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Indigenous Palm Wine Yeasts as Novel Starter Cultures for Mead Production: A Critical Review of Honey Must Chemistry, Fermentation Biotechnology and Yeast Physiology

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ABSTRACT

Mead, an alcoholic beverage produced through the fermentation of diluted honey, represents one of the oldest fermented beverages known to humankind. Despite renewed commercial interest driven by the global expansion of the craft beverage industry, large-scale mead production remains constrained by the intrinsic physicochemical characteristics of honey must, including low yeast assimilable nitrogen, nutritional imbalance, high osmotic pressure and inconsistent fermentation performance. Recent advances in food biotechnology have identified indigenous yeasts isolated from traditional fermented beverages, particularly palm wine, as promising alternatives to conventional commercial starter cultures because of their unique physiological adaptations, stress tolerance and capacity to generate distinctive sensory characteristics. This review critically synthesises current knowledge regarding fermentation biotechnology, honey chemistry, yeast physiology and palm wine microbial ecology to evaluate the suitability of indigenous palm wine yeasts for mead production. Particular emphasis is placed on the biochemical composition of honey must, fermentation kinetics, nutrient supplementation, osmotic stress management and environmental factors influencing ethanol production. The complementary roles of *Saccharomyces cerevisiae* and non-*Saccharomyces* yeasts in improving fermentation efficiency, flavour complexity and product quality are critically discussed. Furthermore, emerging developments in microbial genomics, adaptive evolution and precision fermentation are examined as tools for improving indigenous yeast performance. Collectively, the available evidence indicates that indigenous palm wine yeasts constitute an underutilised microbial resource capable of improving fermentation efficiency, enhancing regional product identity and promoting sustainable beverage biotechnology. Future investigations integrating genomics, metabolomics and industrial-scale validation are required to facilitate their commercial application in premium mead production.

Keywords: Mead; Honey must; Indigenous yeast; Palm wine; *Saccharomyces cerevisiae*; Non-*Saccharomyces*; Alcoholic fermentation; Food biotechnology.

INTRODUCTION

Fermentation is one of the oldest and most significant biotechnological processes employed in food production, preservation and value addition. Beyond extending shelf life, microbial fermentation improves nutritional quality, enhances digestibility, enriches flavour profiles and contributes to food safety through the production of antimicrobial metabolites. Advances in food biotechnology have transformed fermentation from a traditional

empirical practice into a scientifically controlled process integrating microbial physiology, molecular biology, metabolic engineering and systems biotechnology to optimise product quality, consistency and industrial productivity [1-4]. These developments have substantially expanded the applications of fermentation across the food and beverage industries, including the manufacture of bread, dairy products, vinegar, beer, wine, distilled spirits and functional fermented foods. Among fermented alcoholic beverages, mead occupies a unique historical and scientific position. Produced through the alcoholic fermentation of diluted honey, mead is widely regarded as the earliest known alcoholic beverage, with archaeological evidence indicating its production over 9,000 years ago. Throughout history, mead has held important nutritional, medicinal, cultural and religious significance across numerous ancient civilisations in Asia, Europe and Africa. Although commercial beer and grape wine subsequently dominated the global alcoholic beverage market, increasing consumer preference for natural, artisanal and functional beverages has stimulated a substantial resurgence in mead production worldwide [5-8]. Despite this renewed commercial interest, modern mead production continues to encounter several biological and technological constraints. Unlike grape must, honey contains abundant fermentable sugars but is naturally deficient in assimilable nitrogen, vitamins, minerals and other nutrients essential for optimal yeast metabolism. In addition, the high sugar concentration of honey creates severe osmotic stress that can impair yeast growth, prolong fermentation, reduce ethanol productivity and compromise product consistency. Consequently, successful mead production requires careful optimisation of honey dilution, nutrient supplementation, fermentation conditions and microbial starter selection [9-12]. Commercial mead production has traditionally relied on selected strains of *Saccharomyces cerevisiae* because of their high ethanol tolerance, predictable fermentation kinetics and efficient sugar utilisation. Although these commercial strains consistently produce satisfactory ethanol yields, repeated use often results in relatively uniform sensory characteristics and limited regional differentiation. This limitation has stimulated increasing interest in exploiting indigenous yeast biodiversity as an alternative source of starter cultures capable of producing novel flavour profiles while maintaining desirable fermentation performance [13-16]. Indigenous yeasts isolated from traditional fermented beverages represent a valuable but largely underutilised microbial resource. These microorganisms have naturally evolved under diverse ecological conditions and frequently exhibit desirable physiological characteristics, including thermotolerance, osmotolerance, acid resistance, enhanced stress adaptation and the capacity to synthesise diverse volatile aroma compounds. Such properties are particularly advantageous for fermenting nutritionally challenging substrates such as honey must, where environmental stress frequently limits yeast performance [14,17-19]. Palm wine is among the richest natural reservoirs of indigenous fermentative microorganisms. Produced through spontaneous fermentation of palm sap, palm wine contains dynamic microbial communities comprising *Saccharomyces*, *Pichia*, *Candida*, *Hanseniaspora*, *Torulaspora*, *Metschnikowia* and numerous lactic acid bacteria and acetic acid bacteria. These microbial consortia interact throughout fermentation to produce ethanol, organic acids, esters and numerous volatile metabolites responsible for the beverage's characteristic aroma, flavour and physicochemical properties. Owing to their adaptation to sugar-rich environments, many palm wine yeasts possess considerable potential as alternative starter cultures for honey fermentation [20-24]. Recent advances in microbial genomics, metabolomics, adaptive laboratory evolution and precision fermentation have further strengthened the prospects for exploiting indigenous yeasts in industrial beverage biotechnology. High-throughput sequencing technologies now permit comprehensive characterisation of native yeast biodiversity, while metabolic engineering and adaptive evolution enable the development of strains with enhanced ethanol tolerance, improved nutrient utilisation and superior aroma production. Furthermore, sequential and co-inoculation strategies involving *Saccharomyces cerevisiae* and selected non-*Saccharomyces* yeasts have emerged as effective approaches for combining reliable fermentation performance with enhanced sensory complexity [18, 25-28]. Although previous studies have independently investigated honey chemistry, mead fermentation, indigenous yeast diversity and palm wine microbiology, these research areas remain poorly integrated within the existing literature. Few comprehensive reviews have critically examined the potential of indigenous palm wine yeasts as next-generation starter cultures for sustainable mead biotechnology. Addressing this knowledge gap is essential for developing fermentation strategies that utilise locally available microbial resources while supporting biodiversity conservation, regional product development and sustainable food systems. Therefore, this review critically evaluates current evidence regarding fermentation biotechnology, honey must chemistry, microbial physiology and palm wine microbial ecology to assess the potential of indigenous palm wine yeasts in modern mead production. Particular emphasis is placed on fermentation kinetics, stress adaptation, biochemical mechanisms governing ethanol production and emerging precision fermentation technologies. By integrating these previously disconnected fields, this review provides a comprehensive framework for the development of sustainable, high-quality mead using indigenous African yeast resources while identifying priority areas for future research and industrial application.

