1	The periodic table of fermented foods: limitations and opportunities
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15 Abstract

16 Fermentation is one of the oldest methods of food processing and accounts for a substantial 17 proportion of human foods, including not only staple foods such as bread, cereal porridges or 18 fermented legumes but also fermented vegetables, meats, fish and dairy, alcoholic beverages as 19 well as coffee, cocoa and condiments such as vinegar, soy sauce and fish sauces. Adding the 20 regional varieties to these diverse product categories makes for an almost immeasurable diversity 21 of fermented foods. The periodic table of fermented foods aims to map this diversity on the 118 22 entries of the periodic table of chemical elements. While the table fails to represent the diversity 23 of fermented foods, it represents major fermentation substrates, product categories, fermentation 24 processes and fermentation organisms. This communication addresses limitations of the graphical display on a "periodic table of fermented foods", but also identifies opportunities that relate to 25 questions that are facilitated by this graphical presentation: on the origin and purpose of food 26 27 fermentation, which fermented foods represent "indigenous" foods, differences and similarities in 28 the assembly of microbial communities in different fermentations, differences in the global 29 preferences for food fermentation, the link between microbial diversity, fermentation time and 30 product properties, and opportunities of using traditional food fermentations as template for 31 development of new products.

Keywords. Fermented foods, *Lactobacillus*, *Saccharomyces cerevisiae*, indigenous fermented
 foods.

35 Key points.

- Fermented foods are produced in an almost immeasurable diversity
- Fermented foods were mapped on a periodic table of fermented foods
- This table facilitates identification of communalities and differences of products

40 Introduction

41 Fermented foods have been defined as "foods made through desired microbial growth and 42 enzymatic conversions of food components" (Marco et al. 2021), which emphasizes microbial 43 conversions as the defining characteristic of fermented foods. Fermented foods account for a 44 considerable portion of foods eaten by humans, including not only staple foods such as bread, 45 cereal porridges or beverages and fermented legumes or legume proteins but also fermented meats, 46 fish and dairy, fermented vegetables and alcoholic beverages as well as specialty products and 47 condiments such as vinegar, coffee, cocoa, soy sauce and fish sauces (Steinkraus 1997; Hutkins 48 2019). Fermentation is one of the oldest methods of food processing and has been used since the 49 Neolithic revolution, the transition from hunter-gatherer societies to agricultural societies about 50 14,000 years ago (Hayden et al. 2013; Arranz-Otaegui et al. 2018). Among the fermented foods, 51 the cereal products bread and beer are the oldest fermented food products for which archeological 52 evidence is available (Hayden et al. 2013; Arranz-Otaegui et al. 2018). Just about any agricultural 53 crop or animal product including fruits, cereals, vegetables, milk, fish and meats is fermented at 54 some place in the world, with insect protein as one of few commodities for which traditional 55 fermentation processes have not been described.

The microbiology of food fermentation, which initiated the transition from traditional, indigenous knowledge systems to scientific knowledge systems for production of fermented foods, was first described in 1857, when Louis Pasteur attributed alcoholic fermentation to *Saccharomyces cerevisiae* (Pasteur, 1857 as reproduced by (Brock 1992). The industrial production of baker's yeast for bread leavening started in Vienna only 10 years later (Gélinas 2010). Lactic acid bacteria were first isolated by Joseph Lister in the 1870ties (Lister 1877); a comprehensive description of lactic acid bacteria in food fermentations, which remained relevant for much of the 20th century,

63 was published in 1919 (Orla-Jensen 1919). Undefined bacterial starter cultures for baking and dairy fermentations have been available since the late 19th or early 20th century (Brandt 2007); 64 65 followed by defined strain cultures for dairy, meat, wine, and vegetable fermentations. Food 66 cultures are not only of economic importance but have also been recognized in relation to their 67 beneficial effect on human health (Marco et al. 2017; Wastyk et al. 2021), as microbial cell 68 factories (Sun et al. 2015) and as model systems to study ecology, physiology, and evolution, and 69 domestication of microbes (Wolfe and Dutton 2015; Gallone et al. 2016; Duar et al. 2017b). 70 Evidence for domestication of eukaryotic food fermenting microbes has been provided by large 71 scale comparative genomic analyses of several fermentation organisms including Saccharomyces 72 cerevisiae, Aspergillus oryzae and Penicillium roqueforti. In eukaryotes, domestication resulted in 73 distinct phylogenetic clades that are composed exclusively of isolates from food fermentations 74 with a long history of back-slopping. These isolates also exhibit physiological and genetic traits 75 that differentiate the strains from their "wild" ancestors (Gibbons et al. 2012; Gallone et al. 2016; 76 Dumas et al. 2020). Evidence for domestication of prokaryotes, however, remains much less 77 convincing (van de Guchte et al. 2006; Zheng et al. 2015; Kelleher et al. 2017).

78 Despite the economic impact, cultural significance and scientific relevance of fermented foods, 79 only few dedicated textbooks provide an overview on the diversity of fermented foods (Gänzle 80 2019; Hutkins 2019). Since 2014, I have started to map the diversity of fermented foods on the 81 template of the periodic table of chemical elements, a process that was initiated over a Friday 82 afternoon discussion with colleagues that explored whether a "Periodic Table of Fermented Foods" 83 may be a useful tool for teaching of the science of food fermentations at the University of Alberta. 84 An initial version of the periodic table of fermented foods was published in 2015 (Gänzle 2015) 85 but the table continues to be modified with input from collaborators, colleagues and students in the Nutrition and Food Science undergraduate program of the University of Alberta. This communication will briefly present the Periodic Table of Fermented Foods and its outline its limitations. It also aims to outline whether graphical presentation of the diversity of fermented foods to match the periodic table of chemical elements gives rise to relevant scientific questions and hypotheses.

91 Limitations of the Periodic Table of Fermented Foods.

92 The periodic table of chemical elements represents a natural law of the periodicity of the properties 93 of the chemical elements (Balarew 2019). In contrast, a natural law of the periodicity of fermented 94 foods does not exist. Moreover, despite all efforts to reduce the author's ignorance on the diversity 95 of fermented foods, to prioritize those fermented foods for which data is available in the scientific 96 literature, and to avoid cultural or geographic bias in the selection of foods that are represented on 97 the periodic table, the presentation remains incomplete and the selection remains to some extend 98 arbitrary. A table with 118 entries cannot represent the diversity of fermented foods. To provide 99 three examples; the periodic table lists 21 cheeses; however, France alone is thought to produce 100 more than 1000 distinct cheese varieties and a comparable number of varieties is produced other 101 countries with a tradition of cheese making (e.g. http://www.formaggio.it/). Africa is represented 102 on the table with only 10 entries, however, a continent on which 2000 different languages are 103 spoken can be expected to have as many, or more, different fermented foods. Vegetables that are 104 fermented in a brine with about 2% NaCl are represented by a single entry, sauerkraut, but many 105 different products that employ a comparable fermentation process but use different ingredients, 106 spices or condiments and have different designations are widely consumed in Europe, South Asia 107 and East Asia (Table 1).

108 **Opportunities of organizing the diversity in a Periodic Table of Fermented Foods.**

109 What is the merit, then, of omission of a majority of fermented foods for display of 118 entries in 110 a "periodic table"? First, the process of omission forces to emphasize similarities of different 111 products over differences. For example, fermented vegetables are produced by cutting, brining in 112 salt solutions, followed by fermentation in a closed container at ambient temperature (Ashaolu and 113 Reale 2020). The best known products are sauerkraut, which represents this product category in 114 Figure 1, and kimchi, but numerous other products are produced with similar methods and with 115 comparable fermentation organisms in Europe and Asia (Table 1). Likewise, mahewu is produced 116 in Zimbabwe by inoculating a slurry prepared from cooked corn flour with millet malt as a source 117 of amylolytic and proteolytic enzymes, and of fermentation microbiota (Pswarayi and Gänzle 118 2019). Comparable processes and principles are used to prepare cereal beverages in other African 119 countries (Table 2)(Nout 2009; Franz et al. 2014). From a culinary and cultural perspective, these 120 products are very different; from the perspective of the fermentation process or the principles of the assembly of microbial communities, these products share enough similarities to warrant only 121 122 a single entry that represents all comparable products.

A graphical display with 118 entries also allows a quick overview on fermentation substrates, products and fermentation organisms that cannot be provided in a larger figure with several thousand entries to fully map the diversity of fermented foods. Some of these questions – which fermentations include acetic acid bacteria? Which type of products are produced from fish? How is red wine produced from colorless cereal flours? - are readily answered by consulting Figure 1. Other questions that arise from a representative overview rather than a comprehensive display are discussed in more detail below.

