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Annual Review of Food Science and Technology

Starter Culture Development and Innovation for Novel Fermented Foods

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Keywords

Lactobacillus, *Bacillus*, *Saccharomyces cerevisiae*, plant-based cheese analogs, nonalcoholic fermented beverages, minimally processed foods

Abstract

Interest in fermented foods is increasing because fermented foods are promising solutions for more secure food systems with an increased proportion of minimally processed plant foods and a smaller environmental footprint. These developments also pertain to novel fermented food for which no traditional template exists, raising the question of how to develop starter cultures for such fermentations. This review establishes a framework that integrates traditional and scientific knowledge systems for the selection of suitable cultures. Safety considerations, the use of organisms in traditional food fermentations, and the link of phylogeny to metabolic properties provide criteria for culture selection. Such approaches can also select for microbial strains that have health benefits. A science-based approach

to the development of novel fermented foods can substantially advance their value through more secure food systems, food products that provide health-promoting microbes, and the provision of foods that improve human health.

1. INTRODUCTION

Fermented foods are produced “through desired microbial growth and enzymatic conversions of food components” (Marco et al. 2021, p. 197). The oldest food fermentations, unleavened flatbread and alcoholic cereal beverages, are documented for the Natufian culture about 14,000 years ago (Arranz-Otaegui et al. 2018, Liu et al. 2018) and substantially predate the Neolithic (agricultural) revolution. In preindustrial human agricultural societies, fermented foods have accounted for a substantial portion of the diet. Food fermentations serve multiple purposes: to (a) reduce the content of antinutritive or toxic components in plant foods (Gänzle 2020); (b) convert perishable raw materials into products that can be stored for several months and traded over long distances; (c) produce alcoholic beverages; and (d) produce sauces and condiments (**Figure 1**) (Gänzle 2022, Hutkins 2019). **Figure 1** provides an overview of the diversity of fermented foods and the communities of microbes that are recruited for food fermentations using the format of the periodic table of chemical elements (Gänzle 2022). From a North American and European perspective, the discussion of food fermentations typically defaults to fermented vegetables, cereal, meats, and dairy products as well as fermentations to produce alcoholic beverages, which are primarily conducted with yeasts and lactic acid bacteria. However, the diversity of fermented foods, substrates used for fermentation, and fermentation microbes is much greater and reflects the global diversity of human cultural traditions (**Figure 1**).

For thousands of years, the production of fermented foods relied on traditional practices, e.g., back-slopping or spontaneous fermentations. Spontaneous food fermentations recruit environmental microbes that are present in the raw materials and are often members of the microbiota of the phyllosphere (Miller et al. 2019, Mudoor Soorsh et al. 2023, Pswarayi & Gänzle 2019), whereas back-slopped fermentations often select for fermentation microbes that are autochthonous to other establishment niches, including intestinal environments (Li & Gänzle 2020, Su et al. 2012). The production of most fermented foods in developed countries has been industrialized in the past century on the basis of scientific knowledge systems (Fox et al. 2017, Gobbetti & Gänzle 2023, Leroy et al. 2015). Industrial production of fermented foods often relies on starter cultures to control the communities of microbes during fermentation, standardize product quality, and reduce the risk of fermentation failure. The development of starter cultures has been based on the following steps: (a) isolation and taxonomic characterization of microbial strains from high-quality reference products; (b) *in vitro* determination of desirable and undesirable physiological properties; (c) *in situ* determination of ecological fitness in the fermentation substrate and beneficial impact on product quality; and (d) adaptation of the strain for large-scale production of biomass (Daniell & Sandine 1981, Hammes & Hertel 1996). In the past decade, genome sequencing was added as a routine method for characterization of starter cultures (Garrigues et al. 2013). In developing countries, however, fermented foods often continue to be produced at the household level (Pswarayi & Gänzle 2022), or at a small to medium scale by specialized producers operating on the basis of traditional knowledge systems. In addition, food fermentations that rely on surface-associated biofilms (pellicles) such as kefir (Blasche et al. 2021) or kombucha (Baschali et al. 2017) have not been replicated by industrial production at a large scale.

In recent years, interest in fermented foods has increased for multiple reasons: (a) The food industry aims to employ microbes in food production to reduce the number of ingredients

The periodic table of fermented foods. Fermented foods are arranged in groups by fermentation substrate; most of the products shown represent similar products that are produced in different regions with different names. For each element, the region where the product is traditionally produced is indicated as well as major fermentation organisms, time of fermentation, and the pH and water activity of the final product, where information is available. Back-slopped fermentations are underlined; major groups of fermentation organisms are color coded. A high-resolution PDF file for large-format printing, which is periodically updated, is available under a Creative Commons license on the author's personal website (<https://apps.ualberta.ca/directory/person/mgaenzle>). Figure adapted from Gänzle (2022) (CC BY-SA 4.0).

that are used in food products and produce minimally processed foods (Brandt et al. 2023, Jahn et al. 2023); (b) many consumers in developed countries are rediscovering household-level food production by fermentation, a trend that was accelerated by the COVID-19 pandemic (<https://trends.google.com>, with keyword sourdough, yogurt, or pickles); (c) food fermentations provide unique opportunities in the culinary arts to generate novel menu items (Redzepi & Zilber 2018); (d) food producers and particularly breweries are exploring nontraditional fermentations for production of nonalcoholic cereal beverages or lactic acid-fermented fruit juices to take advantage of growth opportunities that are no longer available in the market for beer and wine; (e) food fermented or supplemented with specific probiotic strains combines the sensory appeal of fermented foods with the health benefits of probiotic microbes (Marco et al. 2021, Tuorila et al. 1998); and (f) a shift from animal-protein to plant-protein foods also necessitates the development of plant-based fermented analogs of fermented meats and dairy products (Grasso et al. 2021, Jahn et al. 2023).

This resurging interest in fermented foods thus relates to not only traditional fermented foods but also novel foods for which no closely related traditional template exists. A nonexhaustive list of examples of such novel fermented foods is provided in **Table 1**. For these novel fermented foods, the conventional approach to the selection of starter cultures is not applicable because traditionally fermented templates do not exist or differ substantially from the intended product in terms of production process and sensory properties. This raises the question of how we select starter cultures for novel food fermentations. This article aims to outline approaches that integrate traditional and scientific knowledge systems to guide the selection of suitable cultures.

2. PROPERTIES OF MAJOR BACTERIAL FOOD-FERMENTING ORGANISMS

Bacterial Diversity in Food Fermentations

The International Dairy Federation (IDF) maintains an inventory of food cultures. The current version lists 3 bacterial phyla, Actinomycetota, Bacillota (previously Firmicutes), and Pseudomonata, which are represented by 17 families and several hundred different bacterial species, and 3 fungal phyla that are represented by 13 families and more than 100 fungal species (Bourdichon et al. 2022). Currently, the selection of starter cultures for novel (plant) food fermentations often defaults to *Lactiplantibacillus plantarum* (Jeske et al. 2018), but the diversity of microbes that can be used is much greater.

How Can We Select Bacteria for Novel Food Fermentations from the Immense Diversity of Fermentation Microbes?

A first criterion is provided by regulatory approval for the use of microbes in food and feed fermentations. The European Food Safety Authority (EFSA) (Koutsoumanis et al. 2022) and the US Food and Drug Administration (FDA) list microbes with Qualified Presumed Safety and Generally Recognized as Safe, respectively, for use in food and feed. The safety assessment of bacteria

Table 1 Examples of novel fermented foods for which no direct traditional template exists