Fermentation Biotechnology and the Emerging Importance of Indigenous Yeasts

Fermentation in Food Biotechnology

Fermentation is one of the most important biological processes underpinning modern food biotechnology and remains fundamental to the production, preservation and value enhancement of foods and beverages. The process involves the enzymatic conversion of carbohydrates into ethanol, organic acids, carbon dioxide and numerous secondary metabolites by microorganisms under anaerobic or microaerophilic conditions. Beyond extending product shelf life, fermentation improves nutritional quality, enhances digestibility, increases the bioavailability of micronutrients and generates unique sensory characteristics that determine consumer acceptance [29-32]. Recent advances in biotechnology have transformed fermentation from a largely empirical practice into a precisely controlled industrial process. The integration of microbial physiology, systems biology, genomics, metabolomics and biochemical engineering has enabled optimisation of fermentation kinetics, microbial strain selection and product consistency. These advances have also facilitated the exploitation of microbial biodiversity from traditional fermented foods as valuable sources of industrial starter cultures capable of improving fermentation performance while preserving regional product identity [30, 33, 34]. Increasing consumer demand for natural, minimally processed and functional foods has renewed scientific interest in indigenous fermentation systems. These traditional fermentation ecosystems harbour diverse microbial populations that possess desirable metabolic characteristics often absent in commercial starter cultures. Consequently, indigenous microorganisms are increasingly recognised as valuable biological resources for developing novel fermented beverages with enhanced nutritional, sensory and functional properties while promoting sustainable food production and circular bioeconomy initiatives [31, 35].

Microbial Fermentation in Alcoholic Beverage Production

Alcoholic fermentation represents one of the most economically important applications of microbial biotechnology. During this process, fermentative microorganisms convert fermentable sugars into ethanol while simultaneously producing numerous secondary metabolites, including esters, higher alcohols, aldehydes, volatile acids and sulfur-containing compounds that collectively determine beverage aroma, flavour and mouthfeel [36, 37]. Among fermentative microorganisms, *Saccharomyces cerevisiae* remains the dominant industrial yeast because of its exceptional fermentative capacity, high ethanol tolerance, rapid sugar utilisation and remarkable genetic stability. These characteristics have made *S. cerevisiae* the preferred starter culture for beer, wine, spirits and mead production worldwide [38, 39]. Nevertheless, recent studies have demonstrated that fermentation performance depends not only on ethanol production but also on the production of volatile metabolites that contribute significantly to product quality. Consequently, increasing attention has shifted towards non-*Saccharomyces* yeasts, including species belonging to the genera *Pichia*, *Candida*, *Hanseniaspora*, *Metschnikowia*, *Torulaspora* and *Lachancea*. Although these species generally exhibit lower ethanol tolerance than *S. cerevisiae*, they produce diverse volatile esters, higher alcohols and organic acids capable of enhancing flavour complexity and improving the sensory characteristics of fermented beverages [19, 27, 40]. The growing adoption of mixed-culture fermentations combining *Saccharomyces* and non-*Saccharomyces* species has therefore emerged as a promising strategy for balancing efficient ethanol production with superior organoleptic quality. Such approaches are increasingly being investigated for premium mead production where flavour differentiation is an important commercial objective [18, 19].

Indigenous Yeasts as Emerging Starter Cultures

Commercial fermentation industries have traditionally relied on a relatively limited number of genetically similar yeast strains. Although these cultures provide excellent process reproducibility, their widespread use has contributed to reduced microbial diversity and relatively homogeneous sensory profiles across fermented beverages [14, 16]. Indigenous yeasts, isolated from natural ecosystems and traditional fermented products, have therefore attracted considerable research interest because they represent an extensive reservoir of unexplored microbial diversity. Unlike commercial strains that have undergone prolonged industrial domestication, indigenous yeasts have evolved under diverse ecological conditions and frequently exhibit adaptive physiological traits that enhance survival under environmental stress [13, 14]. Several indigenous yeast species have demonstrated remarkable tolerance to osmotic pressure, elevated temperatures, low pH and nutritional deficiency, characteristics that are particularly advantageous during honey fermentation. Furthermore, many indigenous yeasts possess unique enzymatic activities, including β-glucosidase, esterase and glycosidase production, which facilitate the release of aroma-active compounds from honey and other natural substrates, thereby increasing flavour complexity [19, 41]. An additional advantage of indigenous yeasts lies in their contribution to microbial terroir. This concept describes the influence of regional microbial communities on the distinctive sensory characteristics of fermented foods and beverages. Indigenous starter cultures therefore provide opportunities to develop geographically unique meads with enhanced commercial value while preserving local microbial biodiversity and traditional fermentation practices [15, 42]. Recent developments in adaptive laboratory evolution, comparative genomics and metabolic engineering have further strengthened the industrial relevance of indigenous yeasts. Rather than replacing commercial starter

cultures entirely, indigenous strains can now be selectively improved or incorporated into mixed-culture fermentations to combine robust fermentation performance with desirable sensory attributes [16, 25].