130 Origin and purpose of food fermentation

131 Publications on fermented foods emphasize the aspect of food preservation and food safety as a 132 motivation for fermenting foods (Nout and Motarjemi 1997; Steinkraus 1997). Preservation is 133 indeed a major aspect in the fermentation of vegetables, dairy products, fish, and fermented meats 134 (groups 12 to 18 in Figure 1). Food fermentations preserve vegetables as a source of vitamins in 135 winter, when fresh vegetables are not available in temperate climates. Fermentation also converts 136 the perishable animal products milk, meat and fish to commodities that can stored and traded over 137 long distances (Kindstedt 2012). Animal agriculture emerged, however, several thousand years 138 after the cultivation and fermentation of the cereal crops (Rowley-Conwy 2011; Arranz-Otaegui 139 et al. 2018) and preservation is thus an unlikely driver for the first food fermentations during the 140 Neolithic revolution.

141 A second major reason for fermentation of fruits, tubers and cereals is the human desire for 142 intoxication, which motivates production of alcoholic beverages in virtually all cultures and on all 143 continents (groups 1 through 4, marihuana edibles and spirits in Figure 1) and has been proposed 144 to be one of the drivers for the first food fermentations in the Natufian (Hayden et al. 2013). 145 Because beer is also a source of energy and nearly isotonic, hydration with low-alcohol beer may 146 be advantageous over water. The notion that medieval city dwellers consumed beer with low 147 ethanol content to avoid contaminated drinking water, however, was identified as a myth 148 (Mortimer 2009; Fusco et al. 2019).

A third motivation for food fermentations is the facilitation of milling of cereals and removal of anti-nutritive compounds including phenolic compounds, enzyme inhibitors and phytate, and an improved digestibility of plant crops (Gänzle 2020). Replacing a diverse hunter-gatherer diet with cereal grains, legume seeds, and tubers is a poor proposition unless the palatability and digestibility

153 of these crops and the availability of micro-nutrients is improved by milling, fermentation and 154 heating (Kayodé et al. 2013; Montemurro et al. 2019). In some cases, fermentation is a necessity 155 to remove toxic plant secondary metabolites, e.g. cyanogenic β -glucosides in cassava (group 5), 156 which cause debilitating disease unless they are removed by fermentation or other suitable 157 processes (Kobawila et al. 2005; Nzwalo and Cliff 2011). Steeping of grains also reduces the effort 158 that is needed for wet milling of the grains (Gänzle and Salovaara 2019); an advantage that remains 159 relevant in areas where cereals are processed at the household level. Examples include mawé and 160 ogi produced in Benin (Houghouigan et al. 1993; Greppi et al. 2013) and koko and kenkey 161 produced in Ghana (Halm et al. 1993; Lei and Jakobsen 2004). Extended steeping of cereal grains 162 not only facilitates wet milling but also initiates fermentation, which continues after the milled 163 grains are further processed to porridges or beverages.

Last but not least, fermented foods such as miso, soy sauce, vinegar, coffee or vanilla are produced with the purpose to please the palate. While some of the products, e.g. soy sauce analogues or coffee, can be produced with alternative enzymatic or chemical processes that do not involve microbial conversions (Suzuki et al. 2017), fermented products avoid the use of ingredients or additives, and often have superior sensory properties.

169 Few, if any, of the fermented foods are "ethnic" but almost all represent "indigenous" foods

Figure 1 represents the geographic origin of each product in the upper right of each box, which is colored green if lactic acid bacteria are major members of fermentation microbiota. In recognition to the link of food fermentations to geographic locations and cultures, numerous publications refer to fermented foods outside of Europe and North America as "ethnic fermented foods" (Kwon 2015) or "indigenous fermented foods". The term "ethnic foods" was defined as "an ethnic group's or a country's cuisine" (Kwon 2015) or, in a narrower ethnographic meaning, as "food prepared

or consumed by members of an ethnic group as a manifestation of its ethnicity" (Anonymous) and thus includes ancestry in the definition of ethnicity. The term "indigenous", defined by the Merriam-Webster online Dictionary as "produced (...) in a particular region or environment", is not specific to nations, countries or ethnicity but accommodates fermented foods that are produced by specific to a particular town or other narrowly defined geographic locations that may or may not relate to ethnicity or nationality.

182 A vast majority of fermented foods are specific to, or originate from, specific cultures or regions 183 (Figure 1) and are in some cases a matter of fierce national pride (Jang et al. 2015). This strong 184 link to geography is determined by climate and geography, which determine the availability of 185 fermentation substrates; by the economic constitution of societies, which determines whether 186 fermented foods are produced at the household level, by trades, or in large industrial operations; 187 and by local cultural or religious traditions that define the indigenous knowledge systems on which 188 the fermentation processes are based and the cultural or social context in which fermented foods 189 are consumed (Ströbele 2010). Most fermented foods were produced before scientific knowledge 190 systems were applied for food production. With few exceptions that are discussed below, 191 fermented foods can thus generally be designated as "indigenous foods".

Community assembly in food fermentations: Differences and similarities between different fermentations.

194 Color coding of the fermented foods informs on the main groups of fermentation organisms; 195 representative microbial species are also indicated. The diversity of fermented foods is matched 196 by the diversity of fermentation organisms. In 2022, an inventory of food cultures with beneficial 197 technological use that has been compiled by the International Dairy Federation included more than 198 226 bacterial and 95 fungal species (Bourdichon et al. 2012; Bourdichon et al. 2022). The characterization of fermentation microbiota by full shotgun metagenomic sequencing (Cao et al.
200 2017) and the description of more than 100 new species of food-fermenting organisms
201 (www.lactobacillus.ualberta.ca/)(Zheng et al. 2020) continues to increase the known diversity of
202 food cultures.

203 Despite this large diversity of fermentation organisms, common patterns for community assembly 204 can be derived from the periodic table of fermented foods. The assembly of communities of 205 organisms is determined by dispersal, selection, speciation and drift (Vellend 2010). Of these four, 206 drift, designating random events, can be ignored if the totality of fermentations rather than an 207 individual fermentation batch is considered. The relevance of dispersal depends on whether the 208 fermentations is controlled by back-slopping (thick box outline and underlined product name in 209 Figure 1)(Li and Gänzle 2020) or relies on the microorganisms that are associated with the raw 210 materials or the processing environment (Miller et al. 2019; Pswarayi and Gänzle 2019). Back-211 slopping eliminates dispersal limitation and allows recruitment of highly specialized and niche-212 adapted fermentation organisms (Gänzle and Zheng 2019; Marco et al. 2021). Examples include 213 the host adapted Streptococcus thermophilus, Lactobacillus helveticus and L. delbrueckii in dairy 214 fermentations (Li and Gänzle 2020); the co-existence of Lactobacillus and Limosilactobacillus 215 species, which is characteristic for the intestinal microbiota of many animals but also observed in 216 back-slopped cereal fermentations (Walter 2008; Duar et al. 2017a; Gänzle and Zheng 2019); and 217 the presence of *Fructilactobacillus sanfranciscensis*, an organism that is likely adapted to insect 218 hosts, in sourdoughs (Gänzle and Zheng 2019). The selective pressure that is exerted by 219 fermentation conditions and raw materials is independent of the geographic location. Each of the 220 three examples indicate above is documented by multiple products from multiple countries 221 representing at least three continents (Figure 1).

222 Spontaneous fermentations that are not controlled by back-slopping or starter cultures also exhibit 223 reliable and globally uniform communities of fermentation microbes that have a stable association 224 with the raw material. This is best exemplified with spontaneous plant fermentations, which are 225 characterized by a consistent succession of fermentation microbiota. Spontaneous plant 226 fermentations are initiated by plant associated Enterobacteriaceae including Cronobacter, 227 Kosakonia, Klebsiella and Citrobacter, which are among the most abundant representatives of 228 commensal plant microbiota (Schmid et al. 2009; Allahverdi et al. 2016; Pavlova et al. 2017; Taulé 229 et al. 2019). Enterobacteriaceae are followed by the more acid tolerant enterococci, lactococci, 230 Leuconostoc and Weissella species. Eventually the acid tolerant Lp. plantarum or pediococci in 231 association with Lm. fermentum or Lv. brevis prevail (Jung et al. 2012; Wuyts et al. 2018; Pswarayi 232 and Gänzle 2019). This succession of microorganisms is comparable at the family level 233 (Enterobacteriaceae) or at the genus level (lactic acid bacteria) for most spontaneous plant 234 fermentations including cereal products or tubers in groups 5 to 7, vegetable fermentations (group 235 12), and coffee and cocoa (Figure 1). Community assembly can be manipulated by addition of salt 236 (e.g. Fu-Tsaii, # 112)(Chao et al. 2009) or by addition of acids to inhibit the initial growth of 237 Enterobacteriaceae. Convergence of fermentation communities is also observed for alcoholic 238 fermentations, which all include Saccharomyces cerevisiae as a major fermentation organism. All 239 fermentations that include addition of more than 10% NaCl include, irrespective of the substrate, 240 include *Tetragenococcus halophilus* (Figure 1).