Food	Purpose of fermentation	Closest traditional templates	References
Garum	Combination of umami tastants and flavor compounds derived from the raw material	Garum (antique fish sauce), East Asian fish sauces, kharoli (fermented mustard seed), gochujiang (fermented rice with <i>Capsicum</i> peppers)	Bora et al. 2022, Kim et al. 2010, Redzepi & Zilber 2018
Gluten-free bread	Improved texture, taste, and flavor	Sourdough bread, African traditional fermentations of gluten-free cereals	Moroni et al. 2009, Pswarayi & Gänzle 2022, Taylor & Duodu 2019
Nonalcoholic cereal beverages	Balance of carbonation or fizz, sweetness, and acidity in nonalcoholic cereal beverages	Water kefir, kombucha, kvas	Gänzle 2022, Waldherr et al. 2010
Sourdough bread (household level)	Replacement of baker's yeast as leavening agent at times of global pandemics	Sourdough bread	Landis et al. 2021
Sourdough bread (industrial production)	Replacement of ingredients and additives with novel fermentation processes and organisms Inclusion of waste streams of food production (bran, brewers' spent grains, okara) in breads	Sourdough bread	Brandt et al. 2023, Neylon et al. 2021, Pontonio et al. 2023
Plant-based cheese and meat analogs	Replacement of animal protein with plant or insect protein, generation of desired texture and flavor	Cheese, douchi (fermented tofu), fermented pulses (e.g., idli)	Grasso et al. 2021, Liu et al. 2022
Yosa	Yogurt-type product fermented with probiotic strains of <i>Lactobacillus acidophilus</i>	Yogurt	Marco et al. 2021, Tuorila et al. 1998

for food and feed use by EFSA is based on taxonomic identification by whole-genome sequencing; documentation of a safe history of food use; the absence of virulence factors, toxins, or biogenic amines; and the absence of transferable antimicrobial resistance (EFSA 2012, Rychen et al. 2018). The list includes organisms such as *Lactocaseibacillus rhamnosus*, which rarely causes systemic infections in humans but recognizes that living microbes may cause infections in critically ill individuals even if virulence determinants other than tolerance of oxygen are absent (Koutsoumanis et al. 2023). Several reports attributed *L. rhamnosus* infections in critically ill patients to strains administered as probiotics (Koutsoumanis et al. 2023), emphasizing the importance of the susceptibility to therapeutic antibiotics when assessing the safety of food cultures. The hurdles for the applications of microbes in foods are higher for those microbes that do not have a safe history of use in food and/or have not been subject to prior evaluation by the FDA, EFSA, or regulatory agencies in other jurisdictions. Microbes without prior assessment of their safety include most lactic acid bacteria in families other than the Lactobacillaceae and most bacilli outside of the Bacillaceae. There are therefore challenges to exploiting all the microbes that are used in traditional fermentations as commercial starter cultures, irrespective of their potential beneficial contribution to food quality. Prime examples are enterococci, which beneficially contribute to food safety and quality as fermentation organisms but also are a member of the illustrious group of ESKAPE pathogens (Franz et al. 2003, Pendleton et al. 2013), and the plant-associated Enterobacteriaceae. Enterobacteriaceae are part of microbial communities in many fermented plant foods, including sauerkraut, douchi, daqu, and spontaneously fermented cereal beverages (**Figure 1**) (Comasio et al. 2020,

Nie et al. 2015, Wang et al. 2018, Wiesel et al. 1997), but also include several taxa that contribute to nosocomial infections with antibiotic-resistant microbes (Pendleton et al. 2013). The beneficial contribution of Enterobacteriaceae to product quality, if any, remains unproven and the group of organisms is unlikely to be approved as microbes for safe use in food fermentations.

Traditional knowledge systems provide a second criterion for selection of fermentation microbes (**Figure 1**). Specific fermentation microbes that are frequently present in traditional fermentations of specific substrates likely also perform well in novel fermentations of the same substrates, e.g., cereal, pulse, fruit, or vegetable fermentations. Traditional food fermentations also document that specific fermentation microbes are dominant if specific environmental conditions are met, e.g., *Tetragenococcus halophilus* in fermentations with a high (>12%) salt content, *Oenococcus oeni* in fermentations with a low pH and a high ethanol content, and *Staphylococcus* species in protein-rich foods (meat, fish, pulse protein) with an elevated salt content (**Figure 1**).

Scientific knowledge systems provide a third criterion for the selection of fermentation microbes. When sketching the picture with a bold stroke, lactic acid bacteria contribute to the preservation and taste by conversion of carbohydrates to organic acids and amino acids to umami tastants. Heterofermentative lactobacilli additionally produce CO₂ and acetate and control lipid oxidation and disulfide-bond cross-linking of proteins by NAD(P)H-dependent oxidoreductases (Loponen et al. 2008, Sugahara et al. 2022). In addition, enzymes that produce γ -glutamyl-dipeptides that are active as kokumi tastants are virtually exclusive to heterofermentative lactobacilli (**Figure 2**) (Gänzle 2015, Toelstede et al. 2009, Xie & Gänzle 2021). The strain-specific production of bacteriocins by lactic acid bacteria contributes to the control of gram-positive pathogens, particularly *Listeria monocytogenes* (Drider et al. 2006). Yeasts, which are discussed in more detail below, contribute CO₂, ethanol, and flavor volatiles that are synthesized through diverse metabolic pathways (Dzialo et al. 2017). Mycelial molds and bacilli excel at producing extracellular proteases, glycosyl hydrolases, and phytases (Z. Li et al. 2023b, Owusu-Kwarteng et al. 2020, Zhu & Tramper 2013). In addition, bacilli produce antimicrobial lipopeptides and polyglutamate (Cochrane & Vederas 2016, Ho et al. 2006, Z. Li et al. 2023a), and mycelial molds contribute to the color and flavor of surface-ripened meats and cheeses (Galli et al. 2016, Toelstede & Hofmann 2009). In traditional fermented foods, propionibacteria are solely used as secondary ripening cultures in specific cheeses. Their metabolic traits, however, also support innovative applications that exploit their ability to metabolize organic acids and diols and synthesize cobalamin (**Figure 1**) (Dank et al. 2023). Acetic acid bacteria are essential in the production of vinegars but also contribute to the flavor of coffee, cocoa, Lambic beer, and diverse nonalcoholic fermented beverages (**Figure 1**) (De Roos & De Vuyst 2018). Staphylococci occur in fermented protein foods, including meat and fish fermentations, where they contribute to the removal of hydrogen peroxide, reduction of nitrate, and flavor formation (**Figure 1**) (Sánchez Mainar et al. 2017). Existing and proposed applications in novel fermented foods include the fermentation of insect proteins and the conversion of nitrate to nitrite to use green leafy vegetables as curing agents (Kewuyemi et al. 2020, Sebranek et al. 2012).

Use of Genomic, Transcriptomic, and Metabolomics Data for Selection of Novel Bacterial Cultures

Knowledge of the contribution of specific microorganisms to biochemical conversions during traditional food fermentations and food quality, and the determination of their genetic potential for metabolic conversions by genomic analyses, can be directly used in the selection of starter cultures for novel fermented foods. The phylogeny of food-fermenting organisms provides a first indication of their potential for use in specific food fermentations. Examples of the juxtaposition of

Figure 2 (Figure appears on preceding page)

