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

One sentence summary: review and synthesis of microbial ecology and metabolites in palm wine fermentation across geography and their contribution to cultural food systems

I Nyoman Sumerta[1,2], Xinwei Ruan[1], and Kate Howell[1]*

[1]School of Agriculture, Food and Ecosystem Sciences, Faculty of Science, The University of Melbourne, Victoria 3010, Australia

[2]National Research and Innovation Agency (BRIN), Jakarta 10340, Indonesia

***Corresponding author**: Kate Howell, khowell@unimelb.edu.au

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. Lesser known than other types of wines, palm wine is made by spontaneous fermentation of palm sap by naturally occurring microbial communities. The palm sap ecosystem has unique microbial composition and diversity, which determines the composition of the eventual wine and is likely affected by geographical distinctiveness. While these features are well understood in grape and rice wine, these features have not been understood in palm wine. In this review, we gather information of microbial communities and metabolite profiles from published studies, covering a wide range of methodologies and regions, to better understand the causal links between the principal microbial species and major metabolites of palm wine. We assess palm wine quality across production regions and local practices to provide general characteristics of palm wine and identify specific regional information. These will provide better understandings to the function of microbial communities and metabolite diversity, the contribution of regional variations and to ensure product quality in this important and widespread, yet overlooked, fermented beverage.

Keywords: fermentation, metabolite profiling, microbial ecology, palm wine, traditional beverages, wine variety

1. Introduction

Fermenting microbial communities form beverage aromas and flavours, by release or transformation of chemical compounds in the substrate, creation of small molecules during microbial metabolism and as a result of ecological interactions (Conacher et al., 2021; Liu et al., 2019; Smid & Lacroix, 2013). Other contributing factors to the determination of beverage sensory characteristics are regional variations of plant species and cultivar, genetic diversity of plant and microbes, all of which affect the chemical profile of the end product (Bokulich et al., 2016; Liu et al., 2020). We know that there are a multitude of dynamic and complex microbial and metabolic interactions, which impact upon the product quality of fermented beverages and this has been a major challenge for product development (Gobert et al., 2022). In grape growing and winemaking, understanding and defining the distinctiveness of microbes in fermentation preserves sensory diversity and increases the product value (Bokulich et al., 2016). For example, protecting designations of origins (PDOs) and geographical indication (GIs) of fermented beverages have a significant impact in economic aspect of the product (Candiago et al., 2022; Deselnicu et al., 2013).

Palm wine is less acknowledged compared to the better-known fermented beverages made from grapes and rice. Palm wine is an extremely important commodity in many tropical countries as a traditional beverage, contributing to local economies and with distinctive impacts upon culture and community (Das & Tamang, 2021; Djeni et al., 2020; Santiago-Urbina & Ruíz-Terán, 2014; Wijaya et al., 2024). Palm wine is produced as a traditional practice and is treated differently based on its origin, which leads to distinctive regional variation. In common to all production systems is the collection of palm sap from fruiting bodies and fermentation.

The fermentation of palm wine relies on native microbial communities, which are likely have adapted to local biogeographical constraints to conduct the biotransformations (Astudillo-Melgar et al., 2019). Some microbial species (including yeasts) have evolved to occupy a niche to engage with a wider range of ecological interactions (Gray & Head, 2008). However, biotic and abiotic factors can

specifically modify microbial community structure (Zhou et al., 2021), and drive the differentiation of evolutionary traits and chemical release of the principal fermentative species, *Saccharomyces cerevisiae* (Knight et al., 2015). Understanding biogeographical ranges of microbial communities will contribute to the comparison of global populations, especially on domestication trajectory of palm wine's principal species (De Guidi et al., 2023; Ezeronye & Legras, 2009; Tra Bi et al., 2019) 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 lead to flavour formation in the finished beverage. Understanding microbial ecology is important to develop a consistent beverage product (Ciani et al., 2012). However, published reports of palm wine ecology, especially covering microbial and metabolite profiles and with broad geographical origins are limited. 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 influence product specificity (Bokulich et al., 2016; Knight et al., 2015). 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.

This review focuses on gathering the principal microbial communities and chemical compounds found during palm sap fermentation, that represent the characteristics of palm wine linked to ecology and geography. We begin by discussing the distinctive composition of palm wine and the geographical areas of palm wine production. We synthesise information from published studies to explain the contribution of ecological factors on the fermentation process and the likely effects on organoleptic properties of palm wine. 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 (Anderson & Wittwer, 2015; Bokulich et al., 2016). 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 (Santiago-Urbina & Ruíz-Terán, 2014). Palm wine is derived from palm sap, which is tapped form the blossom or apical structure of palm tree (Djeni et al., 2020; Hebbar et al., 2018). The fresh sap drips from the cutting part with slightly white turbid colour and moderate sweetness (Chandrasekhar et al., 2012), containing sugars (predominantly sucrose) (Naknean et al., 2010; Limtong et al., 2020). In grapes, fructose and glucose predominate (Corbin et al., 2015) 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 (Lee et al., 2022). In contrast, palm sap can be directly fermented after tapping without any pre-processing steps. After fermentation, palm wine has about 4-6% ethanol by volume (Das & Tamang, 2021; Santiago-Urbina & Ruíz-Terán, 2014), which is relatively similar to sweet rice wine 4.53% (v/v) (Yang et al., 2022). On the other hand, grape wine is higher about 11-15% (v/v) (Fontoin et al., 2008) and has more total phenolics at around 1103 mg/L (Ivanova et al., 2010), compared to palm wine up to 340 mg/L (Das & Tamang, 2023) and 250 mg/L in sweet rice wine (Yang et al., 2022). For total flavonoids content, palm wine has higher value up to 490 mg/L (Das & Tamang, 2023) than red grape wine in 237 mg/L (Ivanova et al., 2010) and 10 mg/L in sweet rice wine (Yang et al., 2022). Despite the variance in these substrates, these plant substrates all support the growth of yeast and bacteria during fermentation.