Speciation or domestication of bacterial species in food fermentation organisms has not been convincingly demonstrated. Although the molecular clock of bacterial evolution is poorly calibrated (Duchêne et al. 2016), the domestication of bacterial organisms with genetic and physiological traits that differentiate fermentation organisms from their "wild" ancestors likely requires more time than elapsed since the onset of back-slopped food fermentations (Duar et al. 2017b). Eukaryotes evolve with different mechanisms and at a different pace, though, and domestication of food fermenting yeasts and fungi was demonstrated for *Aspergillus oryzae* from koji fermentation, *S. cerevisiae* from beer and sourdough, and for *Penicillium roqueforti* (Gibbons et al. 2012; Gallone et al. 2016; Dumas et al. 2020; Bigey et al. 2021).

In short, the comparison of fermentation microbiota in different fermented foods worldwide demonstrates that, while the fermented products have a strong link to specific regions or countries, the composition of fermentation organisms is globally uniform if comparable substrates and fermentation processes are employed.

254 North and South, East and West

255 The periodic table of fermented foods highlights preferences for fermentation substrates and 256 fermentation processes at a global scale (Fig. 1 and Fig. 2). Bread has traditionally been produced 257 in all temperate climates that support cultivation of wheat or rye (Gänzle and Zheng 2019; Arora 258 et al. 2021). In East Asia, steamed bread is preferred (Yan et al. 2019); South Asia, the Middle 259 East and North Africa traditionally produce flat breads; in Europe, bread is baked in loaves. 260 Conversely, fermented cereal foods in Sub-Saharan Africa are consumed predominantly as 261 porridges or non-alcoholic beverages, which are not as common in other parts of the world (Fig. 262 2) (Nout 2009; Franz et al. 2014). The color coding in Figure 2 accounts for the documentation 263 that fermentation cultures that are used in the Americas and Oceania are "immigrants" that were 264 brought by the European that settled on these continents (Salama et al. 1991; Gallone et al. 2016). 265 In Europe and Africa, starch saccharification to produce alcoholic beverages, non-alcoholic 266 beverages or vinegar is achieved by the use of malt; barley malt in Europe or millet and sorghum 267 malts in Africa. In East Asia, starch saccharification is achieved by microbial saccharification

268 cultures. Koji, a back-slopped and domesticated cultures of Aspergillus soyae or Aspergillus 269 oryzae, is used in Japan (Gibbons et al. 2012). Daqu, a spontaneous fermentation that recruits 270 bacilli, plant-associated *Enterobacteriaceae* and lactic acid bacteria as well as yeasts and moulds 271 to produce amylases and proteases that hydrolyse starch and proteins in a subsequent mash 272 fermentation, is used in China (Fig. 2)(Zheng et al. 2012; Mu et al. 2014). In addition, the 273 traditional use of *Monascus purpureus* to produce red- or yellow-coloured cereal foods is unique 274 to South-East Asia (Lin et al. 2008). Efforts to use the organisms in fermentations in Europe and 275 North America have stalled as the production of red or yellow pigments is invariably associated 276 with the production of the mycotoxin citrinin (Patakova 2013).

277 Milk has traditionally been used for cheese production in Europe, the Mediterranean, the Middle 278 East and the Eurasian Steppes. Communities in Africa and South Asia ferment milk predominantly 279 to yoghurt and comparable set but not strained dairy products (Jans et al. 2017). Conversely, 280 fermentation of legume (soy) protein to diverse products including *tempe*, *natto*, *sufu* or stinky *tofu* is common on East Asia but not in other regions of the world (Fig. 2)(Han et al. 2004; Nout and 281 282 Kiers 2005; Inatsu et al. 2006). The use of precipitated soy proteins as fermentation substrate also 283 recruits fermentation organisms that are not observed in other parts of the world, e.g. Rhizopus 284 stolonifer for production of tempe (Nout and Kiers 2005) and Bacillus subtilis, which is used for fermentation of natto (Tsuji et al. 2015). 285

Fish fermentations have traditionally been used in Scandinavian countries and in South East Asia. Examples for Scandinavian fermentations include *harkarl*, fermented shark produced in Iceland, and *surströmming* in Sweden (Skåra et al. 2015). East Asia produces fermented fish sauces, where the composition of fermentation microbiota is controlled by addition of more than 10% NaCl, and fermented sour fish were the composition of fermentation microbiota is controlled by addition of 291 carbohydrates including starch (rice) or sugars and / or addition of salt (Paludan-Müller et al. 2002). The author is unaware of comparable fermented products in other regions of the world 293 where seafood is available. The production of *garum*, however, a fish sauce that was produced in 294 ancient Rome but came out of fashion after the fall of the Roman Empire (Corcoran 1963), 295 indicates that this is a question of preference.

296 Microbial diversity and product properties

297 The arrangement of selected fermented foods in the periodic table of fermented foods roughly 298 matches the flavor intensity within each groups, with the blandest examples at the left and top and 299 the product with the most intense flavor at the right and bottom (Figure 1). This arrangement 300 indicates that long fermentation times and / or a diverse fermentation microbiota results in a more 301 intense flavor. The case can be convincingly made with two somewhat exotic examples, 302 surströmming, a fermented fish product from Sweden, and kopi luwak (civet coffee). The 303 fermented fish product surströmming is produced with diverse fermentation organisms that 304 represent several bacterial phyla including Firmicutes, Bacteriodetes, gamma-Proteobacteria and 305 Actinobacteria. The resulting product smells somewhat intense (Belleggia et al. 2020). Kopi 306 Luwak is produced by feeding civet cats with coffee fruits and collecting the excreted beans after 307 fermentation by the intestinal microbiota of civet cats. Intestinal microbiota of the civet cat are 308 dominated by acetic acid bacteria, lactic acid bacteria and Enterobacteriaceae (Watanabe et al. 309 2020), which overlaps with those organisms dominating wet fermentation process of coffee beans 310 (de Melo Pereira et al. 2017) but includes additional organisms as well as digestive enzymes of 311 the civet cat.

The case can also be made with the more commonly consumed fermented products bread and cheese. Long-term cheese ripening recruits non-starter lactic acid bacteria that contribute to flavor 314 formation in addition to the starter cultures (Lo et al. 2018). During cheese ripening, casein is 315 hydrolysed to taste-active peptides and amino acids, in particular glutamate, which can accumulate 316 to levels exceeding the taste threshold more than 500-fold (Toelstede and Hofmann 2008; 317 Hillmann et al. 2016). Straight-dough bread is fermented only with baker's yeast while sourdough 318 baking includes a contribution of lactic acid bacteria and sourdough yeast, predominantly 319 Kazachstania humilis, to biochemical conversions during bread-making, and generally involves 320 extended fermentation times (Gänzle 2014; Gänzle and Zheng 2019; Arora et al. 2021). In 321 comparison to straight dough bread, sourdough bread is characterized by a greater diversity and 322 higher concentration of taste-active compounds and odour volatiles (Hansen and Schieberle 2005; 323 Zhao et al. 2015). A last example relates to the comparison of two distilled grain liquors, whisky 324 and *baijou*. Whisky is fermented with *S. cerevisiae* with a variable contribution of lactobacilli (van 325 Beek and Priest 2000); odorants are additionally derived from the malt, the peat smoke used for 326 drying of the malt and the casks used for maturation (Jeleń et al. 2019). The fermentation process 327 for grain liquors in China includes contributions from diverse microbes including yeasts, fungi, 328 bacilli, gamma-Proteobacteria and beta-Proteobacteria, and Firmicutes which include but are not 329 limited to Lactobacillales (lactic acid bacteria) (Zheng and Han 2016). Again, the higher diversity 330 of microbes that is recruited for *baijou* fermentation results in a higher diversity and intensity of 331 flavor volatiles (Jeleń et al. 2019; Chen et al. 2021).