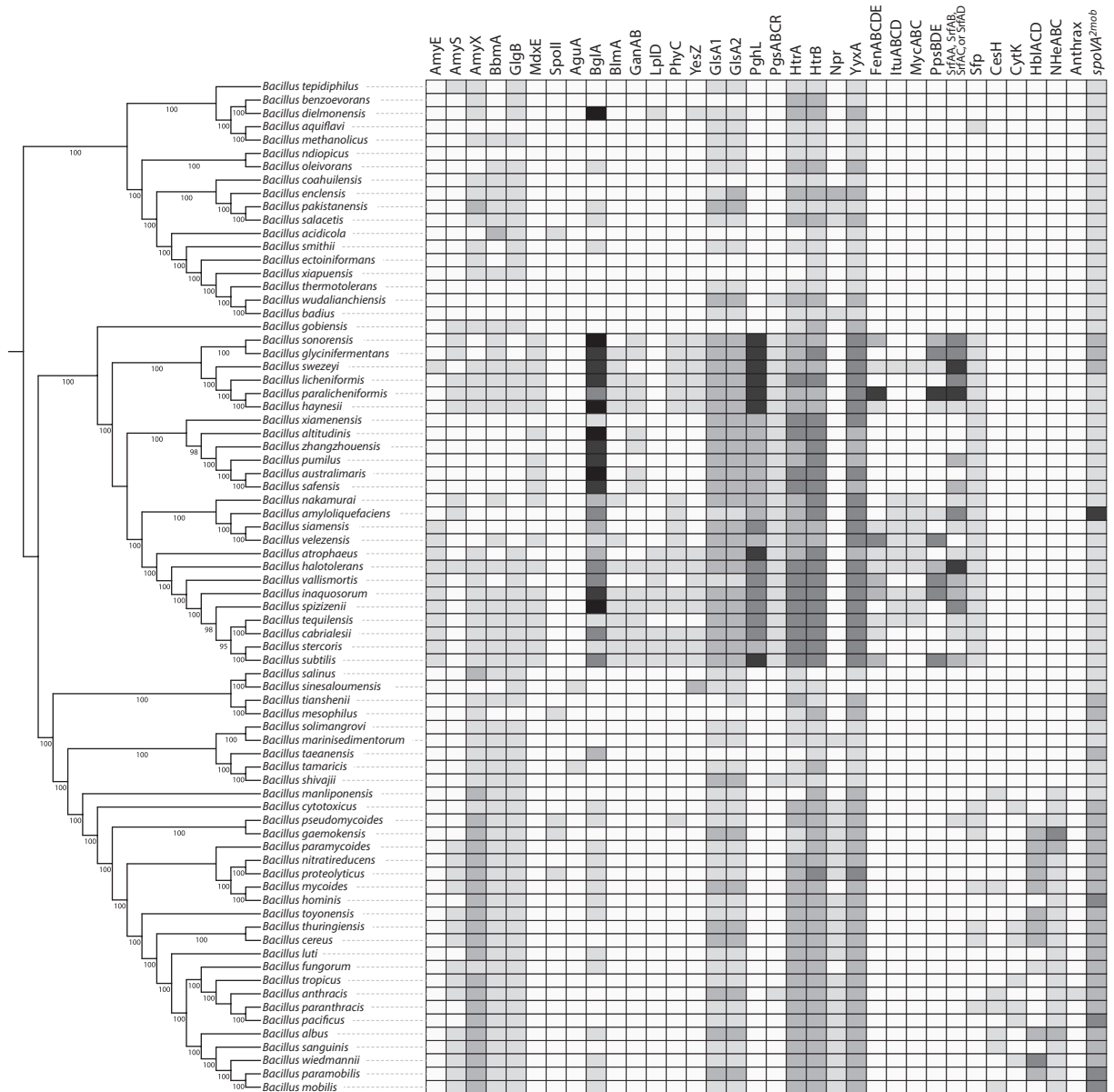
Phylogenetic tree of species in the Lactobacillaceae and a heatmap depicting the presence of genes coding for selected physiological traits. The genome set for preparation of these figures was rarefied to type strains and consequently does not reveal the intraspecific variation of beneficial or undesirable metabolic traits. The phylogenetic tree was calculated with the methodology described by Zheng et al. (2015), using all 355 type strains of validly or effectively published species for which genome sequence data were available in May 2023. The heatmap was generated by BLASTp analysis as described by Zheng et al. (2015), with the threshold values 40% amino acid identity and 70% coverage. Protein query sequences are provided by Gaur & Gänzle (2023) and Zheng et al. (2015). Abbreviations: Central carbon metabolism: CitDEFG, citrate lyase; AldA, lactaldehyde dehydrogenase; MDH, mannitol dehydrogenase; MLE, malolactic enzyme; PduCDE, diol dehydratase; PFK, phosphofructokinase; PFL, pyruvate formate lyase; PKT, phosphoketolase; TAK, transketolase; TAL, transaldolase. Amino acid metabolism: ArcA, arginine deiminase; GadB, glutamate decarboxylase; Gcl, glutamate cysteine ligase; Gls3, glutaminase; GshAB, two domain glutathione synthase; HdcA, histidine decarboxylase; TyrDC, tyrosine decarboxylase. Oligosaccharide metabolism: AmyX, extracellular amylase; BfrA, β -fructan hydrolase; DexB, oligo- α -(1 \rightarrow 6)-glucosidase; GlgP, glycogen phosphorylase; GtfA, glucansucrase; LacG, phospho- β -galactosidase; LacZ and LacLM, β -galactosidases; MalEFG, ABC transporter for malto-oligosaccharide; MalH, maltose-6-phosphate glucosidase; MalN, α -glucosidase; Malp, maltose phosphorylase; MelA, α -galactosidase; MsmEFG, ABC transporter for fructo-oligosaccharides; PTS, fructose-oligosaccharide (sucrose) phosphotransferase system; SacA, β -sucrose hydrolase; ScrP, sucrose phosphorylase. Proteins for glycosyl hydrolase with activity on glycosylated phytochemicals and extracellular protease: LcGUS30, glucuronidase; PrtH3, extracellular proteinase lactoepin; Ram1, Ram2, and RamALa, rhamnosidases; rBGLa, β -glucosidase.

the phylogeny of lactobacilli and bacilli and their genetic potential for beneficial metabolic traits are provided in **Figure 2** (Lactobacillaceae) and **Figure 3** (*Bacillus* spp.).

The ecology of lactobacilli and hence the adaptation to specific ecological niches with corresponding adaptation to substrate and growth conditions are shared among specific phylogenetic groups (Duar et al. 2017). The adaptation to vertebrate hosts by most members of the genera *Lactobacillus*, *Ligilactobacillus*, and *Limosilactobacillus* is an important selection criterion for probiotic strains of lactobacilli (Sanders et al. 2018). Among the lactobacilli, homofermentative and heterofermentative lactobacilli differ in multiple aspects other than the major pathway for hexose metabolism (**Figure 2**). Clade-specific traits include the lactate conversion to acetate, propanol, and propionate (Gänzle 2015), which is observed predominantly in the heterofermentative genera *Lentilactobacillus*, *Secundilactobacillus*, *Paucilactobacillus*, and *Furfurilactobacillus* (**Figure 2**), and the formation of extracellular glucansucrases or glucanotransferases (Gangoiti et al. 2018). Glucansucrases are frequently expressed by strains of the genera *Liquorilactobacillus*, *Limosilactobacillus*, *Leuconostoc*, and a few *Weissella* spp. (Meng et al. 2016), whereas glucanotransferases with activity on starch have to date been characterized only in limosilactobacilli (Gangoiti et al. 2018). Glutaminase is expressed only by *Lactobacillus* and *Limosilactobacillus* species, whereas glutamyl-cysteine-ligases that convert amino acids to taste-active compounds are frequently found only in the genera *Limosilactobacillus* and *Lentilactobacillus* (**Figure 2**) (Xie & Gänzle 2021). A key metabolic trait that is relevant in fermentation of plant foods but not in fermentations of animal proteins is the hydrolysis of glycosides of phytochemicals. Glycosides of phytochemicals often impart a bitter taste to plant foods (Yan & Tong 2023) but also include compounds that are toxic, such as cyanogenic glucosides (Alitubeera et al. 2019, Gänzle 2020). The deglycosylation of phytochemicals, e.g., isoflavones in soy or glucovanillin in vanilla beans (Chen et al. 2015, Li et al. 2021), can also increase a beneficial biological activity of compounds. Although *Lactiplantibacillus* and *Lacticaseibacillus* possess enzymes with known activity on glycosides of phytochemicals, strains of other, less widely used genera, including *Bacillus* spp., *Companilactobacillus*, *Schleiferilactobacillus*, *Levilactobacillus*, and *Lentilactobacillus*, have a much broader set of enzymes to convert glycosylated phytochemicals (**Figure 2** and **Figure 3**) (Gaur & Gänzle 2023). A key trait for fermentation

of legumes and legume proteins is the alcohol dehydrogenase activity of heterofermentative lactobacilli, which eliminates the beany flavor of pulse (protein) preparations (Sugahara et al. 2022).

In the genus *Bacillus*, desirable and undesirable traits are also assigned to specific phylogenetic groups. Genes for the formation of diarrheal toxins and the emetic toxin cereulide, which preclude Qualified Presumed Safety as defined by EFSA (Koutsoumanis et al. 2022), are present only in the *Bacillus cereus* clade (Figure 3). Conversely, beneficial metabolic traits, including extracellular hydrolytic enzymes, antifungal lipopeptides, polyglutamate synthesis, and glutaminases, are



(Caption appears on following page)

Figure 3 (Figure appears on preceding page)

Phylogenetic tree of 76 species in the genus *Bacillus* for which genome sequence data were available in May 2023 and genes coding for useful enzymes or toxins in these type strains. The methodology as well as the accession numbers of query sequences were published previously (Z. Li et al. 2023b). The genome set for preparation of these figures was rarefied to type strains and consequently does not reveal the intraspecific variation of beneficial or undesirable metabolic traits. Shown from left to right are the amylolytic system, other glycosyl hydrolases, glutaminases, polyglutamate synthesis, proteases, antimicrobial lipopeptides, enterotoxins of *B. cereus*, the anthrax toxin, and the *spoVA^{2mob}* operon that confers extreme heat resistance to spores. Abbreviations: AmyE, α -amylase; AmyS, heat-stable α -amylase; AmyX, pullulanase; BbmA, β -amylase; BlmA, maltogenic amylase; GlgB, branching enzyme; MdxE, maltose-binding proteins; SpoII, β -amylase. Other glycosyl hydrolases and phytase: AguA, thermostable xylanase; BglA, β -glucosidase; GanA, endo- β -galactosidase; GanB, exo- β -galactanase; LplD, α -galactosidase; PhyC, phytase; YesZ, β -galactosidase. Glutaminases: GlsA1 and GlsA2, glutaminases. Polyglutamate synthesis: PghL, poly- γ -glutamate hydrolase; PgsABCR, poly- γ -glutamate synthetase, and regulatory genes. Proteolytic system: HtrA and HtrB, envelope-associated serine proteases; YyxA, uncharacterized serine protease. Antimicrobial lipopeptides: FenABCDE, fengycin synthase; ItuABCD, iturin synthase; MycABC, mycosubtilin synthase; PpsBDE, plipastatin synthase; SrfAA, SrfAB, SrfAC, and SrfAD, surfactin synthases; Sfp, surfactin synthetase-activating enzyme. Toxins: CesH, cereulide synthetase; CytK, cytotoxin K; HblACD, hemolysin BL; NheABC, Nhe enterotoxin; *spoVA^{2mob}*, operon conferring heat resistance depending on the copy number.

frequently present only in the *Bacillus subtilis* clade (**Figure 3**) (Z. Li et al. 2023b). Phytase activity of bacilli hydrolyzes phytic acid in legume fermentations (Tsuji et al. 2015) and consequently increases the bioavailability of phytate-bound divalent cations, including Mg^{2+} , Mn^{2+} , and Ca^{2+} . Glutaminases of bacilli not only convert glutamine to the umami tastant glutamate but also form kokumi-active γ -glutamyl peptides (Yang et al. 2017).