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 (Doddipalla et al., 2022; Naknean et al., 2010; Nwaiwu et al., 2016; Pammi et al., 2021), vitamins (Barh & Mazumdar, 2008; Zongo et al., 2020), proteins (Pammi et al., 2021), phenolics (Xia et al., 2011), and minerals (Barh & Mazumdar, 2008). A shift from sugar fermentation

113 to acidic fermentation generates a variety of derivative products, such as palm sugar, alcoholic
114 beverages, and palm vinegar (González & De Vuyst, 2009; Limtong et al., 2020; Somawiharja et al.,
115 2018; Zongo et al., 2020). The fresh sap can be refined to obtain palm sugar and left naturally at room
116 temperature to produce palm wine. Palm wine typically has shelf life only for 1-2 days of
117 fermentation for drinking pleasantly before a subsequent acidic fermentation, which change the
118 flavour. Palm wine can be distilled to produce spirits, which has more than 40% ethanol (v/v)
119 (Pratiknjo & Mambo, 2019). A longer fermentation generates organic acids as a source to produce a
120 palm vinegar. In all cases, the typical fermentation is conducted by palm's natural microbial
121 community without addition of cultured microbes and in general swift and dynamic fermentation
122 process occur (Das & Tamang, 2021; Djeni et al., 2020).

123 **3. Biogeographical perspectives of palm wine**

124 Palm trees are differently distributed across sub-tropical and tropical countries. The use of specific
125 palm species and the influence of ecological factors may mediate microbial ecology, which
126 determines the distinctiveness of palm wine sensory attributes. We have compiled recent studies to
127 construct a clear picture of palm wine usage and tapping practices. By collated data from 47 studies,
128 specifically focused on microbial and biochemical diversity topics within various approaches
129 (**Supplementary Fig. S1**). Based on our compiled studies, palm wine has been studied across three
130 continents over 14 tropical and subtropical countries (**Fig. 2A**). More than half of the studies have
131 originated in Africa, where reports from production practices in Burkina Faso predominate,
132 particularly in metabolite and microbial studies, followed by India. Each continent uses specific palm
133 species for palm wine making; *Nypha* sp. in Asia and *Acrocomia* sp. in Central America, while
134 *Elaesis* spp. and *Raphia* spp. are specifically found in Africa. The traditional names of palm wine vary
135 across the world. In Burkina Faso and Cote d'Ivoire, palm wine is widely known as *Bandji*
136 (Karamoko et al., 2012; Ouoba et al., 2012); *Mimbo* in Cameroon (Ciani et al., 2012; Jespersen,
137 2003); *Akpeteshie* in Ghana (Amoa-Awua et al., 2007); *Toddy* in India (Tamang, 2022); *Tuak* in
138 Indonesia (Hermansyah et al., 2015; Wijaya et al., 2024); *Taberna* or *Tavern* in Mexico (Coutiño et
139 al., 2020; Santiago-Urbina & Ruíz-Terán, 2014); *Ogogoro* in Nigeria (Ikeh et al., 2021); *Tuba* in

Philippines (Gregorio, 2023); *Ra* in Sri lanka (Ciani et al., 2012); *Songkhla* in Thailand (Naknean et al., 2010); *Lagmi* in Tunisia (Malek et al., 2017).

3.1 Geography and palm species affects palm wine production

Environmental variables have a significant role on palm sap production and characteristics (Ziadi et al., 2014). 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. (2019) 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.

Although palms are mostly observed in coastal areas of tropical and sub-tropical countries (Moore & Uhl, 2019), the variety of local factors could also impact the diversity of microbial community. Barata et al. (2012) 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 (Zhou et al., 2021); however, there is a lack information on arboreal microbes correlated to palm sap tapping. A study by Ziadi et al. (2014) 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 (Barata et al., 2012). Yet there is no information on the effect of dry and wet season to imply tropical variations in palm wine composition, which is likely to vary considerably. 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 limited studies, and further work here will 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 (Bokulich et al., 2016; Knight et al., 2015; Liu et al., 2019).

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 (Hebbar et al., 2018). 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 (Barh & Mazumdar, 2008; Djeni et al., 2022). 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. 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**).

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 (Naknean et al., 2010; Santiago-Urbina et al., 2015; Djeni et al., 2020). Insects and microbes have an intimate relationship with plants, signalling symbiotic associations to help them detecting nutrient, protecting from pathogens, and as parasites (Becher et al., 2018; Douglas, 2011). Insects find sugar source through the detection of released volatile compounds by plants (Becher et al., 2018; Madden et al., 2018). 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 (Evans & Schwarz, 2011). Wasps and vinegar flies are often observed in sugar-rich environments in other fermentations (Lam & Howell, 2015; Stefanini et al., 2012). 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 deliberate 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% of the sap production (Ziadi et al., 2014). Slicing stress during the tapping process is likely related to the decrease of palm sap nutritive value after 10 weeks consecutive tapping and impacts the 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 step for product hygiene and sustainability of sap production.

