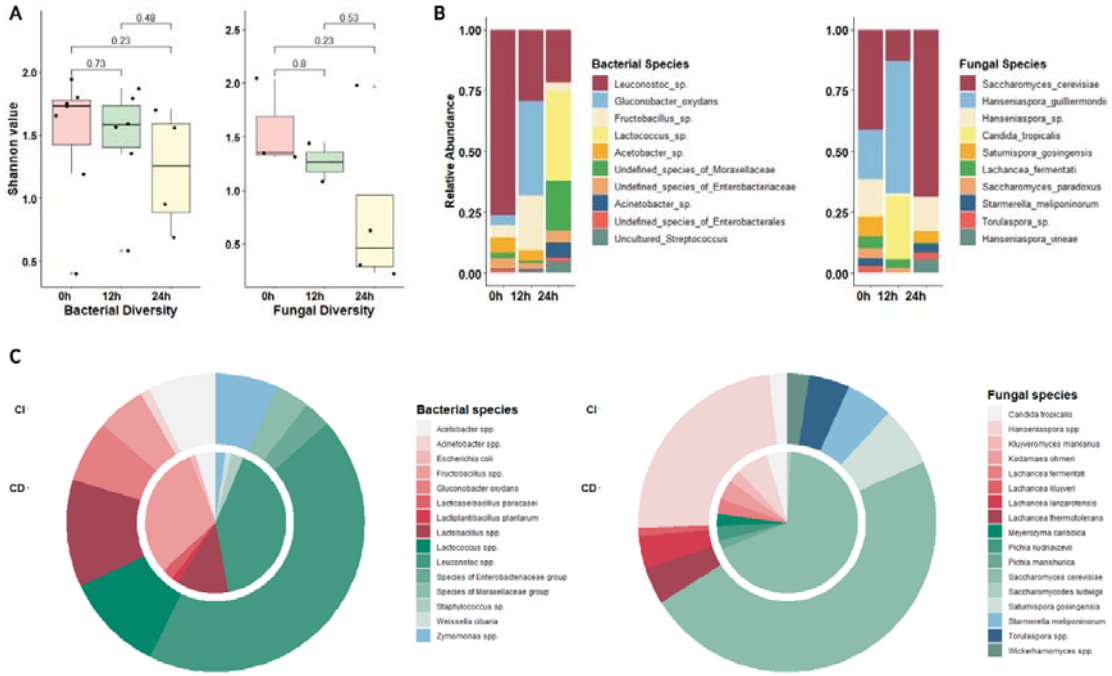

A
Shannon value
0.49
0.23
0.73
0h
12h
24h
Bacterial Diversity
0.53
0.23
0.8
Fungal Diversity
B
Relative Abundance
Bacterial Species
Leuconostoc_sp.
Gluconobacter_oxydans
Fructobacillus_sp.
Lactococcus_sp.
Acetobacter_sp.
Undefined_species_of_Moraxellaceae
Undefined_species_of_Enterobactaceae
Acinetobacter_sp.
Undefined_species_of_Enterobacterales
Uncultured_Streptococcus
Fungal Species
Saccharomyces_cerevisiae
Hanseniaspora_guilliermondii
Hanseniaspora_sp.
Candida_tropicalis
Saturnispora_gosingensis
Lachancea_fermentati
Saccharomyces_paradoxus
Starmerella_meliponinorum
Torulaspora_sp.
Hanseniaspora_vineae
C
CI
CD
Bacterial species
Acetobacter spp.
Acinetobacter spp.
Escherichia coli
Fructobacillus spp.
Gluconobacter oxydans
Lacticaseibacillus paracasei
Lactiplantibacillus plantarum
Lactobacillus spp.
Lactococcus spp.
Leuconstoc spp.
Species of Enterobacteriaceae group
Species of Moraxellaceae group
Staphylococcus sp.
Weissella cibaria
Zymomonas spp.
Fungal species
Candida tropicalis
Hanseniaspora spp.
Kluyveromyces marxianus
Kodamaea ohmeri
Lachancea fermentati
Lachancea kluyveri
Lachancea lanzarotensis
Lachancea thermotolerans
Meyerozyma caribbica
Pichia kudriavzevii
Pichia manshurica
Saccharomyces cerevisiae
Saccharomycodes ludwigii
Saturnispora gosingensis
Starmerella meliponinorum
Torulaspora spp.
Wickerhamomyces spp.