Mead: Historical Development and Industrial Significance

Historical Evolution of Mead

Mead is widely regarded as the earliest alcoholic beverage intentionally produced by humans. Archaeochemical investigations have identified fermented honey beverages dating back approximately 9,000 years, demonstrating that honey fermentation preceded the domestication of cereal crops used in brewing beer and the cultivation of grapes for wine production [5, 6]. The word *mead* originates from the Proto-Indo-European root *medhu*, meaning honey or sweet intoxicating drink, reflecting the historical importance of honey in early human societies. Throughout antiquity, mead occupied a central role in religious ceremonies, medicinal practices and social celebrations across Asia, Europe and Africa. References to honey wine appear in the Rigveda of ancient India, Greek and Roman literature, Norse mythology and numerous African cultural traditions, where mead symbolised fertility, prosperity and longevity [7, 43]. Despite its ancient heritage, industrial production of mead declined following the widespread commercialisation of beer and grape wine. Limited honey availability, relatively high production costs and inconsistent fermentation performance contributed to its reduced popularity during the nineteenth and twentieth centuries [44]. However, the global expansion of the craft beverage industry has stimulated renewed interest in mead production. Modern consumers increasingly seek artisanal beverages characterised by natural ingredients, regional authenticity and functional properties, creating new opportunities for innovative mead products produced using indigenous microbial resources and advanced fermentation technologies [8, 45].

Types of Mead and Their Functional Characteristics

Modern mead exhibits remarkable diversity, reflecting variations in formulation, fermentation strategies and ingredient selection. Traditional mead consists solely of honey, water and yeast and remains the standard reference for evaluating fermentation performance and microbial physiology [8]. Several specialised mead styles have subsequently evolved to satisfy changing consumer preferences and expand product functionality. Melomel incorporates fruits, thereby increasing concentrations of vitamins, organic acids and polyphenolic antioxidants while enhancing colour and flavour complexity. Metheglin contains herbs and spices that contribute antimicrobial activity and distinctive aromatic characteristics. Other commercially important styles include pyment (honey and grape juice), cyser (honey and apple juice) and braggot (a hybrid of mead and beer containing malted cereals) [46-48]. These formulations differ considerably in sugar composition, acidity, antioxidant content and nutrient availability, all of which influence microbial metabolism and fermentation kinetics. Consequently, selecting appropriate yeast strains according to mead style has become an important component of modern fermentation management aimed at optimising ethanol yield, flavour development and product stability [47, 48].

Traditional versus Modern Mead Production Technologies

Traditional mead production relied primarily on spontaneous fermentation using indigenous microorganisms naturally associated with honey, fermentation vessels and the surrounding environment. Although these fermentations frequently produced beverages with distinctive regional characteristics, they were often characterised by prolonged fermentation periods, inconsistent alcohol production and substantial batch-to-batch variability [7, 9]. Modern industrial mead production has largely overcome these limitations through controlled fermentation systems incorporating selected starter cultures, temperature regulation, pH control, nutrient supplementation and oxygen management. Advances in analytical instrumentation, including gas chromatography-mass spectrometry (GC-MS), high-performance liquid chromatography (HPLC) and Fourier-transform infrared spectroscopy (FTIR), now enable continuous monitoring of fermentation kinetics, volatile compound formation and product quality throughout fermentation [8,11,49]. More recently, researchers have begun integrating indigenous yeast isolates into modern fermentation systems. This strategy combines the robustness and predictability of industrial fermentation with the sensory diversity characteristic of traditional spontaneous fermentations. Mixed-culture fermentations involving *Saccharomyces cerevisiae* and carefully selected indigenous non-*Saccharomyces* yeasts have demonstrated considerable potential for producing premium meads with improved flavour complexity while maintaining efficient ethanol production [18, 19, 27].

Honey Must as a Fermentation Substrate

Composition and Physicochemical Properties of Honey Must

Honey must, the aqueous solution prepared by diluting honey before fermentation, serves as the primary substrate for mead production and largely determines fermentation performance, microbial metabolism and final beverage quality. Unlike grape must, which naturally contains a balanced composition of sugars, organic acids, minerals and nitrogenous compounds, honey must is characterised by an abundance of fermentable carbohydrates but a marked deficiency in assimilable nitrogen, essential vitamins and several micronutrients required for optimal yeast growth. Consequently, the biochemical composition of honey must presents unique physiological challenges that distinguish mead fermentation from other alcoholic beverage fermentations and necessitate careful optimisation of substrate

composition and fermentation conditions [50-53]. The physicochemical characteristics of honey are influenced by multiple factors, including floral origin, geographical location, climatic conditions, bee species, harvesting practices and post-harvest handling. As a result, substantial variation exists in the chemical composition of honey used for mead production. Moisture content typically ranges from 15% to 20%, while carbohydrates account for approximately 75 - 82% of total solids, making honey one of the most concentrated natural sugar sources available for industrial fermentation [51, 54]. Minor constituents, including proteins, enzymes, amino acids, minerals, vitamins, organic acids and phenolic compounds, collectively constitute less than 5% of honey but exert disproportionate effects on microbial metabolism, antioxidant capacity and sensory quality [55, 56]. One of the defining characteristics of honey is its exceptionally low water activity (a_w), generally ranging between 0.50 and 0.65. This low water activity, combined with high osmotic pressure, acidic pH and the presence of antimicrobial compounds such as hydrogen peroxide and bee-derived peptides, inhibits the growth of most spoilage microorganisms and contributes to honey's remarkable shelf stability [57, 58]. However, these same physicochemical properties also create an unfavourable environment for fermentative yeasts once honey is diluted to prepare must. During the initial stages of fermentation, yeast cells encounter considerable osmotic stress arising from elevated extracellular sugar concentrations, leading to cellular dehydration, reduced membrane fluidity and delayed metabolic activation [59, 60].