4 Incidence, interactions, and flavour outcome of palm wine fermentations

The nature of palm wine fermentation is vigorous and complex, where available sugars are rapidly consumed (Das & Tamang, 2023; Djeni et al., 2020). Spontaneous fermentations allow natural microorganisms to deplete organic resources without deliberate addition of selected yeast strains. The fermentation environment is a significant factor, which alters microbial interactions and ecological dynamics (Haloin & Strauss, 2008; Kowallik, 2015). As a result, a change in microbial structure is often observed during the fermentation process. To see microbial diversity and dynamic along the fermentation process, we reanalysed data from published studies conducting next generation sequencing (NGS), which is from 7 abstracted studies with further data from Sumerta et al. (2024); (**Supplementary Table S4**). We subsequently selected data of several studies by inclusion criteria, representing a vast diversity change in 24 hours fermentation (**Fig. 3A & 3B)**.

220 Comparison within country or region, type of sample, and some time frames are less informative
221 because of the limitation in comparable parameters, such as research focus, methodology, and data
222 distribution. Since palm wine fermentation is swift, the species loss of fermenting microbial
223 communities is seen after 24 hours; demonstrated by the decrease in Shannon index during
224 fermentation (**Fig. 3A;** 0, 12, and 24 hours of fermentation). Higher diversity is observed in early
225 stage of the fermentation and decrease to the following process (Alcántara-Hernández et al., 2010).
226 Nwachukwu et al. (2017) used isolation methods and found a diversity loss because of succession of
227 some microbial species. Djeni et al. (2022) reiterated that microbial diversity loss was due to a unique
228 inhabitant species in every stage of palm wine fermentation, that dominates growth.
229
230 The relative abundance of bacterial and fungal amplicons from next generation sequencing
231 demonstrates while the initial microbial populations may be maintained for 12 hours, the dominance
232 of *Lactococcus* and *Saccharomyces* is evident (**Fig. 3B**). There are 10 studies that describe a collapse
233 of one microbial group in every stage of palm wine fermentation (**Supplementary Table S6**).
234 Microbial species fluctuate over 24 hours fermentation of palm wine (**Fig. 3B**). The decrease of
235 *Leuconostoc* and the growth of *Lactococcus* present in early stage, with a concurrent drop in
236 *Hanseniaspora* species occurrence and the increase of *Saccharomyces* species. A shift between
237 *Saccharomyces* and non-*Saccharomyces* is inevitable in every stage of the fermentation (Das &
238 Tamang, 2023; Djeni et al., 2022; Gopal et al., 2021; Nwachukwu et al., 2017). This succession of
239 microbial composition over the fermentation process is identified as a key feature to determining palm
240 wine characteristics (Djeni et al., 2022).

241 **4.1 *Saccharomyces cerevisiae* is prominent in palm wine fermentations**

242 In a natural fermentation, the complex microbial interactions may result in the dominance of certain
243 species. We sought to find the microbial species most regularly associated with palm fermentation
244 Through the comparison of a conventional microbial isolation and species inferred from amplicon
245 sequencing, we selected data of top 10 abundance of culturable species (CD) (**Supplementary Table**
246 **S1)** and amplicon sequence variants (CI) (**Supplementary Table S4)**. We compared and 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 (Das & Tamang, 2021; Djeni et al., 2022). 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 (Li & Liu, 2016; Pietrafesa et al., 2020).

4.1.1 What circumstances allow for the dominance of *S. cerevisiae*?

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. (Alcántara-Hernández et al., 2010), 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 can 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 (Ciani et al., 2010; Fleet, 2003). 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 (Perrone et al., 2013; Pietrafesa et al., 2020; Wang et al., 2015).

S. cerevisiae is widely regarded as the most tolerance species to ethanol, acidity, and physical interactions (Ma & Liu, 2010; Henderson & Block, 2014; Albergaria & Arneborg, 2016; Pérez-Torrado et al., 2017). Perrone et al. (2013) 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 (Goddard & Greig, 2015). *ADH1* gene