Figure 3

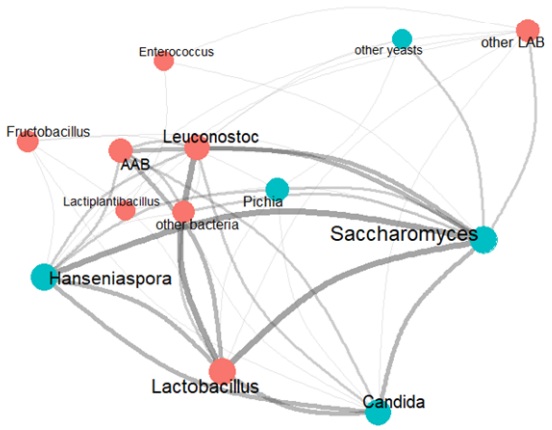
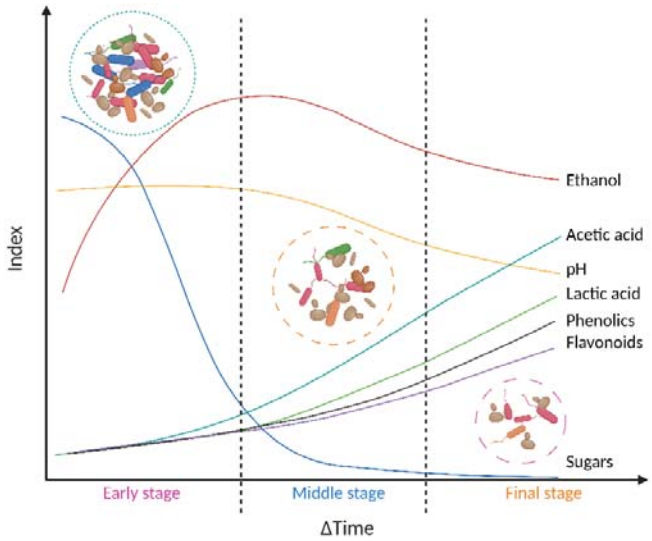
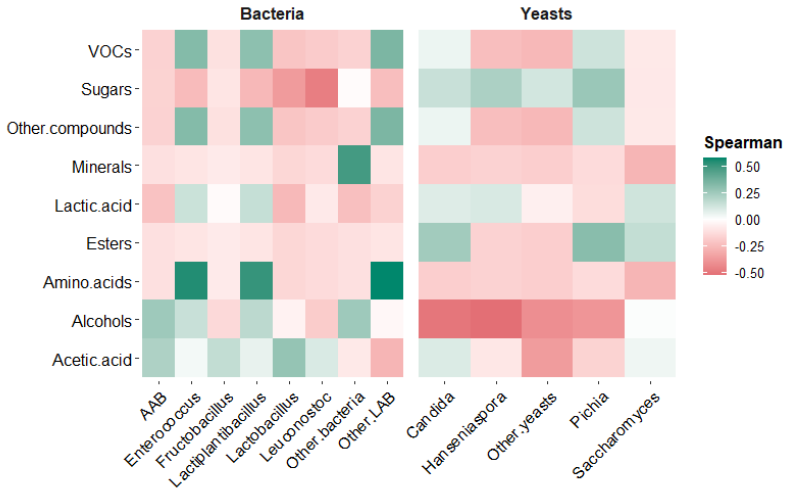

Enterococcus
other yeasts
other LAB
Fructobacillus
Leuconostoc
AAB
Lactiplantibacillus
Pichia
other bacteria
Saccharomyces
Hanseniaspora
Lactobacillus
Candida

Figure 4



Criteria	Early	Middle	Final	Reference
Total Sugars	11%	5%	3%	Amoa-Awua et al., 2007
Ethanol	34 g/L	35 g/L	30 g/L	Tapsoba et al., 2016
Acetic acid	0.50%	0.60%	3%	Amoa-Awua et al., 2007
Lactic acid	0.20%	0.30%	2.80%	Amoa-Awua et al., 2007
pH	4.38	3.54	3.53	Alcantara-Hernandez et al. 2020
Total Phenolics	70 mg/L	100 mg/L	150 mg/L	Das & Tamang 2023
Total Flavonoids	40 mg/L	90 mg/L	150 mg/L	Das & Tamang 2023

Figure 5


Bacteria
Yeasts
VOCs
Sugars
Other.compounds
Minerals
Lactic.acid
Esters
Amino.acids
Alcohols
Acetic.acid
AAB
Enterococcus
Fructobacillus
Lactiplantibacillus
Lactobacillus
Leuconostoc
Other.bacteria
Other.LAB
Candida
Hanseniaspora
Other.yeasts
Pichia
Saccharomyces
Spearman
0.50
0.25
0.00
-0.25
-0.50

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