The pH of honey generally ranges from 3.2 to 4.5, depending on botanical origin, while diluted honey must commonly exhibits pH values between 3.5 and 4.2 following formulation. This acidic environment inhibits many bacterial contaminants while remaining favourable for yeast proliferation. Nevertheless, excessive acidification during fermentation may suppress yeast growth, reduce fermentation rates and influence the formation of volatile aroma compounds. Maintaining appropriate pH therefore represents a critical aspect of fermentation management, particularly when indigenous yeasts are employed, as different strains exhibit varying degrees of acid tolerance [52, 61]. Electrical conductivity and ash content provide additional indicators of honey composition and are frequently used to distinguish floral varieties. Dark honeys generally possess higher mineral concentrations, greater antioxidant capacity and increased electrical conductivity than lighter honeys. These compositional differences may influence fermentation kinetics by altering nutrient availability and buffering capacity, ultimately affecting ethanol production, yeast viability and flavour development [54, 62]. Beyond serving as a carbon source, honey contains numerous bioactive constituents that influence fermentation behaviour. Flavonoids, phenolic acids, enzymes and volatile compounds contribute not only to the nutritional value of honey but also to its antimicrobial activity and oxidative stability. During fermentation, many of these compounds undergo enzymatic transformation by yeast, generating new metabolites that enhance the complexity of mead aroma and flavour. Consequently, honey should not be regarded merely as a source of fermentable sugars but rather as a chemically complex fermentation matrix that actively modulates microbial physiology and metabolic pathways throughout fermentation [55, 63]. The diversity of honey composition presents both opportunities and challenges for industrial mead production. While botanical variability enables the manufacture of regionally distinctive products with unique sensory characteristics, inconsistent substrate composition frequently contributes to variability in fermentation performance. Standardisation of honey must through adjustment of sugar concentration, pH, nutrient availability and dilution ratio has therefore become an important objective in contemporary mead biotechnology. Advances in physicochemical characterisation and metabolomic profiling now permit more precise evaluation of honey composition, facilitating improved process control and greater reproducibility during industrial fermentation [11, 49, 64]. From a biotechnological perspective, honey must should be considered a dynamic biochemical environment rather than a passive fermentation substrate. The interactions among sugars, organic acids, minerals, phenolic compounds and microbial metabolism collectively determine fermentation efficiency, ethanol productivity and the development of desirable sensory attributes. Understanding these interactions is therefore essential for the rational selection of indigenous yeast strains capable of efficiently exploiting the nutritional characteristics of honey while overcoming its inherent physiological limitations. Such knowledge forms the basis for developing robust fermentation strategies that maximise product quality while preserving the unique characteristics associated with different honey varieties [18, 25, 65].

Carbohydrates and Fermentable Sugars in Honey Must

Carbohydrates constitute the principal nutritional component of honey must and serve as the primary carbon and energy source driving alcoholic fermentation. The quantity, composition and relative proportions of fermentable sugars directly influence yeast physiology, fermentation kinetics, ethanol yield and the sensory characteristics of the final mead. Unlike grape must, where glucose concentrations generally exceed those of fructose during ripening, honey exhibits a unique carbohydrate profile dominated by the monosaccharides fructose and glucose, together accounting for approximately 85–95% of total fermentable sugars. The remaining carbohydrate fraction comprises a complex mixture of disaccharides, trisaccharides and higher oligosaccharides whose concentrations vary according to botanical origin, environmental conditions and post-harvest processing [66-69]. Fructose is generally the most

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abundant sugar in natural honey, representing approximately 35–45% of total carbohydrates, whereas glucose contributes between 25% and 40%. Minor sugars include sucrose, maltose, turanose, trehalose, isomaltose, melezitose, raffinose, erlose and several oligosaccharides present at considerably lower concentrations. Although these minor carbohydrates contribute relatively little to total ethanol production, they influence sweetness, viscosity, osmotic pressure and microbial metabolism during fermentation. Their gradual utilisation by yeast may also affect fermentation duration and residual sugar content, thereby influencing the sensory balance and stability of finished mead [51, 54, 66]. The predominance of monosaccharides provides honey with a distinct biotechnological advantage because glucose and fructose can be transported directly across the yeast plasma membrane without prior extracellular hydrolysis. These hexoses enter central carbon metabolism through glycolysis following phosphorylation by hexokinase and fructokinase, allowing rapid ATP generation and ethanol production under anaerobic conditions [70, 71]. However, despite the simultaneous availability of both sugars, many *Saccharomyces cerevisiae* strains preferentially metabolise glucose before fructose owing to glucose repression mechanisms that regulate sugar transporter expression and intracellular metabolic pathways. This preferential utilisation frequently results in sluggish fructose consumption during the later stages of fermentation, increasing the risk of residual sweetness and incomplete fermentation [72, 73]. Fructose metabolism represents a particularly important consideration in mead biotechnology because honey typically contains higher fructose concentrations than grape must. While fructose contributes desirable sweetness and mouthfeel, excessive residual fructose following fermentation may compromise microbiological stability and increase susceptibility to spoilage by osmophilic yeasts and lactic acid bacteria. Consequently, selection of fructophilic or fructose-efficient yeast strains has become an important objective in modern mead production. Several indigenous yeasts isolated from spontaneous fermentations, including certain strains of *Saccharomyces cerevisiae*, *Zygosaccharomyces rouxii*, *Torulaspora delbrueckii* and *Metschnikowia* spp., exhibit enhanced fructose utilisation and may therefore improve fermentation completeness in high-sugar substrates such as honey must [18,74-76]. The exceptionally high sugar concentration of undiluted honey also imposes significant osmotic stress on fermentative microorganisms. Elevated extracellular osmolarity causes rapid efflux of intracellular water, resulting in reduced cell turgor, impaired membrane function, altered enzyme activity and delayed initiation of cell division. To survive these conditions, yeast cells activate the High Osmolarity Glycerol (HOG) signalling pathway, inducing intracellular synthesis of compatible solutes such as glycerol and trehalose that restore osmotic balance and protect cellular structures. Although this adaptive response enhances stress tolerance, diversion of carbon flux towards osmoprotectant synthesis reduces ethanol productivity and may prolong fermentation time [60, 77, 78]. Appropriate dilution of honey before inoculation is therefore essential to establish favourable fermentation conditions. Most commercial mead formulations adjust soluble solids to approximately 20–30 °Brix, depending on the desired alcohol content and mead style. Lower sugar concentrations generally promote faster fermentation and greater yeast viability, whereas higher sugar concentrations favour production of dessert meads with elevated residual sweetness but require more robust yeast strains and intensive nutrient management. Optimising initial sugar concentration therefore involves balancing ethanol yield, fermentation efficiency and product quality while minimising osmotic inhibition [52, 64, 79]. Beyond serving as fermentable substrates, honey carbohydrates influence numerous physicochemical properties of the fermentation medium. Fructose possesses greater hygroscopicity than glucose, contributing to honey's low water activity and prolonged shelf stability. Glucose, conversely, exhibits lower solubility and is primarily responsible for honey crystallisation during storage. Crystallisation alters sugar availability and may affect the homogeneity of honey dilution before fermentation. Consequently, gentle warming and complete dissolution of crystallised honey are recommended during must preparation to ensure uniform sugar distribution and reproducible fermentation performance [51, 54]. The carbohydrate composition of honey also influences flavour development through its interactions with yeast metabolism. During alcoholic fermentation, glycolytic intermediates serve not only as precursors for ethanol production but also as substrates for the biosynthesis of glycerol, succinic acid, higher alcohols, aldehydes and volatile esters. These secondary metabolites collectively determine the aroma complexity, sweetness perception and mouthfeel of finished mead. Carbon flux through central metabolic pathways is therefore strongly influenced by sugar composition, nutrient availability and the genetic characteristics of the fermenting yeast strain [80-82].