275 regulates the fermentation process to produce ethanol, while *ADH2* gene is responsible to transferring
276 energy from ethanol conversion. Non-*Saccharomyces* species are vulnerable and not competitive in
277 higher alcohol fermentations and are affected by other environmental factors (Pérez-Torrado et al.,
278 2017). *S. cerevisiae* may secrete compounds, such fungicide like mycosin and perform cell-contact
279 abundance and triggering to the death of other species in mixed culture fermentation (Kemsawasd et
280 al., 2015; Wang et al., 2015). Albergaria et al. (2010) found that the 2-10 kDa size of peptides
281 secreted by *S. cerevisiae* can inhibit the growth of *Kluyveromyces marxianus, Kluyveromyces*
282 *thermotolerans, Torulaspora delbrueckii* and *Hanseniaspora guilliermondii*. The type of cell-to-cell
283 contact and antibiotic production mechanism can also result in the death of certain species
284 (Kemsawasd et al., 2015). Meanwhile, cell-to-cell contact induces the metabolites properties of the
285 species and affect cell viability in late stage of the fermentation (Pietrafesa et al., 2020; Wang et al.,
286 2015). However, physical contact is not the major factor to decrease the presence of non-
287 *Saccharomyces* and confirmed that the metabolites produced by *S. cerevisiae* mostly sharps the non-
288 *Saccharomyces* population (Wang et al., 2015). With the efficiency of energy use, less osmotic stress,
289 high ethanol production, tolerant to lower pH, and enable to inhibit other species, *S. cerevisiae* often
290 survives until the final stage of fermentation (Tra Bi et al., 2019). It is likely that many of these
291 characteristics may also be true of *S. cerevisiae* found in palm wine environments, but these
292 mechanisms have not been directly shown.
293
294 **4.1.2 Diversity of *Saccharomyces* and the implications for palm wine fermentations**
295 *S. cerevisiae* is a model species for genomics and plays a pivotal role in many food systems, having
296 been selected, adapted, and well domesticated across human history (Aa et al., 2006; Gibbons &
297 Rinker, 2015; Steensels et al., 2019; Steensels & Verstrepen, 2014). Peter et al. (2018) described that
298 the highest variation in *S. cerevisiae* genomes is correlated to the wider differences of phenotypic
299 characters, and it is these characters that are responsible for the signature and originality of
300 fermentation products. The evolutionary process of *S. cerevisiae* at genome level can be modified by
301 human interferences, and the yeasts adapt to various growth conditions, alter phenotypes, and change
302 reproductive mode (Gallone et al., 2016; Liti et al., 2009). In natural conditions, the population

303 structure of *S. cerevisiae* is primarily shaped by ecology (Han et al., 2021). *S. cerevisiae* evolution can
304 be triggered by its response to ecological interactions in harsh fermentation environments (Conacher
305 et al., 2021).
306
307 Spontaneous fermentation on fermented beverage making has been reproducibly conducted and if it
308 effects on microbial diversity loss, this potentially leads to a species domestication (Friedrich et al.,
309 2023). Interaction with the natural environment is often possible, where new strains may contribute,
310 and experience variable abiotic conditions (Gallone et al., 2016; Gibbons & Rinker, 2015). Legras et
311 al. (2007) stated that a rich environmental condition, geographical condition, and repetitive use in the
312 same condition results in gradual genotypes evolution, species distinction, and suggest local
313 domestication patterns. However, if spontaneous fermentation of palm wine generates domestication
314 is an open question (Fay & Benavides, 2005). Some reports released that the genome of *S. cerevisiae*
315 populations of African palm wine is admixed compared to global references, showing a unique
316 signature relative to different continents, niches, and favour strain migration through human
317 interference (Ezeronye & Legras, 2009; Tra Bi et al., 2019). Tra Bi et al. (2019) showed that the
318 genetic relationship of *S. cerevisiae* in palm wine is significantly related to ecological niches, that
319 sharing the similar geographical origin generates lower genetic diversity. A local domestication may
320 be attributed to *S. cerevisiae* from palm wine strains, which are observed as homozygous strains
321 (Ezeronye & Legras, 2009; Tapsoba et al., 2015). Further studies with diverse isolates of *S. cerevisiae*
322 genomes will help unravel this question.

323 **4.2 Interactions amongst microbes in fermentation**

324 We conducted a network analysis of the co-occurrence of species groups from compiled studies which
325 used culture-dependent methods to assess microbial diversity (**Fig. 4A**). The contribution of
326 *Saccharomyces* is dominant and acts as a central hub to other species group in palm wine
327 fermentation. It also has a strong relationship to other yeast genera (*Hanseniaspora, Candida*, and
328 *Pichia*) and the core bacteria in organic acids production, such as *Lactobacillus*, *Leuconostoc*, and
329 acetic acid bacteria (AAB). These show a vital connection pattern of those microbial groups on

330 constructing palm wine characters and suggest a fermentation model retrieved from multi-
331 geographical studies. This pattern reveals a network of microbial ecology, and reveals potential
332 microbial interactions which may be able to predict the occurrence of unwanted species (Fuhrman,
333 2009).
334
335 In spontaneous fermentation, interactions have a significant role on driving the fermentation process,
336 involving various microbial groups. Interactions among microbial species may deliver positive and
337 negative impacts, which determine the product formation (Ciani & Comitini, 2015; Cordero & Datta,
338 2016; Viljoen, 2001; Zuñiga et al., 2017). In spontaneous fermentations, synergistic interactions
339 among different species mediate tolerance to the robustness of dynamic condition in particular level.
340 Mutualism and commensalism interaction are attributed to the synergistic interaction with cross-
341 feeding mechanism or supporting certain metabolite producer (Silverstein et al., 2023; Smid &
342 Lacroix, 2013). For instance, yeasts ferment the sugar into ethanol while acetic acid bacteria convert
343 the ethanol into acetic acid which is not affect the yeast (De Vuyst & Leroy, 2020). Lactic acid
344 bacteria and yeast sometimes support each other by exchanging some metabolites for their
345 metabolism (Smid & Lacroix, 2013). Each group of microbial species has different way to develop its
346 functionality by interacting with other species. Fleet (2003) highlighted the interaction among yeast
347 species contributes to the fermentation behaviour while yeast-bacteria interactions determine the
348 ecological dynamic. This interesting feature of complex microbial communities interaction can be
349 proposed as new model of the fermentation to create flavourful product (Ciani et al., 2010). Specific
350 interactions between microbes have not been described in a palm wine environment, but they are
351 likely to occur.