332 Tradition and innovation

The industrialization of food production also resulted in the industrialization of the production of fermented foods. This process generally involved scaling of traditional fermentation processes and transition from traditional, indigenous knowledge systems to scientific knowledge systems; in short, moving from "art to science". Currently, food fermentations extend to products for which 337 no traditional template exists. In these cases, the periodic table of fermented foods can guide the 338 development of fermentation processes in the absence of a traditional template. Examples include 339 the fermentation of insects (Kewuyemi et al. 2020) or the production of plant cheeses (Jeewanthi 340 and Paik 2018), where information on fermentation of other protein foods (soy, groups 10 and 11, 341 dairy, groups 13 - 16 and fish and meat, groups 17 and 18) may provide useful information on the 342 use of fermentation organisms and enzymes to improve product quality. Moreover, fermentation 343 of vegetables has re-emerged as a method to provide high-quality food not only at the household 344 level but also by chefs and small start-up companies. The corresponding products are not limited 345 to those for which traditional templates exist (Redzepi and Zilber 2018).

346 Current commercial relevance for novel, non-traditional fermented foods relate for example to 347 alcohol-free fermented cereal beverages and gluten free bread. Fermentation of malt with lactic 348 acid bacteria or acetic acid bacteria allows adjusting the level of sweetness, acidity and carbonation 349 or "fizz" to levels that meets consumer's expectations (Bronnmann and Hoffmann 2017). Non-350 alcoholic fermented cereal beverages are widely consumed in Africa and, to a lesser extend, in 351 East Europe but not in Central or Western Europe (Taylor 2016). Element # 102, Bionade, provides 352 an example of a non-traditional fermented "designer" food. Likewise, the development of gluten-353 free bread in the last two decades necessitated building on information related to traditional 354 fermentation of sorghum, millet or corn fermentations to develop a fermented food for which no 355 traditional template is available (Gallagher et al. 2004).

356 Concluding remarks.

357 Mapping the diversity of fermented foods on a simple graphical display is impossible in a world 358 that is inhabited by 8 billion humans where many products are fermented at the household or 359 regional level. The effort to produce such a simple graphical display nevertheless has merit as it 360 necessitates acknowledgement of the - largely unknown - diversity but also allows to derive 361 common patterns in the fermentation of products that, at first sight, appear to be very different. 362 Many of the fermented foods contain live fermentation microbes at the time of consumption 363 (groups 6, 7, 12 to 18, and several elements in the group "tea, coffee, chocolate, and various 364 beverages). Live microbes that are present in fermented foods are increasingly recognized as 365 contributors to human health even if no strain specific health claims were established (Marco et 366 al. 2021; Wastyk et al. 2021). The periodic table of fermented foods also provides an indication of 367 the many fermented foods that are likely to please one's palate but remain to be sampled. Last but 368 not least, many fermented foods negate conventional wisdom and are tasty *and* healthy.

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377 **References**

Allahverdi T, Rahimian H, Ravanlou A (2016) First report of bacterial canker in mulberry caused
by *Citrobacter freundii* in Iran. Plant Dis 100:1774

Anonymous Ethnic Cuisines | Encyclopedia.com.
 https://www.encyclopedia.com/food/encyclopedias-almanacs-transcripts-and-maps/ethnic-

382 cuisines. Accessed 17 Aug 2021

- Arora K, Ameur H, Polo A, Di Cagno R, Rizzello CG, Gobbetti M (2021) Thirty years of
 knowledge on sourdough fermentation: A systematic review. Trends Food Sci Technol
 108:71–83 . https://doi.org/10.1016/J.TIFS.2020.12.008
- 386 Arranz-Otaegui A, Carretero LG, Ramsey MN, Fuller DQ, Richter T (2018) Archaeobotanical
- evidence reveals the origins of bread 14,400 years ago in northeastern Jordan. Proc Natl Acad

388 Sci U S A 115:7925–7930 . https://doi.org/10.1073/pnas.1801071115

- 389 Ashaolu TJ, Reale A (2020) A holistic review on Euro-Asian lactic acid bacteria fermented cereals
- 390andvegetables.Microorganisms8:1176
- 391 https://doi.org/10.3390/MICROORGANISMS8081176
- Balarew C (2019) The periodic table of chemical elements history, nature, meaning. Pure Appl
 Chem 91:2037–2042 . https://doi.org/10.1515/PAC-2019-0902
- 394 Belleggia L, Aquilanti L, Ferrocino I, Milanović V, Garofalo C, Clementi F, Cocolin L, Mozzon
- M, Foligni R, Haouet MN, Scuota S, Framboas M, Osimani A (2020) Discovering microbiota
 and volatile compounds of *surströmming*, the traditional Swedish sour herring. Food
 Microbiol 91:103503 . https://doi.org/10.1016/J.FM.2020.103503
- 398 Bigey F, Segond D, Friedrich A, Guezenec S, Bourgais A, Huyghe L, Agier N, Nidelet T, Sicard
- 399 D (2021) Evidence for two main domestication trajectories in Saccharomyces cerevisiae
 400 linked to distinct bread-making processes. Curr Biol 31:722-732.e5 .
- 401 https://doi.org/10.1016/J.CUB.2020.11.016
- 402 Bourdichon F, Budde-Niekiel A, Dubois A, Fritz D, Hatte J-L, Laulund S, McAuliffe O,
 403 Ouwehand AC, Yao S, Zgoda A, Zuliani V, Morelli L (2022) Bulletin of the IDF N°514/2022:

- 404 Inventory of microbial food cultures with safety demonstration in fermented food products –
- 405 FIL-IDF. https://shop.fil-idf.org/collections/publications/products/bulletin-of-the-idf-n-514-
- 406 2022-inventory-of-microbial-food-cultures-with-safety-demonstration-in-fermented-food-
- 407 products. Accessed 26 Mar 2022
- 408 Bourdichon F, Casaregola S, Farrokh C, Frisvad JC, Gerds ML, Hammes WP, Harnett J, Huys G,
- 409 Laulund S, Ouwehand A, Powell IB, Prajapati JB, Seto Y, Ter Schure E, Van Boven A,
- 410 Vankerckhoven V, Zgoda A, Tuijtelaars S, Hansen EB (2012) Food fermentations:
- 411 Microorganisms with technological beneficial use. Int J Food Microbiol 154:87–97.
- 412 https://doi.org/10.1016/j.ijfoodmicro.2011.12.030
- 413 Brandt MJ (2007) Sourdough products for convenient use in baking. Food Microbiol 24:161–164
 414 . https://doi.org/10.1016/j.fm.2006.07.010
- 415 Brock TD (1992) Milestones in Microbiology. Science Tech Publishers, Madison, Wisconsin
- 416 Bronnmann J, Hoffmann J (2017) Product differentiation in the German soft drink market: which
- 417 attributes matter? https://doi.org/101080/1350485120171388906 25:968–971 .
- 418 https://doi.org/10.1080/13504851.2017.1388906
- Cao Y, Fanning S, Proos S, Jordan K, Srikumar S (2017) A review on the applications of next
 generation sequencing technologies as applied to food-related microbiome studies. Front
 Microbiol 0:1829 . https://doi.org/10.3389/FMICB.2017.01829
- 422 Çetin B (2013) Production of probiotic mixed pickles (Tursu) and microbiological properties.
 423 African J Biotechnol 10:14926–14931 . https://doi.org/10.4314/ajb.v10i66.
- 424 Chao SH, Wu RJ, Watanabe K, Tsai YC (2009) Diversity of lactic acid bacteria in suan-tsai and
- 425 fu-tsai, traditional fermented mustard products of Taiwan. Int J Food Microbiol 135:203–210