The gold standard for establishing the link of genotype to phenotype is the generation of isogenic mutants and their use in (model) food fermentations that are analyzed by suitable instrumental methods in conjunction with sensory panels (Lo et al. 2018, Zhao et al. 2015). Once the link from gene to function is established, high-throughput screening of large strain collections is achieved with “omics” technologies, including (meta-)genomic, (meta-)transcriptomic, and metabolomic analyses. Strain-specific genetic traits are readily identified by suitable databases, e.g., BAGEL (<http://bagel4.molgenrug.nl/>) and Antismash (<https://antismash.secondarymetabolites.org>) for antimicrobial metabolites or the CARD database for antibiotic resistance (<https://card.mcmaster.ca/>). As advanced sequencing technologies and metabolomic methods become increasingly available and affordable, the scale of the data that are generated rapidly moves from tebibytes (TiB, 2^{40}) to pebibytes (PiB, 2^{50}). The use of machine learning and artificial intelligence to evaluate the large volume of data that are generated by “omics” technologies becomes increasingly helpful in predicting the performance of microbial communities in novel fermented foods (Galimberti et al. 2021, Wels et al. 2019). Several of the strain-specific beneficial or detrimental impacts of fermentation microbes, however, remain difficult to predict from genome sequence data; examples include flavor formation by lactobacilli or yeasts (Dzialo et al. 2017, Lo et al. 2018) and the formation of exopolysaccharides by lactobacilli (Lynch et al. 2018).

3. PROPERTIES OF MAJOR FUNGAL FOOD-FERMENTING ORGANISMS

Fungi have been used for a multitude of food processes for centuries, with both yeast (unicellular fungi) and mold (filamentous fungi) playing key roles. During food production, these fungi have an immense spectrum of properties and functionalities with multiple impacts on food, including flavor, texture, preservation by ethanol production, nutritional improvement, and improved digestibility. **Figure 4** provides an overview of approaches for the innovative use of fungi in food fermentations.

DIFFERENT WAYS OF FUNGAL-DRIVEN INNOVATIONS IN FERMENTED PRODUCTS

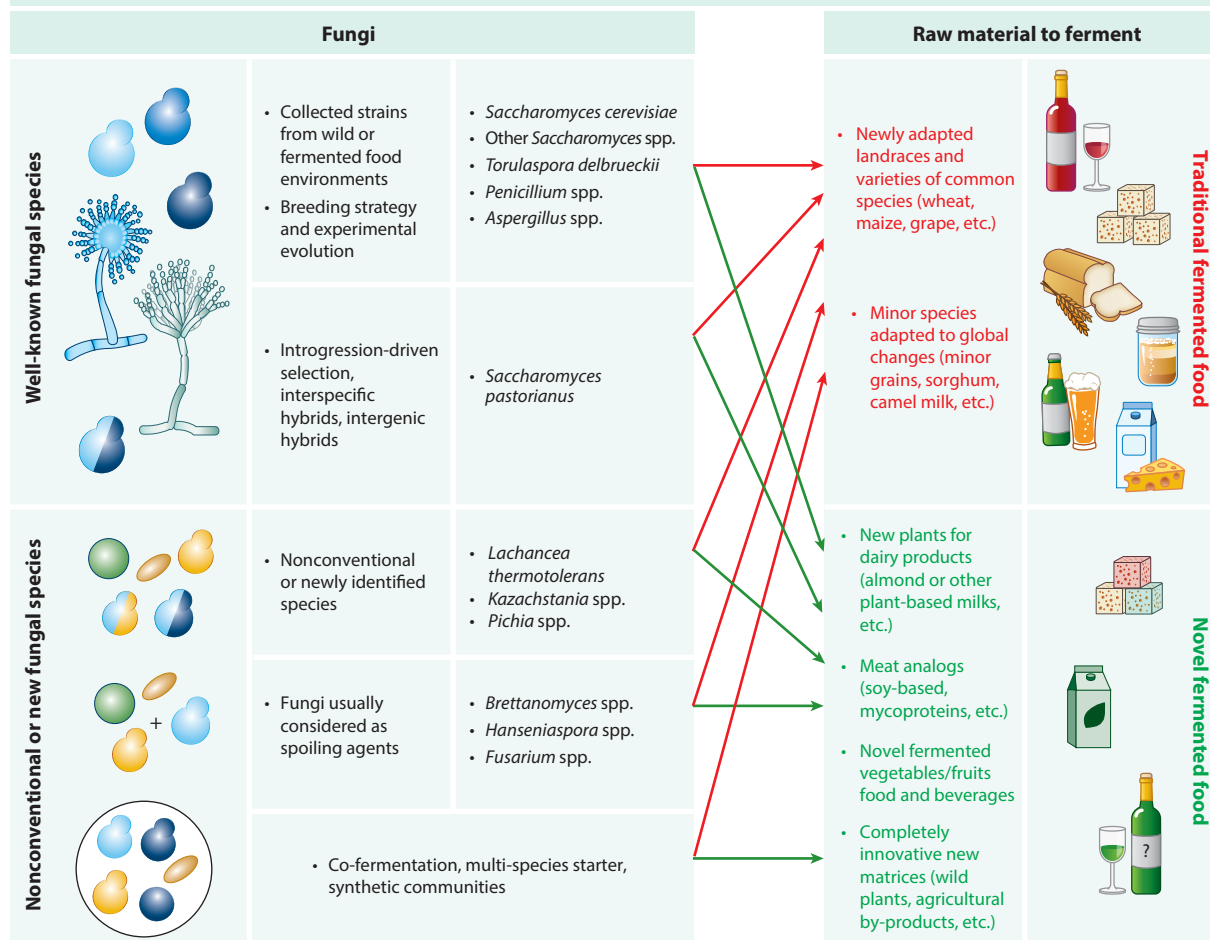


Figure 4

Overview of different approaches of selecting or developing fungal starter cultures for novel fermented food products. Shown are approaches that are based on improvement of well-known fungal species by expanded strain collections, experimental evolution, and intra-specific or inter-specific hybrids as well as approaches that are based on exploitation of nonconventional or new fungal species or fungal communities.

Nonconventional Fungi for Food Innovation

To date, fungal starters used to develop fermented products are based on only a few species, such as *Saccharomyces cerevisiae*, commonly used for wine, beer, or bread fermentations. With time, an increasing number of fungal strains have been made available for industrial purposes, expanding the diversity of fermented food properties.

New strains of commonly found species that were isolated from wild or different agri-food environments can potentially have new properties. For instance, *Saccharomyces* strains isolated from wine, kombucha, or sourdough have interesting potential in brewing, such as aroma compounds production, improved fermentation performance, and fermentation of low-alcohol beer (Bruner et al. 2021, Rossi et al. 2018, Siesto et al. 2023). Nonconventional yeast species have also shown

potential in bread production to increase aroma complexity (Aslankoochi et al. 2016, Timmermans et al. 2023). Environments that are not food related are also reservoirs for biodiversity (Crequer et al. 2023, Mozzachiodi et al. 2022). Fungi are found on flowers, fruits, plant exudates, bark, and animals, which represent interesting environments for new biological resources (Alsammar & Delneri 2020, Cubillos et al. 2019). For instance, yeasts isolated from snails were found to have potential biotechnological value for wine (Akan et al. 2020).

Traditional fermented products can unravel fungi with similar or even enhanced functional properties to those strains commonly used as starters. Fermented foods, including cheeses or cereal-based fermented products, harbor an unexpected diversity of unknown filamentous fungal or yeast species with potential for use in food fermentation. Cheese isolates belonged to the Nectriaceae family, with four new species described, including two *Bisifusarium* spp. and two species of the new genus *Longinectria* (Savary et al. 2022). These species also have technological properties of interest for fermentation, including lipolysis, proteolysis, formation of volatiles, and no mycotoxin production (Savary et al. 2023). Cereal isolates belong to the genus *Kazachstania* and include the new species *Kazachstania bozae* and *Kazachstania saulgeensis* (Gouliamova & Dimitrov 2020, Michel et al. 2023). Therefore, exploring the diversity of known and unknown species can reveal novel or enhanced functional properties for novel foods.