352 **4.3 The implications of metabolite release on fermentation dynamics**

353 The associations of microbial communities and chemical release have a major contribution on
354 constructing palm wine characteristics. A wide range of microbial groups occupies in every stage of
355 the fermentation process but following the depletion of sugar in the fermentation process, microbial
356 diversity decreases because of biochemicals alteration and ecological interactions. Here, we abstracted

357 10 studies (**Supplementary Table S6**), exploring both in microbial communities and chemical
358 composition along the fermentation stages, representing palm wine fermentation dynamics and
359 summarised in **Fig. 5**. The abundance of ethanol is likely attributed to the presence of *Saccharomyces*
360 yeasts during fermentation. Lactic acid bacteria (LAB) and acetic acid bacteria (AAB) grow on palm
361 wine fermentation related to the significant number of organic acids in final stages of fermentation
362 (Adamu-Governor et al., 2018; Kouame et al., 2020; Ouoba et al., 2012; Somashekaraiah et al., 2019).
363 Total phenolics and flavonoids impact shifts in microbial community composition through the
364 fermentation process (Das & Tamang, 2023). We presented the examples of chemical yield in the
365 table, which represents the gradual change in line graph. It is important to note that chemical content
366 of palm wine ultimately depends on, geographical location, palm species, and the way analytical
367 process and research design conducted, so the results vary among studies. By summarising related
368 studies, the general pattern was demonstrated to provide a better understanding of palm wine
369 fermentation.
370
371 We simulated the co-occurrence of microbial groups and compounds based on the correlation analysis
372 of each microbial group follows the biochemical pattern (**Fig. 4B**). Data was summarised from the
373 frequency of microbial groups and metabolite components presented in each study. Lactic and acetic
374 acid production in the final stage of palm wine fermentation positively corelate to the frequency of
375 lactic acid and acetic acid bacteria group while *Saccharomyces* and *Candida* group may also have
376 similar contribution. These compounds reduce the pH and alter the microbial diversity. Since pH
377 decreasing, the evaporation of volatile fatty acids is possibly high (Derikx et al., 1994). Meanwhile in
378 alcohol production, non-*Saccharomyces* yeasts have a negative correlation compared to bacterial
379 groups and *Saccharomyces*. This simulation provides the influence of metabolite components on the
380 composition of microbial diversity, which can demonstrate the fermentation dynamics.
381

5 The intersection of culture for palm wine production in modern food systems

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 (Djeni et al., 2020). 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 (Limtong et al., 2020). 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 (Wijaya et al., 2024). 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 (Jakl, 2021). 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 (Barh & Mazumdar, 2008; Hebbar et al., 2018; Laklaeng & Kwanhian, 2020; Leida et al., 2020; Mia et al., 2020; Senghoi & Klangbud, 2021). Palm wine contains phenolic compounds that may contribute to antioxidant activity in the plasma (Hebbar et al., 2018; Xia et al., 2011) and modulate the growth of gut microbiota (Cardona et al., 2013; Nash et al., 2018; Queipo-Ortuño et al., 2012). A probiotic-type microbiome that benefits for digestive system is also found in fresh palm sap (Gopal et al., 2021) and fermented sap showed bioactive chemical activities (Kurniawan et al., 2018). We suggest that basic information on microbial community structure and dynamic of metabolite profile benefits local and traditional practices, that support regional identity and preservation of traditional practices.

Understanding microbial ecology and controlling microbial composition are pivotal to beverage quality and a major challenge for future product development (Gobert et al., 2022). In general, inconsistent sensory characteristics results from spontaneous fermentation as it is difficult to control product quality and consistency. The presence of spoilage bacteria is inevitable amid a spontaneous fermentation, for example lactic acid and acetic acid bacteria, that can compete for nutrients and produce lactic and acetic acids, which limit the ethanol production during the fermentation process (Beckner et al., 2011). Intervention at harvesting may obtain higher ethanol production before the spoilage bacteria rapidly conducts the acidic fermentation. Deploying defined starter cultures may obtain consistent, efficient, and desired quality of the alcohol products; however, the end-products might lack complexity of organoleptic characteristics (Steensels & Verstrepen, 2014). The fermentation process has evolved to current commercial practices with selected yeast strains (Cavalieri et al., 2003; Steensels & Verstrepen, 2014) to enhance aroma and flavour (Medina et al., 2013; Rodríguez-Lerma et al., 2011). Although this practice yet applicable in palm wine, co-culturing with selected strain could be considered in the future. We recognise there is a need to retain and foster traditional food products, which may at odds with the use of commercial starter cultures.