426

. https://doi.org/10.1016/J.IJFOODMICRO.2009.07.032

- 427 Chen S, Tang J, Fan S, Zhang J, Chen S, Liu Y, Yang Q, Xu Y (2021) Comparison of potent
 428 odorants in traditional and modern types of Chinese *Xiaoqu* liquor (*Baijiu*) Based on Odor
 429 Activity Values and Multivariate Analyses. Foods 2021, Vol 10, Page 2392 10:2392 .
 430 https://doi.org/10.3390/FOODS10102392
- 431 Corcoran TH (1963) Roman Fish Sauces. Class J 58:204–210
- 432 de Melo Pereira GV, Soccol VT, Brar SK, Neto E, Soccol CR (2017) Microbial ecology and starter
- 433 culture technology in coffee processing. https://doi.org/101080/1040839820151067759
- 434 57:2775–2788 . https://doi.org/10.1080/10408398.2015.1067759
- 435 Duar RM, Frese SA, Lin XB, Fernando SC, Burkey TE, Tasseva G, Peterson DA, Blom J, Wenzel
- 436 CQ, Szymanski CM, Walter J (2017a) Experimental evaluation of host adaptation of
- 437 *Lactobacillus reuteri* to different vertebrate species. Appl Environ Microbiol 83:e00132-17.
- 438 https://doi.org/10.1128/AEM.00132-17
- 439 Duar RM, Lin XB, Zheng J, Martino ME, Grenier T, Pérez-Muñoz ME, Leulier F, Gänzle M,
- 440 Walter J (2017b) Lifestyles in transition: evolution and natural history of the genus
- 441 *Lactobacillus*. FEMS Microbiol Rev 41:S27–S48 . https://doi.org/10.1093/femsre/fux030
- 442 Duchêne S, Holt KE, Weill FX, Le Hello S, Hawkey J, Edwards DJ, Fourment M, Holmes EC
- 443 (2016) Genome-scale rates of evolutionary change in bacteria. Microb Genomics 2:e000094
 444 . https://doi.org/10.1099/MGEN.0.000094
- 445 Dumas E, Feurtey A, Rodríguez de la Vega RC, Le Prieur S, Snirc A, Coton M, Thierry A, Coton
 446 E, Le Piver M, Roueyre D, Ropars J, Branca A, Giraud T (2020) Independent domestication
- 447 events in the blue-cheese fungus Penicillium roqueforti. Mol Ecol 29:2639-2660 .

448 https://doi.org/10.1111/mec.15359

- 449 Franz CMAP, Huch M, Mathara JM, Abriouel H, Benomar N, Reid G, Galvez A, Holzapfel WH
- 450 (2014) African fermented foods and probiotics. Int J Food Microbiol 190:84–96.
- 451 https://doi.org/10.1016/j.ijfoodmicro.2014.08.033
- 452 Fusco DO De, Madaleno LL, Bianchi VL Del, Bernardo A da S, Assis RR, Teixeira GH de A
- 453 (2019) Development of low-alcohol isotonic beer by interrupted fermentation. Int J Food Sci
- 454 Technol 54:2416–2424 . https://doi.org/10.1111/IJFS.14156
- 455 Gadaga TH, Mutukumira AN, Narvhus JA, Feresu SB (1999) A review of traditional fermented
- 456 foods and beverages of Zimbabwe. Int J Food Microbiol 53:1–11
- Gallagher E, Gormley TR, Arendt EK (2004) Recent advances in the formulation of gluten-free
 cereal-based products. Trends Food Sci Technol 15:143–152 .
 https://doi.org/10.1016/j.tifs.2003.09.012
- 460 Gallone B, Steensels J, Prahl T, Soriaga L, Saels V, Herrera-Malaver B, Merlevede A, Roncoroni
- 461 M, Voordeckers K, Miraglia L, Teiling C, Steffy B, Taylor M, Schwartz A, Richardson T,
- 462 White C, Baele G, Maere S, Verstrepen KJ (2016) Domestication and divergence of
- 463 Saccharomyces cerevisiae beer yeasts. Cell 166:1397-1410.e16 .
 464 https://doi.org/10.1016/j.cell.2016.08.020
- Gänzle M (2019) Fermented foods. In: Michael P. Doyle MP, Diez-Gonzalez F, Hill C (eds) Food
 Microbiology: Fundamentals and Frontiers, 5th edn. wiley, pp 855–900
- 467 Gänzle M, Salovaara H (2019) Lactic acid bacteria in cereal-based products. In: Vinderola G,
- 468 Ouwehand AC, Salminen S, von Wright A (eds) Lactic acid bacteria: Microbiological and
- 469 functional aspects, Fith Editi. CRC Press, pp 199–213

470	Gänzle M, Zho	eng J (2	2019) Life	estyles of so	ourdoug	sh lac	tobacilli	– do they ma	tter for microb	ial
471	ecology	and	bread	quality?	Int	J	Food	Microbiol	302:15-23	•
472	https://doi	.org/10	.1016/j.ijf	oodmicro.20)18.08.0	019				

- 473 Gänzle MG (2014) Enzymatic and bacterial conversions during sourdough fermentation. Food
 474 Microbiol 37:2–10 . https://doi.org/10.1016/j.fm.2013.04.007
- 475 Gänzle MG (2015) Lactic metabolism revisited: Metabolism of lactic acid bacteria in food
 476 fermentations and food spoilage. Curr Opin Food Sci 2:106–117 .
 477 https://doi.org/10.1016/j.cofs.2015.03.001
- 478 Gänzle MG (2020) Food fermentations for improved digestibility of plant foods an essential ex
 479 situ digestion step in agricultural societies? Curr Opin Food Sci 32:124–132 .
 480 https://doi.org/10.1016/j.cofs.2020.04.002
- 481 Gélinas P (2010) Mapping early patents on baker's yeast manufacture. Compr Rev Food Sci Food
 482 Saf 9:483–497 . https://doi.org/10.1111/J.1541-4337.2010.00122.X
- 483 Gibbons JG, Salichos L, Slot JC, Rinker DC, McGary KL, King JG, Klich MA, Tabb DL,
- 484 McDonald WH, Rokas A (2012) The evolutionary imprint of domestication on genome
- 485 variation and function of the filamentous fungus *Aspergillus oryzae*. Curr Biol 22:1403–1409
- 486 . https://doi.org/10.1016/J.CUB.2012.05.033
- 487 Greppi A, Rantsiou K, Padonou W, Hounhouigan J, Jespersen L, Jakobsen M, Cocolin L (2013)
- 488 Determination of yeast diversity in ogi, mawè, gowé and tchoukoutou by using culture-
- 489 dependent and -independent methods. Int J Food Microbiol 165:84–88
- 490 https://doi.org/10.1016/J.IJFOODMICRO.2013.05.005
- 491 Halm M, Lillie A, Sørensen AK, Jakobsen M (1993) Microbiological and aromatic characteristics
 - 23

492

of fermented maize doughs for kenkey production in Ghana. Int J Food Microbiol 19:135-

493 143 . https://doi.org/10.1016/0168-1605(93)90179-K

- Han BZ, Cao CF, Rombouts FM, Nout MJR (2004) Microbial changes during the production of
 Sufu A Chinese fermented soybean food. Food Control 15:265–270 .
 https://doi.org/10.1016/S0956-7135(03)00066-5
- Hansen A, Schieberle P (2005) Generation of aroma compounds during sourdough fermentation:
 applied and fundamental aspects. Trends Food Sci Technol 16:85–94 .
 https://doi.org/10.1016/J.TIFS.2004.03.007
- Hayden B, Canuel N, Shanse J (2013) What was brewing in the natufian? An archaeological
 assessment of brewing technology in the Epipaleolithic. J Archaeol Method Theory 20:102–
 150. https://doi.org/10.1007/s10816-011-9127-y
- Hillmann H, Behr J, Ehrmann MA, Vogel RF, Hofmann T (2016) Formation of kokumi-enhancing
 γ-glutamyl dipeptides in Parmesan cheese by means of γ-glutamyltransferase activity and
 stable isotope double-labeling studies. J Agric Food Chem 64:1784–1793 .
 https://doi.org/10.1021/acs.jafc.6b00113
- Houghouigan DJ, Nout MJR, Nago CM, Houben JH, Rombouts FM (1993) Characterization and
 frequency distribution of species of lactic acid bacteria involved in the processing of mawe,
 a fermented maize dough from Benin. Int J Food Microbiol 18:279–287 .
 https://doi.org/10.1016/0168-1605(93)90151-6
- 511 Hutkins RW (2019) Microbiology and Technology of Fermented Foods, 2nd Edition. Wiley512 Blackwell, Hoboken, New Jersey
- 513 Inatsu Y, Nakamura N, Yuriko Y, Fushimi T, Watanasiritum L, Kawamoto S (2006)
 - 24