Innovative genetic strategies for selection expand the means for starter development. In traditional fungal cultures, several interesting technological properties originated from interspecies hybridization, introgression, and even interkingdom horizontal gene transfer (Cheeseman et al. 2014, Coelho et al. 2013, Legras et al. 2018, Naumova et al. 2005). Breeding processes such as controlled hybridization, artificial introgression, and experimental evolution have been extensively used to develop new strains (Pérez-Torrado et al. 2015, Steensels et al. 2014). Key examples pertain to yeasts, especially hybrids of *Saccharomyces* spp. As a traditional template, *Saccharomyces pastorianus* (syn. *Saccharomyces carlsbergensis*), a lager yeast used in beer production, is a natural hybrid between *S. cerevisiae* and *Saccharomyces eubayanus* obtained approximately 5,000 years ago (Hebly et al. 2015). Several hybrids between *S. cerevisiae* and *Saccharomyces kudriavzevii* have been isolated from the wine environment (Erny et al. 2012). De novo laboratory hybrids have also been generated between these and other species of *Saccharomyces* to expand the functional diversity of yeast strains. This strategy combines well-known microorganisms (here *S. cerevisiae*) and wild isolates for “the best of both worlds,” as quoted in the work of Hebly et al. (2015) (Álvarez et al. 2023, Pérez-Través et al. 2012). A recent study on *Penicillium roqueforti* has described five genetically distinct cheese and noncheese lineages within this species, with lineages showing distinct phenotypes, including beneficial traits for cheese production among the cheese lineages (Crequer et al. 2023). Crosses between these genetically distinct food and nonfood lineages may lead to improved strains with enhanced functional traits. Intergenous hybrids are generated more rarely. This strategy relies on the same basis as interspecific and intragenous hybrids, with a well-known species on one hand and a nonconventional one on the other hand (Carrau et al. 1993).

Innovation can also take advantage of the genetic diversity of spoilage microbes to determine whether these organisms are beneficial in a different context or environment (Padilla et al. 2016). This is the case for *Brettanomyces* yeasts in wine and beer fermentations. *Brettanomyces* have also been described as beneficial for other fermented beverages such as kombucha and may impact product quality by producing specific volatile compounds and organic acids (Coton et al. 2017, Savary et al. 2021). Other examples include the *Hanseniaspora* genus. Yeasts of this genus contribute to aroma and organic acid production in cocoa, coffee, citrus, and apple-based products (Martin et al. 2018, van Wyk et al. 2024). Strains of additional genera, including *Torulasporea*, *Metschnikowia*, and *Lachancea*, are now commercially used as starters (Roudil et al. 2020) with various technological

properties, including wine acidity modulation, lowering alcohol content, aroma improvement, and bioprotection against spoilage microorganisms (Capece et al. 2018, Chu et al. 2023).

New Matrices for Fungal Fermentations to Answer Global Challenges

Novel raw materials for fermentation alone or in combination with more common raw materials also resulted in innovative fermentation microbes. Animal and plant agriculture are changing their production systems to adapt to climate change. The development of new varieties, landraces, and agro-ecological crop systems provide increased diversity of raw ingredients with new properties, which needs to be taken into account in fermentation processes. This is also the case for selection of the most appropriate microorganisms. Adapting to novel fermentation processes can be based on the know-how of producers of traditionally fermented products, which are often confronted with heterogeneous matrices and adapt their practices accordingly. This can be observed in French farmer-bakers where sourdough bread-making practices are directly adapted to terroir diversity, wheat populations, milling techniques, and seasonal environmental changes (Michel et al. 2023).

New fungal-based fermented products have been developed using underexploited nutrient-rich food sources, e.g., cereals like millet and sorghum or camel milk, that are better adapted to global warming. One example is *Penicillium roqueforti*, which was tested using solid-state fermentations of kodo millet grains to produce a new cereal-based product in India named nilamadana (Dwivedi et al. 2015). This model organism can thus be adapted to a new substrate and actually enhance the overall nutritional value of the final product, as the fermented product contains potentially bioactive phytochemicals of interest for human health. More generally, fermented minor grain foods have unique nutritional value and functional characteristics, which are important for developing dietary culture worldwide (Pswarayi & Gänzle 2022, Qin et al. 2022). Functional components of barley, sorghum, or millet include polyphenols, β -glucans, alkaloids, and a small quantity of anthraquinones. However, these grains also have nutritional deficiencies such as the absence of proteins and some essential amino acids (lysine), low starch content, and the possible presence of antinutritive factors, particularly phytic acid and proanthocyanidins or 3-desoxyanthocyanidins (Gänzle 2020, Svensson et al. 2010). Besides plant products, the development of minor animal-based fermented products may improve food security. This could be the case for camel milk-fermented products that already play an important role in the nutrition of rural communities in Africa, Asia, and the Middle East, especially for populations in arid and semiarid regions (Shori 2012). The isolation of lactose-nonfermenting yeasts such as *Issatchenkia orientalis* from Gariss and *Kazachstania unispora* from Shubat and lactose-positive yeast such as *Kluyveromyces marxianus* from both products is a first step in understanding and developing these products (Shori 2012).

The increased occurrence of food intolerances and changes in lifestyles (vegetarian, vegan, etc.) also generates a need to ferment alternative plant-based materials, including lactose-free, gluten-free, and often legume-based functional products. To tackle these challenges, fungi are a highly valuable resource to transform many substrates into high-quality fermented products with potentially improved digestibility and nutritional value for humans. Mycelial molds are important contributors to many traditional fermented pulse foods (**Figure 1**). Fungi efficiently degrade not only proteins and polysaccharides but also antinutritional factors commonly found in diverse plant-based sources, cereals, and seeds (Gänzle 2020). Fungal cells that colonize these substrates secrete a multitude of enzymes to hydrolyze the more or less complex polysaccharides, proteins, and lipids (Meyer et al. 2020). The degradation products are used for fungal growth but also impact the overall quality of the final fermented food. Yeast and bacterial fermentations can also improve the nutritional and technological properties of gluten-free or plant-based dairy

products (Tangyu et al. 2019, Zannini et al. 2012). Gluten-free cereal products and beverages as well as fermented plant-based milks are now widely available in Western countries as bakery products, beers, and functional drinks. Apart from these, African and Asian traditional fermented products are good examples (**Figure 1**) (Pswarayi & Gänzle 2022). Moreover, fungi have been recently used to valorize side streams of food production. A good example is found in the production of alcoholic beverages based on spent coffee ground hydrolysates using yeast and lactic acid bacteria (Liu et al. 2023) or in oil cake valorized as food using koji mold (Stodolak et al. 2020).

Making use of fungi for new fermentation conditions and products also requires ensuring consumer safety. This aspect is especially important when selecting filamentous fungal species and strains for fermentations, as they may be producers of mycotoxins that impact human health. Approximately 400 mycotoxins have been described to date, although only 9 mycotoxin categories are regulated in the food chain in the European Union (EC No 1881/2006). Mycotoxin production can be highly variable, as it depends on not only the fungal species and strains but also the substrates. Fungal growth is influenced by many abiotic conditions during fermentation processes (temperature, pH, water activity, etc.), and these same factors may impact mycotoxin biosynthesis. Thus, the use of a fungal strain on one substrate versus another may lead to differences in mycotoxin production, so this should be considered for future strain selection for fermented foods and beverages.

4. THE SOCIAL BEHAVIOR OF STARTER CULTURES

Community Assembly in Fermented Foods

Traditional food fermentations are either spontaneous or back-slopped, and the communities of fermentation microbes are controlled through the application of appropriate fermentation conditions. These practices select for either the most competitive fermentation microbes over time (back-slopping) or those among the most competitive microbes that are associated with the raw materials or the processing environment (spontaneous fermentations). An overview of community assembly in spontaneous and back-slopped food fermentations is provided in **Figure 5**. Spontaneous fermentations are characterized by a succession of microbes that is fairly reproducible at the genus level (Mudoor Soorash et al. 2023). Back-slopped fermentations apply selective pressure that selects for communities of fermentation microbes that are often reproducible at the species level, e.g., for *Lactobacillus delbrueckii* and *Streptococcus thermophilus* in yogurt, *Lactococcus lactis*, *Lactococcus cremoris*, and *Leuconostoc mesenteroides* in back-slopped mesophilic cheese starter cultures and *Fructilactobacillus sanfranciscensis* in Type I sourdoughs (Li & Gänzle 2020, Marco et al. 2017). Both back-slopped and spontaneous fermentations are generally characterized by communities of microbes rather than single strains (Smid & Lacroix 2013). Typically, fermented foods include a small number of dominant strains or species and a larger number of species accounting for less than 1% of the microbial cell counts. Increased diversity of the microbial community in fermented foods has been linked to an increased abundance and diversity of flavor compounds (Gänzle 2022).