Recent metabolomic studies have demonstrated that different honey varieties produce distinct fermentation metabolite profiles owing to differences in carbohydrate composition and associated minor constituents. Floral sources rich in fructose frequently generate higher concentrations of glycerol and fruity esters, whereas glucose-rich honeys may support more rapid ethanol production but lower concentrations of certain aroma-active compounds. These observations suggest that carbohydrate composition should be considered an important determinant of sensory differentiation and regional product identity in premium mead production [83, 84]. The selection of indigenous palm wine yeasts introduces additional opportunities for optimising carbohydrate utilisation. Native yeasts isolated from palm sap have evolved under naturally sugar-rich conditions and frequently exhibit

enhanced osmotolerance, efficient monosaccharide transport systems and broader substrate utilisation capabilities than conventional commercial strains. Several studies have reported that indigenous African *Saccharomyces*, *Pichia* and *Candida* isolates display superior fermentation efficiency in substrates containing elevated concentrations of glucose and fructose, suggesting that these organisms may improve fermentation performance under the challenging osmotic conditions characteristic of honey must [20, 21, 85]. Furthermore, mixed-culture fermentations combining *Saccharomyces cerevisiae* with selected non-*Saccharomyces* species may enhance carbohydrate utilisation through complementary metabolic activities. Certain non-*Saccharomyces* yeasts preferentially consume fructose or synthesise extracellular enzymes capable of modifying carbohydrate availability, while *S. cerevisiae* completes ethanol production during the later stages of fermentation. Such sequential metabolic interactions may reduce residual sugars, improve fermentation completeness and generate more complex aromatic profiles than single-strain fermentations [19, 27, 34].

Advances in systems biology, comparative genomics and metabolic engineering are further expanding understanding of carbohydrate metabolism in industrial yeasts. Identification of sugar transporter genes, regulatory networks governing glucose repression and pathways involved in fructose utilisation has facilitated the development of improved starter cultures capable of maintaining efficient fermentation under conditions of elevated osmotic stress. Adaptive laboratory evolution has similarly demonstrated potential for selecting yeast strains with enhanced sugar tolerance, faster fermentation kinetics and greater ethanol productivity without compromising flavour quality [16, 25, 86]. Collectively, current evidence indicates that the carbohydrate composition of honey must exert profound effects on fermentation performance, yeast physiology and final mead quality. Future research should integrate detailed carbohydrate profiling with metabolomic and genomic analyses of indigenous palm wine yeasts to identify strain-substrate combinations capable of maximising ethanol yield while enhancing sensory complexity. Such approaches will support the development of precision fermentation strategies tailored to specific honey varieties and regional production systems, thereby improving both process efficiency and commercial competitiveness.

Enzymes, Minerals, Organic Acids and Nitrogenous Compounds in Honey Must

Although sugars dominate the composition of honey must, the behaviour of fermenting yeasts cannot be understood from carbohydrate availability alone. Enzymes, minerals, organic acids, proteins, amino acids and vitamins occur in much smaller quantities, yet they exert substantial effects on yeast growth, osmotic adaptation, acid–base balance, and fermentation kinetics and aroma formation. Their concentrations vary considerably with botanical and geographical origin, bee species, climatic conditions, honey maturity, processing and storage. Consequently, two honey musts adjusted to the same sugar concentration may differ markedly in their nutritional adequacy and fermentation performance.

Enzymatic Constituents of Honey Must

The principal enzymes naturally present in honey include invertase, diastase, glucose oxidase and catalase. These enzymes originate mainly from the hypopharyngeal glands of honeybees, although nectar, pollen and associated microorganisms may also contribute to the enzymatic profile. Their activities are influenced by honey freshness, botanical origin, storage duration and exposure to heat. Enzyme activity therefore provides information not only on the functional composition of honey but also on its processing history and suitability for fermentation [87, 88]. Invertase, also known as sucrase or β-fructofuranosidase, hydrolyses sucrose into glucose and fructose during the conversion of nectar into mature honey. Because most sucrose has already been hydrolysed before honey is harvested, its direct contribution during mead fermentation is generally limited. Nevertheless, residual invertase activity may improve the availability of fermentable monosaccharides in honeys containing comparatively high sucrose concentrations. This may be relevant for certain floral honeys or immature honeys in which sucrose levels remain elevated. However, the practical importance of native honey invertase is reduced when the honey is heated during must preparation, because prolonged or excessive thermal treatment progressively inactivates the enzyme [87, 89]. Diastase represents a group of amylolytic enzymes, particularly α- and β-amylases, capable of degrading starch and related polysaccharides into shorter dextrins and maltose. As honey contains little starch, diastase contributes minimally to the direct release of fermentable sugars in conventional mead. Its principal technological relevance lies in its use as an indicator of honey freshness and heat exposure. A low diastase activity may reflect naturally low enzyme content, prolonged storage or excessive heating, whereas preserved activity generally indicates limited thermal deterioration. Thus, although diastase does not substantially drive mead fermentation, it provides an indirect measure of the extent to which honey handling may have altered other heat-sensitive constituents [87, 90]. Glucose oxidase is particularly important because it catalyses the oxidation of glucose to glucono-δ-lactone, which subsequently hydrolyses to gluconic acid, while simultaneously generating hydrogen peroxide. This reaction contributes to the natural acidity and antimicrobial activity of honey. In concentrated honey, glucose oxidase activity is restricted by low water availability; dilution during must preparation can reactivate the enzyme and temporarily increase hydrogen peroxide formation. The resulting oxidative environment may suppress

contaminating microorganisms, but it may also expose inoculated yeast cells to oxidative stress, particularly during the early stages of fermentation [88, 91]. The effect of glucose oxidase on mead production is therefore potentially dual. Moderate activity may improve microbial control and contribute to the formation of gluconic acid, whereas excessive peroxide accumulation may damage yeast membranes, proteins and nucleic acids. Catalase, derived from pollen and other biological sources, partially moderates this effect by decomposing hydrogen peroxide into water and oxygen. The balance between glucose oxidase and catalase activity may consequently influence oxidative pressure during early fermentation, although this relationship remains insufficiently characterised in honey must inoculated with indigenous yeasts [88, 91]. From a processing perspective, pasteurisation can reduce unwanted microbial populations but may simultaneously inactivate beneficial enzymes and alter volatile or phenolic constituents. Mendes-Ferreira et al. demonstrated that honey-must preparation, including controlled heat treatment and nutrient adjustment, significantly influences fermentation performance [52]. For industrial mead production, heat treatment should therefore be sufficiently effective to improve microbial safety without unnecessarily degrading the native enzymatic and sensory properties of the substrate.