514	Characterization of Bacillus subtilis strains in Thua nao, a traditional fermented soybean food
515	in northern Thailand. Lett Appl Microbiol 43:237-242 . https://doi.org/10.1111/J.1472-
516	765X.2006.01966.X
517	Jang DJ, Chung KR, Yang HJ, Kim KS, Kwon DY (2015) Discussion on the origin of kimchi,
518	representative of Korean unique fermented vegetables. J Ethn Foods 2:126-136 .
519	https://doi.org/10.1016/J.JEF.2015.08.005
520	Jans C, Meile L, Kaindi DWM, Kogi-Makau W, Lamuka P, Renault P, Kreikemeyer B, Lacroix
521	C, Hattendorf J, Zinsstag J, Schelling E, Fokou G, Bonfoh B (2017) African fermented dairy
522	products - Overview of predominant technologically important microorganisms focusing on
523	African Streptococcus infantarius variants and potential future applications for enhanced
524	food safety and security. Int J Food Microbiol 250:27-36 .
525	https://doi.org/10.1016/J.IJFOODMICRO.2017.03.012
526	Jeewanthi RKC, Paik HD (2018) Modifications of nutritional, structural, and sensory
527	characteristics of non-dairy soy cheese analogs to improve their quality attributes. J Food Sci
528	Technol 55:4384-4394 . https://doi.org/10.1007/s13197-018-3408-3
529	Jeleń HH, Majcher M, Szwengiel A (2019) Key odorants in peated malt whisky and its

530 differentiation from other whisky types using profiling of flavor and volatile compounds.

531 LWT 107:56–63 . https://doi.org/10.1016/J.LWT.2019.02.070

Jun Z, Shuaishuai W, Lihua Z, Qilong M, Xi L, Mengyang N, Tong Z, Hongli Z (2018) Culturedependent and -independent analysis of bacterial community structure in Jiangshui, a
traditional Chinese fermented vegetable food. LWT 96:244–250 .
https://doi.org/10.1016/J.LWT.2018.05.038

536	Jung JY, Lee SH, I	Lee HJ, S	eo HY,	Park WS, .	Ieon CO (2012)	Effects of Leucon	ostoc
537	mesenteroides st	arter cultu	res on m	nicrobial cor	nmunities and me	etabolites during ki	imchi
538	fermentation.	Int	J	Food	Microbiol	153:378–387	
539	https://doi.org/10.1016/J.IJFOODMICRO.2011.11.030						

- 540 Kayodé APP, Mertz C, Guyot J-P, Brat P, Mouquet-Rivier C (2013) Fate of phytochemicals during
- 541 malting and fermentation of type III tannin sorghum and impact on product biofunctionality.

542 J Agric Food Chem 61:1935–1942 . https://doi.org/10.1021/JF304967T

- Kelleher P, Bottacini F, Mahony J, Kilcawley KN, van Sinderen D (2017) Comparative and
 functional genomics of the *Lactococcus lactis* taxon; insights into evolution and niche
 adaptation. BMC Genomics 18:267 . https://doi.org/10.1186/s12864-017-3650-5
- 546 Kewuyemi YO, Kesa H, Chinma CE, Adebo OA (2020) Fermented edible insects for promoting 547 Africa. food security in Insects 2020, Vol 11. Page 283 11:283 548 https://doi.org/10.3390/INSECTS11050283
- 549 Kindstedt P (2012) Cheese and culture : a history of cheese and its place in western civilization.
 550 Chelsea Green Pub, London
- 551 Kobawila SC, Louembe D, Keleke S, Hounhouigan J, Gamba C (2005) Reduction of the cyanide

552 content during fermentation of cassava roots and leaves to produce bikedi and ntoba mbodi,

- two food products from Congo. African J Biotechnol 4:689–696 .
 https://doi.org/10.5897/ajb2005.000-3128
- 555 Kwon DY (2015) What is ethnic food? J Ethn Foods 2:1 .
 556 https://doi.org/10.1016/J.JEF.2015.02.001
- 557 Lei V, Jakobsen M (2004) Microbiological characterization and probiotic potential of koko and
 - 26

- koko sour water, African spontaneously fermented millet porridge and drink. J Appl
 Microbiol 96:384–397 . https://doi.org/10.1046/j.1365-2672.2004.02162.x
- Li Q, Gänzle MG (2020) Host-adapted lactobacilli in food fermentations: Impact of metabolic
 traits of host adapted lactobacilli on food quality and human health. Curr Opin Food Sci
- 562 31:71–80 . https://doi.org/10.1016/j.cofs.2020.02.002
- Lin YL, Wang TH, Lee MH, Su NW (2008) Biologically active components and nutraceuticals in
 the *Monascus*-fermented rice: a review. Appl Microbiol Biotechnol 77:965–973.
 https://doi.org/10.1007/S00253-007-1256-6
- Lister J (1877) Introductory address delivered in the Medical Department of King's College. Br
 Med J 2:469 . https://doi.org/10.1136/BMJ.2.875.465
- Liu Z, Li J, Wei B, Huang T, Xiao Y, Peng Z, Xie M, Xiong T (2019a) Bacterial community and
 composition in Jiang-shui and Suan-cai revealed by high-throughput sequencing of 16S
 rRNA. Int J Food Microbiol 306: . https://doi.org/10.1016/J.IJFOODMICRO.2019.108271
- 571 Liu Z, Peng Z, Huang T, Xiao Y, Li J, Xie M, Xiong T (2019b) Comparison of bacterial diversity
- 572 in traditionally homemade paocai and Chinese spicy cabbage. Food Microbiol 83:141–149 .
- 573 https://doi.org/10.1016/J.FM.2019.02.012
- 574 Lo R, Ho VTT, Bansal N, Turner MS (2018) The genetic basis underlying variation in production
- of the flavour compound diacetyl by *Lactobacillus rhamnosus* strains in milk. Int J Food
 Microbiol 265:30–39 . https://doi.org/10.1016/J.IJFOODMICRO.2017.10.029
- 570 Interorior 205.50 57 . https://doi.org/10.1010/5.151 OOD interto.2017.10.025
- 577 Marco ML, Heeney D, Binda S, Cifelli CJ, Cotter PD, Foligné B, Gänzle M, Kort R, Pasin G,
- 578 Pihlanto A, Smid EJ, Hutkins RW (2017) Health benefits of fermented foods: microbiota and
- 579 beyond. Curr Opin Biotechnol 44:94–102 . https://doi.org/10.1016/j.copbio.2016.11.010
 - 27

580	Marco ML, Sanders ME, Gänzle M, Arrieta MC, Cotter PD, De Vuyst L, Hill C, Holzapfel W,
581	Lebeer S, Merenstein D, Reid G, Wolfe BE, Hutkins RW (2021) The International Scientific
582	Association for Probiotics and Prebiotics (ISAPP) consensus statement on fermented foods.
583	Nat Rev Gastroenterol Hepatol 2021 183 18:196-208 . https://doi.org/10.1038/s41575-020-
584	00390-5
585	Miller ER, Kearns PJ, Niccum BA, Schwartz JOM, Ornstein A, Wolfe BE, O'Mara Schwartz J,
586	Ornstein A, Wolfe BE, Schwartz JOM, Ornstein A, Wolfe BE (2019) Establishment
587	limitation constrains the abundance of lactic acid bacteria in the Napa cabbage phyllosphere.
588	Appl Environ Microbiol 85:e00269-19 . https://doi.org/10.1128/AEM.00269-19
589	Montemurro M, Pontonio E, Gobbetti M, Rizzello CG (2019) Investigation of the nutritional,
590	functional and technological effects of the sourdough fermentation of sprouted flours. Int J
591	Food Microbiol 302:47-58 . https://doi.org/10.1016/j.ijfoodmicro.2018.08.005
592	Mortimer I (2009) The time traveler's guide to medieval England : a handbook for visitors to the
593	fourteenth century. Simon & Schuster, New York
594	Mu X, Wu Y, Fan W, Wu Q, Wang D (2014) Solid state fermentation alcoholic beverages. In:
595	Chen J, Zhu J (eds) Solid state fermentation for foods and beverages. CRC Press, Boca Raton,
596	pp 288–299
597	Mugula JK, Nnko SAM, Narvhus JA, Sørhaug T (2003) Microbiological and fermentation
598	characteristics of togwa, a Tanzanian fermented food. Int J Food Microbiol 80:187–199
599	Mukisa I, Nsiimire DG, Byaruhanga YB, Muyanja CMBK, Lansgrud T, Narvhus JA (2010)
600	Obushera: Descriptive sensory profiling and consumer acceptability. J Sens Stud 25:190–214
601	. https://doi.org/10.1111/J.1745-459X.2009.00272.X

602Mukisa I, Porcellato D, Byaruhanga YB, Muyanja CMBK, Rudi K, Langsrud T, Narvhus JA603(2012) The dominant microbial community associated with fermentation of Obushera604(sorghum and millet beverages) determined by culture-dependent and culture-independent605methods.IntJFoodMicrobiol160:1–10.