How Do We Use Existing Knowledge to Compose Communities of Microbes for Use as Starter Cultures in Novel Food Fermentations?

Microbes in food fermentations interact by metabolic cooperation, including cross feeding of metabolites, competition, growth inhibition by metabolites, and niche partitioning. Most traditional food fermentations harbor microbial communities that include yeasts, homofermentative lactic acid bacteria, and heterofermentative lactic acid bacteria. In fermented foods, symbiotic

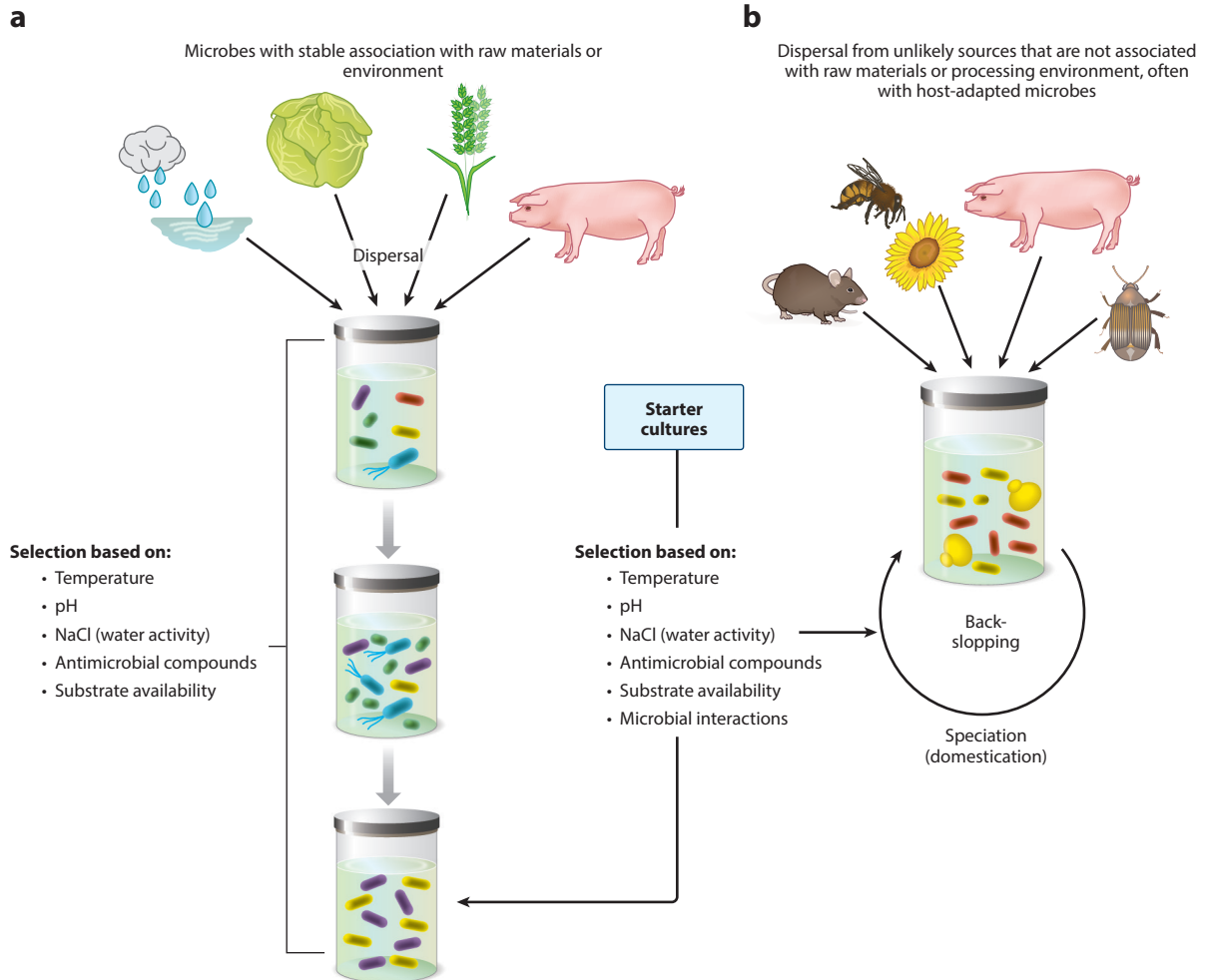


Figure 5

Community assembly in fermented foods. (a) Microbial communities in spontaneous food fermentations originate from raw materials or the processing environment and are determined by dispersal and selection. Most spontaneously fermented plant foods undergo a characteristic succession of fermentation microbes that includes plant-associated Enterobacteriaceae; *Lactococcus*, *Leuconostoc*, and *Weissella*; and *Lactiplantibacillus plantarum* or *Pediococcus* with *Levilactobacillus brevis* or *Limosilactobacillus fermentum*. The use of starter cultures shortcuts this succession of fermentation microbes and thus eliminates an impact of early fermenters on product quality. (b) Community assembly in back-slopped food fermentations is not limited by dispersal, and selection is the major driver for community assembly. Many lactic acid bacteria in back-slopped fermentations are adapted to vertebrate or insect hosts. Several fungal fermentation organisms, including *Saccharomyces cerevisiae* and *Aspergillus oryzae*, were domesticated by long-term back-slopping in fermented foods (Bigey et al. 2021, Dumas et al. 2020, Gallone et al. 2016, Gibbons et al. 2012). The use of starter cultures allows starting a new batch without relying on (unlikely) dispersal from animals or unknown sources and maintains a stable community of microbes despite deficiencies in fermentation control. Figure adapted from Marco et al. (2021) with information provided by Duar et al. (2017), Gänzle & Ripari (2016), Li & Gänzle (2020), and Vellend (2010).

growth of *S. thermophilus* and *L. delbrueckii* subsp. *bulgaricus* is among the best-understood examples. Here, growth of *L. delbrueckii* is favored by formate, CO₂, and fatty acids produced by *S. thermophilus*, whereas *L. delbrueckii* supports growth of *S. thermophilus* by its stronger proteolytic activity (Radke-Mitchell & Sandine 1986, Yamamoto et al. 2021). In traditional sourdoughs,

the yeast *Kazachstania humilis* releases fructose from wheat fructans for use by *F. sanfranciscensis*, whereas maltose metabolism of *F. sanfranciscensis* and acidification of the fermentation substrate shift enzymatic activities of wheat and rye toward glucoamylase and protease activities that release substrates for use by *K. humilis* (Brandt & Hammes 2001, Vogel et al. 1999). More recent discoveries include metabolic interactions by reconstituted microbial communities in kefir grains (Blasche et al. 2021) and sourdough (Maria Calabrese et al. 2022). These metabolic interactions are, however, highly dependent on the fermentation substrates milk, wheat, and rye and thus are not necessarily transferable to novel food fermentations based on different substrates. Traditional food fermentations nevertheless provide templates for reconstitution of microbial communities for use as starter cultures in novel food fermentations.

To briefly outline the selection of communities of microbes for fermentation of those examples of novel fermented foods that are presented in **Table 1**: The revival of garum (Mouritsen et al. 2017, Redzepi & Zilber 2018), antique fish sauces that went out of fashion in Europe when the Roman Empire collapsed, can be based on traditional Asian or African fermented condiments, including kharoli (element 13 in **Figure 1**), gochujang (element 81), and fish sauces produced in Southeast Asia (element 85) (Bora et al. 2022, Owusu-Kwarteng et al. 2020). All these products rely on a combination of mycelial molds or bacilli as a source of proteolytic enzymes, often followed by growth of *T. halophilus* in combination with yeasts to improve flavor and taste (Song et al. 2015). Traditional African cereal fermentations, which are generally based on gluten-free cereals, provide templates for communities of fermentation microbes that are suitable for production of gluten-free bread and nonalcoholic cereal beverages (**Figure 1** and **Table 1**) (Pswarayi & Gänzle 2022). Predicting how fermentation microbes perform in plant-based analogs of cheeses and meats is more difficult, as traditional templates exist (group 12 in **Figure 1**) but the flavor and texture of these products are not appealing to consumers who are used to eating cheese or processed/fermented meats. When assuming that pulse proteins or insect powder provide a comparable substrate composition as meat or fish, a combination of staphylococci and *Latilactobacillus*, *Lacticaseibacillus*, or *Lactiplantibacillus* spp. would likely be successful (Kewuyemi et al. 2020). Communities of microbes also include communities of yeasts or combinations of fungal cultures and bacterial cultures.