Mineral Composition and Fermentation Relevance

Minerals constitute only a small fraction of honey solids, but they perform essential catalytic and structural functions in yeast metabolism. Potassium is generally the most abundant mineral, while calcium, magnesium, sodium, phosphorus, iron, manganese, zinc and copper occur at lower concentrations. Their abundance varies with floral source, soil composition, environmental conditions and geographical origin. Darker and honeydew honeys commonly contain higher ash and mineral concentrations than lighter blossom honeys, although substantial variation occurs among samples [92, 93]. Potassium contributes to intracellular ionic balance, membrane potential and pH regulation. Magnesium serves as a cofactor for numerous enzymes involved in glycolysis, ATP utilisation, nucleic-acid metabolism and stress resistance. It also contributes to membrane stability and may improve yeast tolerance to ethanol and osmotic stress. Phosphorus is required for the formation of ATP, phospholipids and phosphorylated intermediates of central carbon metabolism. Deficiencies in these minerals can impair cell growth and reduce the efficiency with which glucose and fructose are converted into ethanol. Zinc is required for the activity and structural stability of several enzymes, including alcohol dehydrogenase, which catalyses the final reduction of acetaldehyde to ethanol. However, excessive zinc may inhibit microbial growth and disturb cellular homeostasis. Manganese supports antioxidant defence and enzyme activation, whereas iron and copper participate in redox reactions and respiratory metabolism. Their concentrations require careful control because excessive amounts may catalyse oxidative reactions, promote haze formation or adversely affect beverage stability. The mineral profile of honey must may therefore influence both fermentation efficiency and sensory quality. Nevertheless, the total concentration of minerals in honey does not necessarily reflect their biological availability to yeast. Some elements may be bound to proteins, phenolic compounds or insoluble particles, limiting their accessibility. Dilution also substantially reduces the concentration of minerals originally present in honey. Accordingly, honey must prepared from mineral-poor floral varieties may require micronutrient supplementation, particularly where the selected indigenous yeast exhibits high magnesium, zinc or phosphorus requirements. Conversely, indiscriminate supplementation may be counterproductive. Excess mineral addition can create ionic imbalance, increase oxidative stress or alter flavour. Process optimisation should therefore be based on the mineral composition of the honey and the nutritional requirements of the selected starter culture rather than on universal supplementation protocols. Detailed mineral profiling may be especially valuable when comparing indigenous palm wine yeasts because strains adapted to palm sap may differ from commercial wine yeasts in their micronutrient requirements.

Organic Acids and Buffering Behaviour

Organic acids account for approximately 0.5% of the fresh weight of honey and are important determinants of acidity, flavour, electrical conductivity, microbial stability and botanical identity. Gluconic acid is generally the predominant organic acid, but honey may also contain acetic, citric, formic, fumaric, lactic, malic, malonic, oxalic, propionic, pyruvic, quinic, shikimic, succinic and tartaric acids. The precise profile depends on floral origin, bee metabolism, microbial activity and storage conditions [87, 94]. The acidic character of honey must provides an important selective advantage during fermentation because it suppresses many bacterial contaminants while remaining compatible with the growth of acid-tolerant yeasts. However, pH and titratable acidity represent distinct properties. Honey has a relatively low pH but limited buffering capacity because of its low concentrations of proteins, phosphates and other buffering compounds. During fermentation, production of succinic, acetic and other organic acids may therefore cause a rapid decline in pH. An uncontrolled decrease in pH may inhibit yeast proliferation, impair nutrient transport and contribute to sluggish or arrested fermentation. Indigenous yeasts may differ substantially in their tolerance to acidic conditions; therefore, strains isolated from palm wine should not automatically be assumed to perform optimally in honey must. Palm sap and honey must differ in buffering capacity, nitrogen content and acid composition, making direct strain screening under actual mead conditions essential. Organic acids also contribute significantly to sensory balance. Appropriate acidity counteracts the intense sweetness

of residual fructose and improves freshness, whereas excessive volatile acidity may generate vinegar-like or solvent-associated defects. Succinic acid contributes sourness, bitterness and saltiness, while citric and malic acids provide sharper acidity. Acetic acid is desirable only at low concentrations; excessive formation commonly reflects microbial contamination, oxygen exposure or yeast stress. Adjustment of honey-must acidity is therefore frequently necessary. However, acidification should not be regarded simply as a means of achieving a target initial pH. The type of acid used affects buffering behaviour, microbial selection and sensory development. Mendes-Ferreira et al. found that must formulation, including organic-acid addition and nitrogen supplementation, can improve mead fermentation, although the outcome depends on the wider fermentation conditions [52]. Rational acid management should consequently consider initial pH, titratable acidity, buffering capacity, yeast strain and desired product style rather than relying on a fixed acid dose.

Proteins, Amino Acids and Yeast-Assimilable Nitrogen

Proteins and free amino acids occur only in small quantities in honey. Proline is usually the predominant free amino acid and may account for a substantial proportion of the total amino-acid pool. Other amino acids include phenylalanine, glutamic acid, aspartic acid, alanine, arginine, leucine, isoleucine, lysine, serine, threonine and valine. Their concentrations are strongly influenced by floral origin, pollen content and bee-derived secretions [87,95]. Despite the presence of amino acids, honey is generally a poor source of yeast-assimilable nitrogen. This is one of the major reasons mead fermentation is commonly slower and less predictable than grape-wine fermentation. Moreover, proline is poorly utilised by *S. cerevisiae* under the oxygen-limited conditions that predominate during alcoholic fermentation. Consequently, the total amino-acid concentration of honey may overestimate the fraction that is metabolically accessible to fermenting yeast. Nitrogen is required for amino-acid synthesis, protein production, nucleic-acid formation, membrane biogenesis and cell division. Insufficient nitrogen prolongs the lag phase, restricts biomass formation, reduces sugar-consumption rates and increases the risk of incomplete fermentation. Nitrogen limitation may also alter the production of higher alcohols, esters, volatile sulfur compounds and other aroma-active metabolites. The consequences therefore extend beyond fermentation speed to the sensory quality of the resulting mead. Supplementation with ammonium salts, amino-acid mixtures or complex yeast nutrients can improve fermentation performance, but the timing and dose require careful control. Excessive nitrogen may stimulate excessive biomass production, promote microbial instability or cause imbalanced aroma formation. Early supplementation is generally more effective because yeast cells require nitrogen during their growth phase, whereas additions made after substantial ethanol accumulation may be poorly assimilated. The nitrogen requirements of indigenous palm wine yeasts may differ considerably among species and strains. Some isolates may possess efficient amino-acid transport systems or greater tolerance of nitrogen limitation, while others may require substantial supplementation to complete fermentation. Strain selection should therefore incorporate direct measurement of nitrogen demand, fermentation rate and metabolite formation in defined honey must rather than relying solely on ethanol-tolerance screening.