- 606 https://doi.org/10.1016/J.IJFOODMICRO.2012.09.023
- Nguyen DTL, Van Hoorde K, Cnockaert M, De Brandt E, Aerts M, Binh Thanh L, Vandamme P
 (2013) A description of the lactic acid bacteria microbiota associated with the production of
 traditional fermented vegetables in Vietnam. Int J Food Microbiol 163:19–27 .
 https://doi.org/10.1016/J.IJFOODMICRO.2013.01.024
- Nout MJR (2009) Rich nutrition from the poorest–Cereal fermentations in Africa and Asia. Food
 Microbiol 26:685–692
- Nout MJR, Kiers JL (2005) Tempe fermentation, innovation and functionality: update into the
 third millenium. J Appl Microbiol 98:789–805 . https://doi.org/10.1111/J.13652672.2004.02471.X
- Nout MJR, Motarjemi Y (1997) Assessment of fermentation as a household technology for
 improving food safety: a joint FAO/WHO workshop. Food Control 8:221–226 .
 https://doi.org/10.1016/S0956-7135(97)00021-2
- Nzwalo H, Cliff J (2011) Konzo: From poverty, cassava, and cyanogen intake to toxico-nutritional
 neurological disease. PLoS Negl. Trop. Dis. 5:e1051
- 621 Orla-Jensen S (1919) The lactic acid bacteria. Andr Fred Høst and Son, Copenhagen
- Paludan-Müller C, Valyasevi R, Huss HH, Gram L (2002) Genotypic and phenotypic
 characterization of garlic-fermenting lactic acid bacteria isolated from *som-fak*, a Thai low-

- 624 salt fermented fish product. J Appl Microbiol 92:307–314 . https://doi.org/10.1046/J.1365625 2672.2002.01544.X
- Patakova P (2013) *Monascus* secondary metabolites: production and biological activity. J Ind
 Microbiol Biotechnol 40:169–181 . https://doi.org/10.1007/s10295-012-1216-8
- Patra JK, Das G, Paramithiotis S, Shin HS (2016) Kimchi and other widely consumed traditional
 fermented foods of Korea: A review. Front Microbiol 7:1493 .
 https://doi.org/10.3389/FMICB.2016.01493/BIBTEX
- 631 Pavlova AS, Leontieva MR, Smirnova TA, Kolomeitseva GL, Netrusov AI, Tsavkelova EA (2017)
- 632 Colonization strategy of the endophytic plant growth-promoting strains of *Pseudomonas*
- 633 *fluorescens* and *Klebsiella oxytoca* on the seeds, seedlings and roots of the epiphytic orchid,
- 634 Dendrobium nobileLindl. J Appl Microbiol 123:217–232
- Phiri S, Schoustra SE, van den Heuvel J, Smid EJ, Shindano J, Linnemann A (2019) Fermented
 cereal-based Munkoyo beverage: Processing practices, microbial diversity and aroma
 compounds. PLoS One 14:e0223501 . https://doi.org/10.1371/journal.pone.0223501
- 638 Pswarayi F, Gänzle MG (2019) Composition and origin of the fermentation microbiota of mahewu,
- a Zimbabwean fermented cereal beverage. Appl Environ Microbiol 85:e03130-18.
- 640 https://doi.org/10.1128/AEM.03130-18
- Redzepi R, Zilber D (2018) The Noma guide to fermentation: foundations of flavor. Artisan
 Books, New York, New York
- Rowley-Conwy P (2011) Westward Ho! The spread of agriculture from Central Europe to the
 Atlantic. Curr Anthropol 52:S431–S451 . https://doi.org/10.1086/658368
- 645 Salama M, Sandine W, Giovannoni S (1991) Development and application of oligonucleotide 30

- probes for identification of *Lactococcus lactis* subsp. *cremoris*. Appl Environ Microbiol
 57:1313–1318 . https://doi.org/10.1128/aem.57.5.1313-1318.1991
- Schmid M, Iversen C, Gontia I, Stephan R, Hofmann A, Hartmann A, Jha B, Eberl L, Riedel K,
 Lehner A (2009) Evidence for a plant-associated natural habitat for *Cronobacter* spp. Res
 Microbiol 160:608–614 . https://doi.org/10.1016/j.resmic.2009.08.013
- 651 Skåra T, Axelsson L, Stefánsson G, Ekstrand B, Hagen H (2015) Fermented and ripened fish
 652 products in the northern European countries. J Ethn Foods 2:18–24 .
 653 https://doi.org/10.1016/J.JEF.2015.02.004
- Steinkraus KH (1997) Classification of fermented foods: worldwide review of household
 fermentation techniques. Food Control 8:311–317 . https://doi.org/10.1016/S09567135(97)00050-9
- 657 Ströbele W (2010) Zur Geschichte der Reutlinger Mutschel und ihrer Gebraäuche.
 658 https://publikationen.uni-tuebingen.de/xmlui/handle/10900/84636. Accessed 27 Mar 2022

659 Sun Z, Harris HMB, McCann A, Guo C, Argimón S, Zhang W, Yang X, Jeffery IB, Cooney JC,

660 Kagawa TF, Liu W, Song Y, Salvetti E, Wrobel A, Rasinkangas P, Parkhill J, Rea MC,

661 O'Sullivan O, Ritari J, Douillard FP, Paul Ross R, Yang R, Briner AE, Felis GE, De Vos

662 WM, Barrangou R, Klaenhammer TR, Caufield PW, Cui Y, Zhang H, O'Toole PW (2015)

Expanding the biotechnology potential of lactobacilli through comparative genomics of 213
strains and associated genera. Nat Commun 6:8322 . https://doi.org/10.1038/ncomms9322

- Suzuki H, Nakafuji Y, Tamura T (2017) New method to produce kokumi seasoning from protein
 hydrolysates using bacterial enzymes. J Agric Food Chem 65:10514–10519 .
- 667 https://doi.org/10.1021/ACS.JAFC.7B03690

- Tamang B, Tamang JP (2010) *In situ* fermentation dynamics during production of *gundruk* and *khalpi*, ethnic fermented vegetable products of the Himalayas. Indian J Microbiol 2010 501
 50:93–98 . https://doi.org/10.1007/S12088-010-0058-1
- Tamang JP, Tamang B, Schillinger U, Franz CMAP, Gores M, Holzapfel WH (2005)
 Identification of predominant lactic acid bacteria isolated from traditionally fermented
 vegetable products of the Eastern Himalayas. Int J Food Microbiol 105:347–356 .
 https://doi.org/10.1016/J.IJFOODMICRO.2005.04.024
- 675 Taulé C, Luizzi H, Beracochea M, Mareque C, Platero R, Battistoni F (2019) The Mo-and Fe-
- 676 nitrogenases of the endophyte *Kosakonia* sp. UYSO10 are necessary for growth promotion
 677 of sugarcane. Ann Microbiol 69:741–750
- Taylor JRN (2016) Fermentation: Foods and nonalcoholic Beverages. Encycl Food Grains Second
 Ed 3–4:183–192 . https://doi.org/10.1016/B978-0-12-394437-5.00136-4
- 680 Toelstede S, Hofmann T (2008) Quantitative studies and taste re-engineering experiments toward
- the decoding of the nonvolatile sensometabolome of Gouda cheese. J Agric Food Chem
 56:5299–5307 . https://doi.org/10.1021/jf800552n
- Tsuji S, Tanaka K, Takenaka S, Yoshida K (2015) Enhanced secretion of natto phytase by Bacillus
- 684
 subtilis.
 Biosci
 Biotechnol
 Biochem
 79:1906–1914

 685
 https://doi.org/10.1080/09168451.2015.1046366

 <
- van Beek S, Priest FG (2000) Decarboxylation of substituted cinnamic acids by lactic acid bacteria
- 687 isolated during malt whisky fermentation. Appl Environ Microbiol 66:5322 LP 5328 .
- 688 https://doi.org/10.1128/AEM.66.12.5322-5328.2000
- van de Guchte M, Penaud S, Grimaldi C, Barbe V, Bryson K, Nicolas P, Robert C, Oztas S,
 - 32