For wine or beer fermentations, combinations of *S. cerevisiae* with strains of nonconventional yeasts are commercially available (Roudil et al. 2020). Strains selected from complex traditional kombucha fermentations were used to create synthetic microbial communities for kombucha production combining both bacterial and yeast species (Ferremi Leali et al. 2022, Savary et al. 2021). The fungal species *Brettanomyces bruxellensis*, *Hanseniaspora uvarum*, and, in some cases, *Zygosaccharomyces* spp. positively impacted this fermentation by producing volatile compounds and organic acids but also by releasing CO₂ through alcoholic fermentation. These properties enhanced the overall aromatic and sensorial complexity of the product, proving that diverse communities positively impact these fermentations. These studies opened the way to imagine controlled fermentation with more species, increasing the diversity from a simplified consortia of a few strains to more complex synthetic communities (Bagheri et al. 2017, Savary et al. 2021). Multistrain starter cultures or synthetic communities can now be seen as the future for food starters or ripening cultures, but we need to design new breeding methods for fungal cultures (Arias-Sánchez et al. 2019) and rethink the way we use these industrial starters. The use of microbial communities generates the need to fully understand how to maintain microbial communities and promote and/or limit fungal growth while preserving the typical complexity that a given ecosystem brings (Sakandar et al. 2020). Analyzing how raw materials' process parameters shape the community dynamics should shed light on how to maintain diversity.

A third criterion for selecting strains for the design of starter cultures for novel food fermentations is the coexistence of organisms in their natural habitats, i.e., plants, animals, or environmental niches. Lactococci, *Leuconostoc* spp., and *Weissella* spp. coexist in dairy starter cultures and plant microbiomes (Yu et al. 2020) and thus can be expected to also perform well when combined for use in plant fermentations such as plant-based cheese analogs. Likewise, *Lactobacillus* spp. and *Limosilactobacillus* spp. interact and stably coexist in intestinal communities associated with vertebrate animals (Lin et al. 2018, Tannock et al. 2012) and in many cereal fermentations (Gänzle & Zheng 2019). Insect-associated microbial communities are also characterized by the stable coexistence of homofermentative and heterofermentative lactobacilli (Brochet et al. 2021), but, with the exception of *F. sanfranciscensis* and *Fructilactobacillus fructivorans*, none of the insect-adapted lactobacilli occurs in food fermentations.

Last but not least, the list of microbes with documented or potential use in food fermentations includes a few wildcards that remain poorly characterized. For example, *Companilactobacillus* spp., *Schleiferilactobacillus* spp., and *Furfurilactobacillus* spp. often occur in traditional food fermentations but are usually not part of the dominant microbial strains or core communities in specific food fermentations (Zheng et al. 2020). Their contribution to the quality of fermented foods remains largely unexplored.

5. FERMENTED FOODS AS A SOURCE OF HEALTH-BENEFICIAL LIVE MICROBES

Do Fermented Foods Impact the Human Intestinal Microbiome and Human Health?

Humans have evolved with both their microbiome and fermented foods, which has implications for health. The analyses of fecal metagenomes revealed that the transition from hunter-gatherer societies to nonindustrial agricultural societies and the transition from nonindustrialized agricultural societies to industrialized societies had major impacts on human intestinal microbial communities (Wibowo et al. 2021). Microbial communities from hunter-gatherer societies were more similar to preindustrial agricultural societies when compared to metagenomes from industrialized countries (Wibowo et al. 2021). The transition from hunter-gatherer societies and the transition from preindustrial agricultural societies to industrialized societies altered the density of human settlements and the transmission of microbes among humans (Figure 6). Two examples are the evolution of host-adapted serovars of *Salmonella enterica* in response to the larger settlements of agricultural societies and the disruption of the transmission of *Vibrio cholera* by water sanitation (Key et al. 2020, Koch 1893). These impacts on the transmission and dispersal of microbes pertain to not only pathogens but also commensal gut microbes. A substantial portion of gut microbes is shared by strain-level human-to-human transmission (Kort et al. 2014, Valles-Colomer et al. 2023, Yassour et al. 2018), i.e., the conditions of human cohabitation impact the composition of intestinal microbial communities. In addition, zoonotic transmission of gut microbes from domesticated animals that live in close contact with humans was proposed as a relevant route to the acquisition of the accessory intestinal microbiome (F. Li et al. 2023). Human-to-human or zoonotic transmission of gut microbes, however, transfers not only commensal gut microbes but also pathogens (Figure 6) (GBD 2016 Diarrhoeal Dis. Collab. 2018). Prevention of human-to-human or zoonotic transmission of gut microbes has thus greatly improved human health but has also been associated with negative consequences to the diversity of human intestinal microbiota and the health benefits that are associated with this diversity (Figure 6) (Sonnenburg & Sonnenburg 2014).

Differentially abundant bacterial taxa in hunter-gatherer societies, preindustrial agricultural societies, and industrialized societies also include animal-associated microbes, e.g., enterococci,

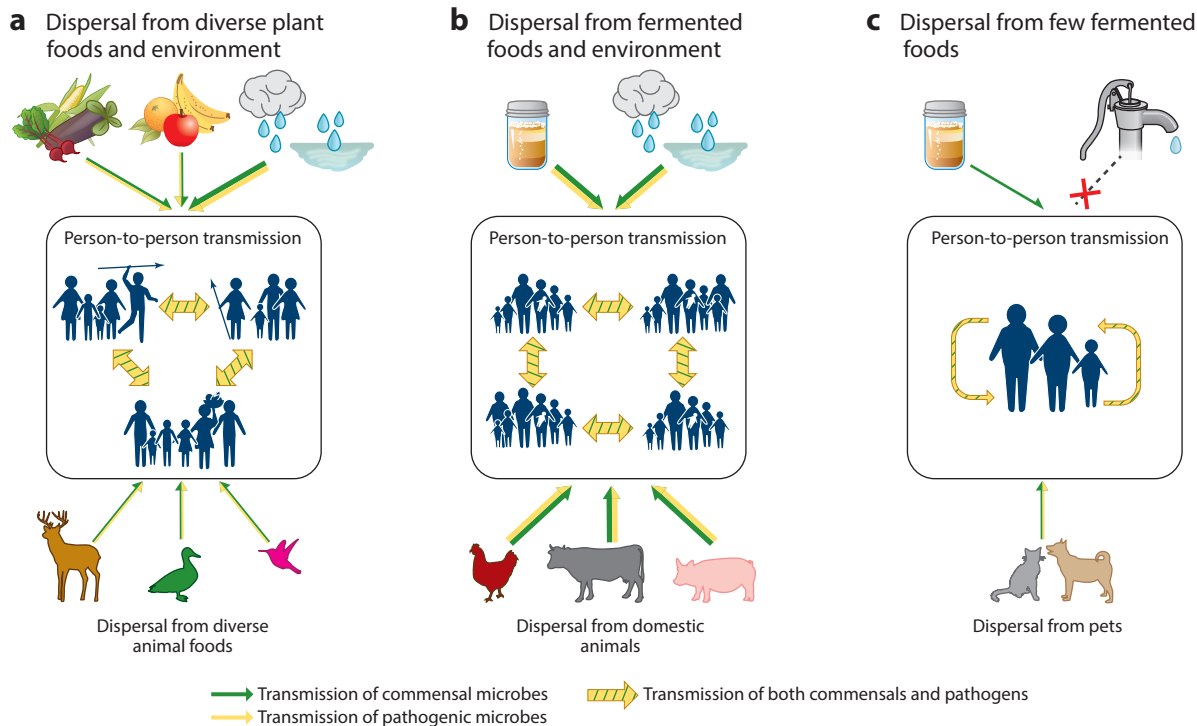


Figure 6

Schematic representation of the transmission path of gut microbes in (a) hunter-gatherer societies, (b) preindustrial agricultural societies, and (c) industrialized societies. Transmission of commensal microbes is indicated by green arrows, transmission of pathogenic microbes is indicated by yellow arrows, and transmission of both commensals and pathogens is indicated by green and yellow hatched arrows. The arrow width is scaled to approximate the relevance of specific transmission paths.

Lactobacillus animalis, and *Ligilactobacillus murinus*, which were more abundant in preindustrial metagenomes, and *S. thermophilus*, which was more abundant in metagenomes from industrialized countries (Wibowo et al. 2021). This comparison also holds true if the majority population in industrialized countries is compared to minorities with the same genetic background but a different lifestyle (Keohane et al. 2020). Several studies of contemporary individuals also report on a differential distribution of lactobacilli. Few, if any, Lactobacillaceae were identified in contemporary hunter-gatherer societies (Clemente et al. 2015, Schnorr et al. 2014), whereas lactobacilli were enriched in African and Papua-New Guinean preindustrial agricultural societies but not in developed societies (De Filippo et al. 2010, Martínez et al. 2015, Shankar et al. 2017, Yatsunenkov et al. 2012). These differences particularly pertained to food-fermenting species or genera, including *Leuconostoc* and *Weissella* and/or lactobacilli, and may suggest that fermented foods with live fermentation microbes contribute to intestinal microbial diversity (Figure 6).