Vitamins and Other Growth Factors

Honey contains small amounts of water-soluble vitamins, including thiamine, riboflavin, niacin, pyridoxine and pantothenic acid. Although present at low concentrations, these compounds function as precursors of coenzymes involved in carbohydrate metabolism, amino-acid synthesis and redox reactions. Thiamine is particularly important for pyruvate decarboxylase activity, while pantothenic acid is required for coenzyme A synthesis. Dilution, heating and storage can further reduce the already limited vitamin content of honey must. Accordingly, complex nutrient supplements containing vitamins may improve yeast growth more effectively than inorganic nitrogen alone. Nevertheless, the nutritional response is strain-dependent, and supplementation strategies should be validated experimentally to avoid unnecessary additions or sensory consequences. Overall, the minor constituents of honey must function as an interconnected nutritional and physicochemical system. Enzymes influence sugar transformation and oxidative conditions; minerals support metabolic catalysis and stress adaptation; organic acids regulate pH and sensory balance; and nitrogenous compounds determine biomass formation, fermentation rate and aroma metabolism. Effective mead biotechnology therefore requires integrated characterisation of these components rather than correction of individual deficiencies in isolation. For indigenous palm wine yeasts, such characterisation is particularly important because their successful transfer from a traditional palm-sap ecosystem to honey must depends on matching strain-specific nutritional requirements with the biochemical properties of the selected honey.

Indigenous Palm Wine Yeasts as Novel Starter Cultures for Mead Production

Traditional mead production has relied predominantly on commercial *Saccharomyces cerevisiae* strains because of their predictable fermentation performance, high ethanol tolerance and efficient sugar utilisation. However, the increasing demand for premium and regionally distinctive fermented beverages has stimulated interest in indigenous yeasts as alternative starter cultures. Native yeasts isolated from traditional fermented beverages possess unique physiological and metabolic characteristics that may enhance fermentation efficiency while generating more complex flavour

profiles than conventional commercial strains [106-109]. Palm wine is one of the richest natural reservoirs of fermentative microorganisms. During spontaneous fermentation of palm sap, a dynamic microbial community develops, comprising *Saccharomyces*, *Pichia*, *Candida*, *Hanseniaspora*, *Torulaspora*, *Metschnikowia* and other yeast genera alongside lactic acid and acetic acid bacteria. The succession of these microorganisms contributes to ethanol production, aroma development and microbial stability, making palm wine an important source of industrially valuable yeast biodiversity [20-24,110]. Among these microorganisms, *Saccharomyces cerevisiae* generally becomes dominant during the later stages of fermentation because of its superior ethanol tolerance and fermentative capacity. In contrast, non-*Saccharomyces* species predominate during the early stages, where they contribute significantly to the production of esters, higher alcohols, glycerol and other volatile compounds that enhance flavour complexity. Sequential or mixed fermentations involving these yeasts have therefore emerged as an effective strategy for balancing ethanol production with improved sensory quality [19, 27, 111]. Indigenous palm wine yeasts possess several physiological characteristics that make them attractive for mead fermentation. Many isolates exhibit high tolerance to osmotic stress, acidic environments and elevated sugar concentrations, conditions commonly encountered in honey must. They also demonstrate efficient glucose and fructose utilisation, rapid adaptation to nutrient-limited environments and enhanced production of aroma-active metabolites, characteristics that may improve both fermentation performance and product quality [85,112]. Despite these advantages, indigenous yeasts exhibit considerable strain-to-strain variability. Comprehensive phenotypic, genomic and metabolomic characterisation is therefore essential before industrial application. Important selection criteria include fermentation rate, ethanol yield, sugar utilisation, stress tolerance, aroma production, flocculation behaviour and microbiological safety. Modern genomic and adaptive evolution approaches now facilitate the identification and improvement of superior indigenous strains for commercial beverage fermentation [16, 25, 113]. Overall, indigenous palm wine yeasts represent an underutilised microbial resource with considerable potential for sustainable mead biotechnology. Their incorporation into controlled fermentation systems could improve fermentation efficiency, diversify sensory characteristics and promote the development of regionally distinctive premium meads while reducing dependence on imported commercial starter cultures.

Fermentation Dynamics and Optimisation Strategies for Mead Production

Successful mead production depends on the interaction between yeast physiology, substrate composition and fermentation conditions. Unlike grape must, honey must is characterised by high sugar concentrations but limited assimilable nitrogen, vitamins and minerals, making fermentation slower and more susceptible to stress. Optimising fermentation parameters is therefore essential for achieving high ethanol yield, efficient sugar utilisation and desirable sensory characteristics [52, 79, 114].

Fermentation Kinetics

Alcoholic fermentation proceeds through four stages: lag phase, exponential growth, stationary phase and maturation. During the lag phase, yeast adapts to the osmotic stress imposed by concentrated honey sugars. This is followed by rapid sugar metabolism during exponential growth, where glucose and fructose are converted into ethanol, carbon dioxide and numerous secondary metabolites, including esters, higher alcohols and organic acids. As nutrients become depleted and ethanol accumulates, fermentation slows until residual sugars are exhausted or yeast activity ceases [71, 80, 115].