6 Conclusions, limitations, and prospects

Palm wine is a unique and culturally important beverage. The fermentation process is challenged by many factors, which contribute to differences of product composition and distinction. Technologically behind from the production of grape and rice wines, there is no standardized procedure widely used to produce palm wine, which remains at extremely small-scale and conducted with traditional methods. We have defined the facets of palm wine fermentation and composition reflecting the importance of ecological specificity on beverage characteristics but encourage addition of further studies across other regions and ecological variations to add to the knowledge of this unique beverage. Further studies will help typical geographical features and help preserve traditional knowledge and distinctive foods for benefit of local communities. We support further actions to strengthen fundamental understandings of palm wine production to support sustainable product development and appreciating 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 methods

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, analysis, writing and editing the manuscript

XR: data analysis supervision and review the manuscript

KH: research design supervision, writing, review and editing the manuscript

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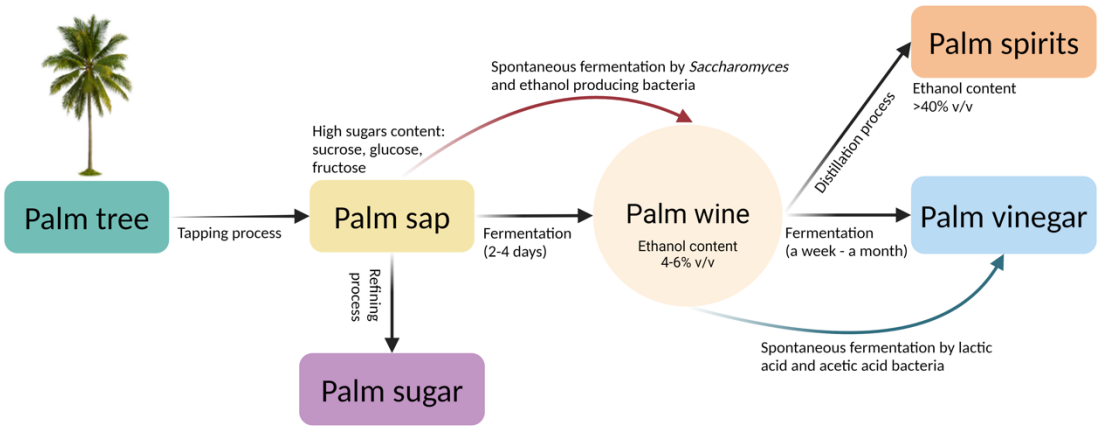
840 **Figure legends**

841 **Fig. 1** Schematic to describe the processing of palm sap with its derivative products. Created with
842 BioRender.com
843
844 **Fig.2** A survey of palm wine studies which include measures of microbial ecology and metabolite
845 profiling (n= 47), details are available on **Supplementary Table S1 & S2**. A) Country distribution of
846 scientific studies in both microbes and metabolites across continents. B) The Venn diagram shows the
847 focus of compiled scientific studies. C) Proportion of the studies of palm species for all compiled
848 studies.
849
850 **Fig 3.** Microbial dynamics and community proportion of palm wine fermentation. Next generation
851 sequencing (NGS) data of 7 abstracted studies with data from Sumerta et al. (2024); **Supplementary**
852 **Table S4**) were analysed together. A) Microbial diversity loss (measured as Shannon index) over 24
853 hours palm wine fermentation (Wilcoxon test; p-value <0.05); B) Change in top 10 abundance of
854 microbial species in 24 hours palm wine fermentation from NGS data. C) The proportion of top 10
855 microbial species, obtained by CD (inner circle; n =33) compared to CI (outer circle; bacteria n=7-1,
856 excluded due to technical limitation; fungi n = 5).
857
858 **Fig 4.** Co-occurrence pattern of microbe-microbe and microbe-metabolite relationships on palm wine
859 fermentation. A) Network analysis of the relationship of microbial group in palm wine fermentation.
860 The contribution of each group is represented as an edge. Different colour showing different microbial
861 group (blue= yeasts, red= bacteria), then different size of font represents the abundance value. The
862 data set used for this study consists of 23 studies based on the abundance and frequency each species
863 group in **Supplementary Table S3**, omitting 7 studies of NGS, where data was abstracted in
864 **Supplementary Table S5** and used R studio adopting the codes by Schweinberger (2024). B)
865 Correlation heatmap between microbial and metabolite groups (n= 23-3, studies which used amplicon

sequencing were disregarded). The frequency of microbial and metabolite groups was abstracted from **Supplementary Table S3** and analysed with Spearman correlations (p value > 0.05).

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.