690	Mangenot S, Couloux A, Loux V, Dervyn R, Bossy R, Bolotin A, Batto J-M, Walunas T,
691	Gibrat J-F, Bessières P, Weissenbach J, Ehrlich SD, Maguin E (2006) The complete genome
692	sequence of Lactobacillus bulgaricus reveals extensive and ongoing reductive evolution.
693	PNAS 103:9274-9279 . https://doi.org/10.1073/pnas.0603024103
694	Vellend M (2010) Conceptual synthesis in community ecology. Q Rev Biol 85:183–206
695	Walter J (2008) Ecological role of lactobacilli in the gastrointestinal tract: Implications for
696	fundamental and biomedical research. Appl Environ Microbiol 74:4985-4996 .
697	https://doi.org/10.1128/AEM.00753-08
698	Wastyk HC, Fragiadakis GK, Perelman D, Dahan D, Merrill BD, Yu FB, Topf M, Gonzalez CG,
699	Van Treuren W, Han S, Robinson JL, Elias JE, Sonnenburg ED, Gardner CD, Sonnenburg
700	JL (2021) Gut-microbiota-targeted diets modulate human immune status. Cell 184:4137-

701 4153.e14 . https://doi.org/10.1016/J.CELL.2021.06.019

- 702 Watanabe H, Ng CH, Limviphuvadh V, Suzuki S, Yamada T (2020) *Gluconobacter dominates* the
- gut microbiome of the Asian palm civet *Paradoxurus hermaphroditus* that produces kopi
 luwak. PeerJ 8:e9579 . https://doi.org/10.7717/PEERJ.9579/SUPP-3
- 705 Wolfe BE, Dutton RJ (2015) Fermented foods as experimentally tractable microbial ecosystems.

706 Cell 161:49–55 . https://doi.org/10.1016/J.CELL.2015.02.034

- 707 Wuyts S, Van Beeck W, Oerlemans EFM, Wittouck S, Claes IJJ, De Boeck I, Weckx S, Lievens
- 708 B, De Vuyst L, Lebeer S (2018) Carrot juice fermentations as man-made microbial
- ros ecosystems dominated by lactic acid bacteria. Appl Environ Microbiol 84:00134-18.
- 710 https://doi.org/10.1128/AEM.00134-18
- 711 Yan B, Sadiq FA, Cai Y, Fan D, Chen W, Zhang H, Zhao J (2019) Microbial diversity in traditional
 - 33

- type I sourdough and jiaozi and its influence on volatiles in Chinese steamed bread. LWT
 101:764–773 . https://doi.org/10.1016/j.lwt.2018.12.004
- Zhao CJ, Kinner M, Wismer W, Gänzle MG (2015) Effect of glutamate accumulation during
 sourdough fermentation with *Lactobacillus reuteri* on the taste of bread and sodium-reduced
 bread. Cereal Chem 92:224–230 . https://doi.org/10.1094/CCHEM-07-14-0149-R
- 717 Zheng J, Wittouck S, Salvetti E, Franz CMAP, Harris HMB, Mattarelli P, O'Toole PW, Pot B,
- 718 Vandamme P, Walter J, Watanabe K, Wuyts S, Felis GE, Gänzle MG, Lebeer S (2020) A
- taxonomic note on the genus *Lactobacillus*: Description of 23 novel genera, emended
- 720 description of the genus *Lactobacillus* Beijerinck 1901, and union of *Lactobacillaceae* and
- *Leuconostocaceae* . Int J Syst Evol Microbiol 70:2782–2858 .
 https://doi.org/10.1099/ijsem.0.004107
- Zheng J, Zhao X, Lin XB, Gänzle M (2015) Comparative genomics *Lactobacillus reuteri* from
 sourdough reveals adaptation of an intestinal symbiont to food fermentations. Sci Rep 5:1–
 11. https://doi.org/10.1038/srep18234
- Zheng X-W, Yan Z, Han B-Z, Zwietering MH, Samson RA, Boekhout T, Nout MJR (2012)
 Complex microbiota of a Chinese "Fen" liquor fermentation starter (Fen-Daqu), revealed by
 culture-dependent and culture-independent methods. Food Microbiol 31:293–300
- 729 Zheng XW, Han BZ (2016) *Baijiu* (白酒), Chinese liquor: history, classification and manufacture.
- 730 J Ethn Foods 3:19–25 . https://doi.org/10.1016/J.JEF.2016.03.001
- 731
- 732

733 Figure legends

734 Figure 1. Periodic element of the fermented foods. The figure aims to provide an overview of the 735 diversity of fermented foods that are produced globally. Indicated are the origin of the food, main 736 ingredients and typical fermentation organisms, pH, water activity and fermentation / ripening 737 time, and major microbial metabolites that relate to product quality. The contribution of major 738 groups of fermentation organisms is color coded as indicated in the legend; back-slopped 739 fermentations are indicated by a thick outline and by an underlined product name. The figure is 740 not provided in this pre-print; the reader is referred to the updated, high resolution file for printing 741 in A0 format that is available on the author's personal website and on:

742 <u>https://drive.google.com/open?id=10cH7XaNqGQAKdL3VHhd1tzWXlGaTdfkV&authuser=mg</u> 743 aenzle%40ualberta.ca&usp=drive fs

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744 **Figure 2.** Global preferences for traditional consumption of different types of fermented foods. 745 Preferences are color coded based national borders, ignoring regional preferences. Panel A. Use 746 of malt (red) or microbial enzymes (blue, koji, daqu) for production of alcoholic beverages or 747 vinegar from grains. Panel B. Consumption of bread as steamed bread (yellow), flat bread 748 (orange), in loaves (red) or consumption of cereal porridges or beverages (blue). Countries are 749 hatched if they are at the intersection of two cultures (e.g. Turkey) or if the preferences of 750 indigenous and immigrant (fermentation) cultures differ (e.g. Brazil, North America). Panel C. 751 Production of isolated, fermented products from soy (blue) or of cheese (red). Countries that 752 produce little, if any, cheese (most African countries), or produce acid-coagulated cheese without 753 fermentation (South Asia) are coloured in orange. Countries are hatched if preferences of 754 indigenous and immigrant (fermentation) cultures differ. Gray, not relevant or insufficient 755 information. Maps were drawn with a template file from www.freeworldmaps.net.

Name	Origin	Main ingredients	References
Sauerkraut / Choucrute	Germany, France, U.K., U.S.A and Canada	cabbage (juniper berries)	(Hutkins 2019)
Tursu	Turkey	cabbage, cucumber, carrot, beet,	(Çetin 2013)
Gundruk	India	Cabbage, mustard leaves, raddish and / or cauliflower	(Tamang and Tamang 2010)
Sinki (raddish)	India, Nepal	radish	(Tamang et al. 2005)
Pao Cai	China	cabbage (red pepper, scallion, ginger, garlic, anchovy)	(Liu et al. 2019b)
Suan-Tsai, Suan Cai	China, Taiwan	Napa cabbage (North China) or green mustard (South and West China, Taiwan)	(Chao et al. 2009; Liu et al. 2019a)
Jianshui	China	Cabbage or celery	(Jun et al. 2018)
Kimchi	Korea	cabbage (red and black pepper, onions, mustard)	(Patra et al. 2016)
Dua muoi or dha muoi	Vietnam	Mustard or beet	(Nguyen et al. 2013)
Ca muoi	Vietnam	Eggplant	(Nguyen et al. 2013)

Table 1. Examples for vegetables that are produced by cutting, brining, and fermentation for

2-4 weeks at ambient temperature, matching element #30, sauerkraut.

Table 2. Examples for non-alcoholic fermented cereal beverages that are produced by fermentation of a cooked cereal slurry with addition of adjuncts as source of enzymes and fermentation microbiota, matching element # 42, mahewu.

Name	Origin	Main ingredients	References
Mahewu, Amahewu, Emahewu, or Mageu	Zimbabwe South Africa, Swaziland	cooked maize with millet or sorghum malt	(Pswarayi and Gänzle 2019)
Togba	Zimbabwe	cooked maize	(Gadaga et al. 1999)
Tobwa	Tanzania	cooked maize with millet or sorghum malt	(Mugula et al. 2003)
Munkoyo (Chimbwantu)	Zambia, Democratic Republic of Congo	cooked maize with millet malt, <i>Rynchosia</i> root, cowpea root or sweet potato peels	(Phiri et al. 2019)
Ekitiribita	Uganda	cooked millet with sorghum malt	(Mukisa et al. 2010; Mukisa et al. 2012)