Optimisation of Fermentation Conditions

Temperature is one of the most influential factors affecting fermentation. Most *Saccharomyces cerevisiae* strains perform optimally between 20 and 25°C, where ethanol production is efficient and aroma compounds are well balanced. Higher temperatures accelerate fermentation but may increase undesirable fusel alcohols, whereas lower temperatures prolong fermentation while enhancing ester production and flavour complexity [116,117]. Maintaining an initial pH of 3.5–4.0 suppresses bacterial contaminants while supporting yeast growth. Likewise, adequate oxygen should be supplied only during the early growth phase to promote sterol and membrane synthesis; prolonged oxygen exposure later in fermentation can increase oxidation and reduce product quality [61, 118].

Nutrient Supplementation

Nitrogen deficiency is the principal nutritional limitation of honey must. Supplementation with yeast-assimilable nitrogen, vitamins and minerals significantly improves yeast growth, fermentation rate and ethanol yield while reducing the risk of sluggish or stuck fermentations. Modern mead production commonly employs staggered nutrient addition, where nutrients are supplied in small doses during the early stages of fermentation rather than as a single addition, improving nutrient utilisation and reducing yeast stress [52, 119].

Process Optimisation and Emerging Technologies

Recent advances in mead biotechnology integrate traditional fermentation with modern analytical tools. Response Surface Methodology (RSM), Artificial Neural Networks (ANNs) and machine-learning algorithms have been used to optimise fermentation variables such as sugar concentration, inoculum size, pH and temperature. Likewise, metabolomics and genomic analyses provide deeper insights into yeast metabolism, enabling the selection of

indigenous strains with superior fermentation performance and aroma-producing capabilities [120-122]. Mixed-culture fermentations involving *Saccharomyces* and selected non-*Saccharomyces* yeasts have also gained attention because they improve flavour complexity while maintaining satisfactory ethanol production. These approaches are particularly promising for indigenous palm wine yeasts, which may combine high stress tolerance with unique aromatic properties not achievable using commercial starter cultures alone [111,123]. Efficient mead fermentation requires careful control of temperature, pH, oxygen availability and nutrient supplementation. Integrating indigenous palm wine yeasts with modern optimisation techniques offers significant opportunities to improve fermentation efficiency, enhance sensory quality and develop premium meads with distinctive regional characteristics.

Future Perspectives and Research Gaps

The renewed interest in mead production has created opportunities to integrate traditional fermentation practices with modern biotechnology. Despite significant advances in yeast physiology and fermentation engineering, commercial mead production remains constrained by inconsistent fermentation performance, prolonged processing times and limited utilisation of indigenous microbial resources. Future research should therefore focus on developing robust starter cultures, optimising honey must composition and applying emerging omics technologies to improve fermentation efficiency and product quality [124-126]. A major research priority is the systematic exploration of indigenous palm wine yeasts. Although numerous studies have reported the microbial diversity of palm wine, relatively few have evaluated these isolates as starter cultures for mead fermentation. Comprehensive screening should include ethanol productivity, sugar utilisation, osmotic tolerance, acid resistance, aroma formation, flocculation behaviour and genomic stability under honey must conditions. Such evaluations would facilitate the selection of strains specifically adapted for industrial mead production rather than relying exclusively on commercial wine yeasts [110,127]. Another important area is the application of multi-omics technologies, including genomics, transcriptomics, proteomics and metabolomics. These approaches provide detailed insights into yeast metabolism, stress responses and flavour biosynthesis, enabling the identification of genetic markers associated with desirable fermentation traits. Coupling multi-omics data with computational modelling and machine learning could accelerate the development of superior indigenous starter cultures with improved fermentation performance and reproducibility [121,128]. Process optimisation also remains an important research need. Advanced optimisation techniques such as Response Surface Methodology (RSM), Artificial Neural Networks (ANNs) and digital fermentation models can simultaneously evaluate multiple fermentation variables, including temperature, pH, nutrient supplementation and inoculum size. These predictive tools offer greater precision than traditional one-factor-at-a-time experiments and can significantly reduce development costs while improving product consistency [120,129]. Sustainability should become a central consideration in future mead biotechnology. Locally isolated palm wine yeasts represent an inexpensive and renewable microbial resource that could reduce dependence on imported commercial starter cultures. Their adoption may also enhance the commercial value of indigenous biodiversity while supporting regional honey industries and promoting sustainable bioeconomy initiatives across Africa and other tropical regions [130]. Despite these promising developments, several knowledge gaps remain. The interactions between indigenous palm wine yeasts and different honey varieties are still poorly understood, particularly regarding nutrient requirements, phenolic biotransformation and long-term fermentation stability. Furthermore, most published studies remain laboratory-based, with limited pilot- or industrial-scale validation. Addressing these gaps will be essential for translating indigenous yeast biodiversity into commercially viable mead production systems. Overall, integrating indigenous palm wine yeasts with modern fermentation biotechnology offers a promising pathway for producing premium meads with improved fermentation efficiency, enhanced sensory complexity and stronger regional identity. Future interdisciplinary research combining microbiology, food biotechnology, metabolomics and process engineering will be instrumental in realising this potential.

CONCLUSION

Honey must is a nutritionally unique fermentation substrate characterised by abundant fermentable sugars but limited assimilable nitrogen, vitamins and minerals. These characteristics create physiological challenges for fermentative yeasts, making nutrient management and process optimisation critical for successful mead production. The composition of honey including its carbohydrates, organic acids, minerals, enzymes and phenolic compounds-collectively influences yeast metabolism, fermentation kinetics, ethanol yield and the sensory quality of the final beverage. Indigenous palm wine yeasts represent a valuable but underexploited microbial resource for mead biotechnology. Their natural adaptation to sugar-rich fermentation environments, coupled with their ability to produce distinctive aroma compounds, positions them as promising alternatives or complements to conventional commercial *Saccharomyces cerevisiae* starter cultures. However, successful industrial application requires comprehensive characterisation of their physiological, metabolic and genomic properties under honey must conditions. Advances in genomics, metabolomics, artificial intelligence and fermentation modelling now provide unprecedented opportunities to optimise yeast selection and fermentation processes. Combining these technologies

with systematic evaluation of indigenous yeasts could improve fermentation reliability, enhance flavour complexity and promote the development of regionally distinctive premium meads. This review proposes that the future of mead biotechnology lies not only in improving fermentation conditions but also in harnessing indigenous yeast biodiversity through precision fermentation approaches. Integrating traditional microbial resources with modern systems biology and process optimisation offers a sustainable strategy for advancing commercial mead production while preserving regional fermentation heritage and expanding the diversity of fermented beverages available to global markets.

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