Figure 1



881 Figure 2

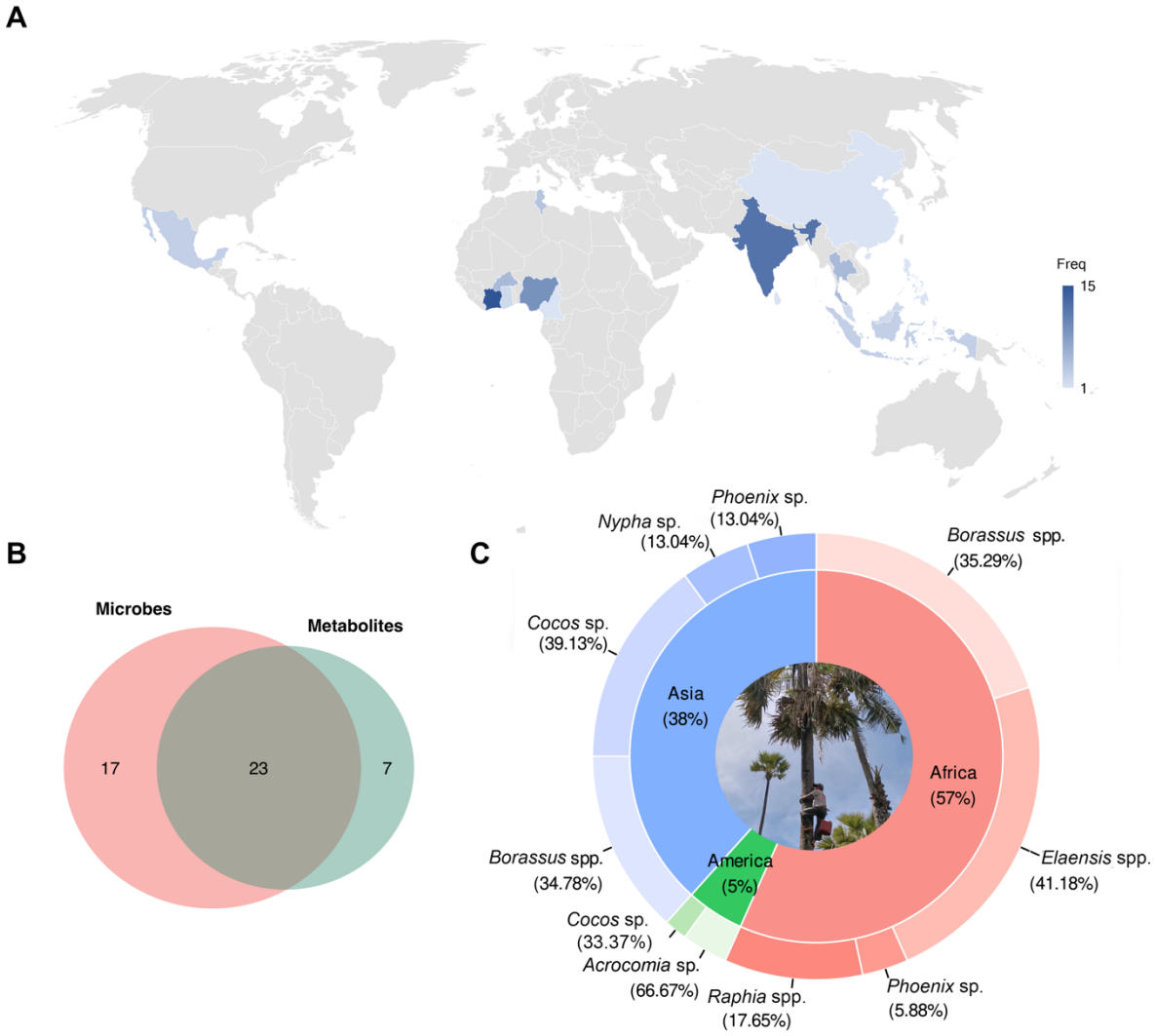


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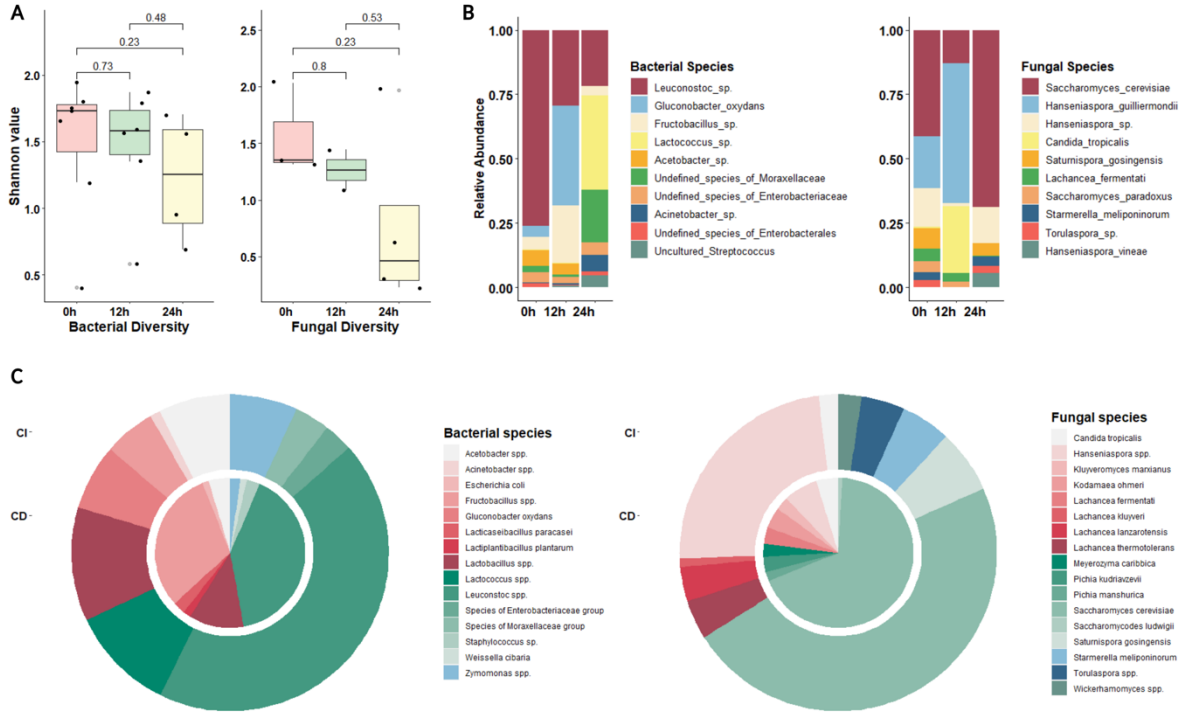
Figure 3


A
Shannon value
0.48
0.23
0.73
0.53
0.23
0.8
0h
12h
24h
Bacterial Diversity
Fungal Diversity
B
Relative Abundance
Bacterial Species
Leuconostoc_sp.
Gluconobacter_oxydans
Fructobacillus_sp.
Lactococcus_sp.
Acetobacter_sp.
Undefined_species_of_Moraxellaceae
Undefined_species_of_Enterobacteriaceae
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.