Most species in the genera *Lactobacillus*, *Ligilactobacillus*, and *Limosilactobacillus* are adapted to vertebrate hosts (Duar et al. 2017), and many of these host-adapted species are also present in food fermentations (Figure 1) (Li & Gänzle 2020, Su et al. 2012). It is increasingly recognized that fermented foods containing live dietary microbes contribute to the human accessory microbiome. Food-fermenting lactobacilli are readily detected and isolated from human fecal samples (Dal Bello et al. 2003, Gelsomino et al. 2003). Large-scale analyses of human fecal metagenomes

confirmed that food-fermenting lactic acid bacteria are present in relatively low abundance but, in some cases, with high prevalence (Pasoli et al. 2020). However, through the reduction of fermented foods in modern diets and the application of starter cultures with limited microbial diversity, the exposure of humans to diverse fermentation microbes was reduced through industrialization.

To what degree fermented food organisms become part of the human microbiota and impact gut microbiome ecology is likely highly variable and dependent on the microbial species. In addition, fermentation microbes differ with respect to their survival during intestinal transit. In general, vertebrate gut-associated microbes are better equipped to withstand environmental insults during gastrointestinal transit by acid- and bile-resistance mechanisms (Krumbeck et al. 2016, Lebeer et al. 2018, Morelli 2000, Zhao et al. 2019). Experiments that used fermentation microbes allochthonous to the human gut have often been studied in probiotic trials, and these experiments clearly showed that these organisms have only a transient and marginal effect on the gut microbiota (Tannock et al. 2000, Walter et al. 2001). The consumption of live fermentation microbes may still have functional consequences when the exposure is high and continuous. Many societies, e.g., in Sub-Saharan Africa, consume fermented foods with live fermentation microbes as daily staples of the diet (Pswarayi & Gänzle 2022).

In addition, analyses of fecal samples may underestimate any impact fermentation microbes have on intestinal microbial ecosystems. A slaughter trial in swine documented that the DNA copy number of live dietary microbes in the stomach and small intestine ranged from 10 to 100% relative to the abundance in feed. In the colon and fecal samples, the abundance was reduced to 1–10% and less than 1%, respectively (Zhao et al. 2019). Microbes from a fermented dairy product accounted for up to 50% of the small intestinal microbiota in ileostomy patients (Zaccaria et al. 2023).

In conclusion, fermented foods have the potential to function as vectors for the dispersal of gut microbes, or allochthonous microbes from other microbiomes, that provide high numbers of microbes that interact with the immune system when fermented foods are consumed (Spencer et al. 2022, Wastyk et al. 2021). It is likely that fermented foods fulfilled this role between the Neolithic revolution and the onset of industrialization (**Figure 6**).

As fermented foods deliver large amounts of live microbes, they have the potential to beneficially influence health. Health benefits are best documented for probiotic microorganisms, i.e., preparations of microbial biomass with high cell counts of strains for which specific health benefits were documented in randomized, placebo-controlled clinical trials (Hill et al. 2014, Merenstein et al. 2020). The current consensus considers the health benefits of probiotics a strain-specific effect; however, specific health benefits, e.g., protective effects in necrotizing enterocolitis or prevention of antibiotic-induced diarrhea (Merenstein et al. 2020), are consistently documented in multiple clinical trials that use taxonomically diverse probiotic strains (Hill et al. 2014, Marco et al. 2021, Merenstein et al. 2020).

Health benefits were also observed for fermented foods that did not include specific probiotic strains, e.g., yogurt; however, clinical trials with fermented foods are rare and often confounded by the simultaneous impact of the food matrix (Bourrie et al. 2020, Marco et al. 2017, Song et al. 2023). Expert panels convened by the International Scientific Association for Probiotics and Prebiotics have reviewed the health effects of fermented food products. These panels clearly differentiated between fermented foods and probiotics (Hill et al. 2014, Marco et al. 2021) but also proposed a minimally recommended intake of microbes (Marco et al. 2020). Early observational studies have detected a modest correlation of live dietary microbes with several positive health outcomes (Hill et al. 2023). A small intervention trial with fermented foods observed a small but significant impact on the gut microbiome and gut metabolome of humans (Taylor et al. 2020). An intervention trial

comparing a high-fiber diet, a diet high in fermented foods, and a control diet reported increased intestinal microbial diversity and reduced inflammatory signals in individuals consuming the diet that was high in fermented foods (Wastyk et al. 2021). None of these three studies screened for specific microbes or specific fermented foods; the correlations were based on comparing fermented foods with high cell counts of any food-fermenting microbe to control diets with much lower microbial cell counts. Although the health effects of fermented foods are enthusiastically praised by lay commentators and some scientists, there are thus far too few well-designed clinical studies that validate effects, and evidence for specific health claims is virtually nonexistent. The clinical validation of the health effects of fermented foods and the underlying mechanisms therefore remains a major area of needed research.

Can Health Benefits of Live Dietary Microbes Be Used to Select Strains to Design Novel Fermented Foods?

When compared to the body of literature documenting the health-beneficial effects of probiotic microbes, the science on the health benefits of fermented foods is still incomplete, fragmented, and evolving. Because the concept of probiotics was developed with fermented dairy products as a conceptual template (Fuller 1992), many of the probiotic strains of lactobacilli also represent food-fermenting organisms, e.g., *Limosilactobacillus fermentum*, *Limosilactobacillus reuteri*, *L. plantarum*, and *Lactocaseibacillus paracasei*. It is therefore often straightforward to select specific strains that serve a dual role as health-beneficial probiotic strains and starter cultures with suitable technological traits (Jahreis et al. 2002, Marco et al. 2021). The selection of strains that modulate the immune system or other host systems can be based on high-throughput genomic analyses and through screening for functional metabolites, e.g., γ -aminobutyrate (Lebeer et al. 2018, Surachat et al. 2021). Preclinical screens also used immune cells, organoids, and other systems (Groeger et al. 2013, Spinler et al. 2014). In addition, the above statement that more diverse communities of fermentation microbes result in a greater diversity and higher concentration of flavor compounds may also relate to health benefits: The selection of diverse communities that include species that are both autochthonous to the human gut and perform well in food fermentations is likely to enhance the impact of live dietary microbes on intestinal microbial communities and host health. Of the diverse transmission paths of gut microbes (**Figure 6**), fermented foods are least likely to have a permanent impact on human intestinal microbiota; however, they also represent the only transmission path that excludes pathogenic microbes and parasites. Fermented foods thus constitute a promising opportunity to redress the deleterious reduction of gut microbial diversity in the industrialized world (Sonnenburg & Sonnenburg 2014).

6. CONCLUSIONS

The diversity of fungal and bacterial cultures for use in novel food fermentations is immense. Safety considerations, the use of organisms in traditional food fermentations with comparable substrates, the link of bacterial phylogeny to ecology and metabolic properties as well as established and emerging computational tools provide criteria for screening this immense diversity and using cultures that are currently not used commercially for food fermentations. Fungi are also key actors in traditional fermented products and a source of innovation for future fermented food and beverages. These innovations can come from two paths, the matrix and the fungi used, that can also work together. Moreover, food fermentation trends tend to promote microbial diversity as well as product diversity and the most suitable starter cultures are likely to often consist of communities of fungi and bacteria.

Interest in food fermentations is likely to increase even further with the transition to sustainable food systems to protect planetary and human health (Jahn et al. 2023). Novel microbial foods in

which most biomass is provided through microbes, novel fermented foods based on plant-derived ingredients, and food ingredients derived from microbial fermentations are promising solutions for more secure food systems with much smaller environmental footprints than traditional (animal) foods. Among others, these solutions are provided by the provision of plant-based alternatives to (fermented) animal protein foods and soft drinks, and by fermentative upcycling of side streams of food production, including those for bran, brewers' spent grains, and okara. In addition, many of the novel fermented foods that contain live dietary microbes meet the recommendation to include minimally processed plant foods with a high content of dietary fiber and phytochemicals that may contribute to the prevention of noncommunicable chronic diseases (Armet et al. 2022). Novel fermented foods thus have the potential to tackle food security and food safety and benefit human health. However, a science-based approach as proposed in this review is required to exploit this potential.

DISCLOSURE STATEMENT

The authors are not aware of any affiliations, memberships, funding, or financial holdings that might be perceived as affecting the objectivity of this review.

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