887 Figure 4

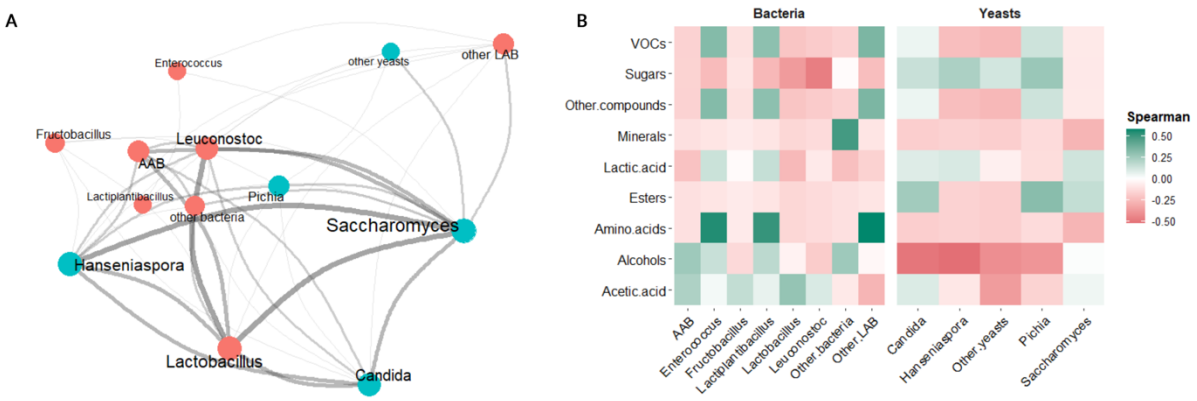


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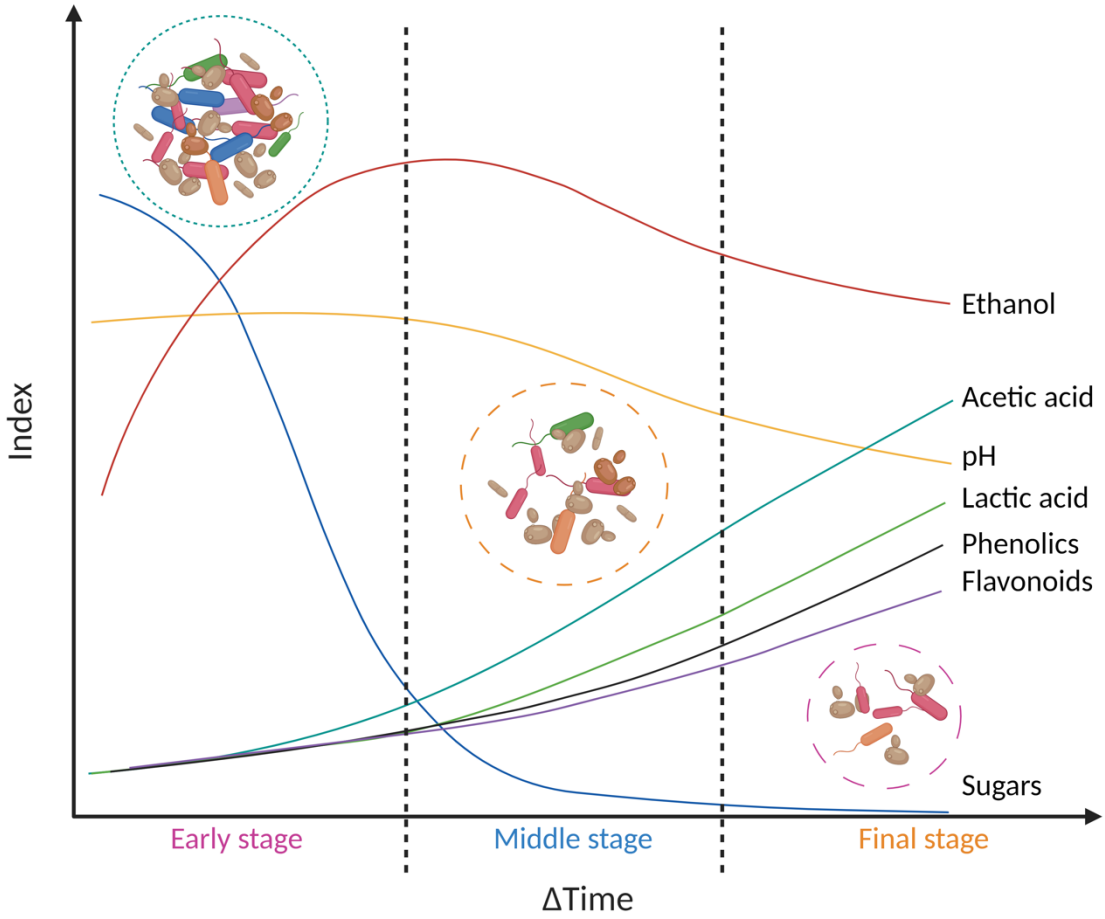
Figure 5



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