

Review

Fermented foods: lessons learned from metagenomicsVincenzo Valentino¹, Francesca De Filippis^{1,2} and
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Thanks to the standard microbiology protocols of isolation and culturing, hundreds of strains have been isolated from fermented foods throughout the last decades, and phenotypic traits linked with pro-technological properties and health claims have been investigated. However, culture-independent metagenomic analyses have revealed an unexpected microbial diversity in foods fermented spontaneously or by undefined starter cultures.

Here, we report the most groundbreaking advancements in the understanding of fermented foods ecology by presenting case studies where metagenomics has been applied, contributing to identifying novel species *in silico* or to deciphering the microbiome structure associated with spontaneous fermentations. We also highlight the potential of metagenomics in supporting the identification of potential probiotics and discuss the future ahead, particularly focusing on the integration of multi-omics approaches.

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Introduction

Proofs of food fermentation trace back to at least 14 000 years BCE [1]. However, it has been hypothesized that unintentionally fermented foods were consumed by hominids at least 10 million years ago, probably as a behavioral heritage from primates [2]. Ancient

populations accidentally fermented a wide range of food matrices in multiple settings throughout the globe [3–6] and thus discovered a convenient and spontaneous way of storing perishable matrices. Since then, consumption of fermented foods has become a staple in different cultures, and has been handed down till modern ages.

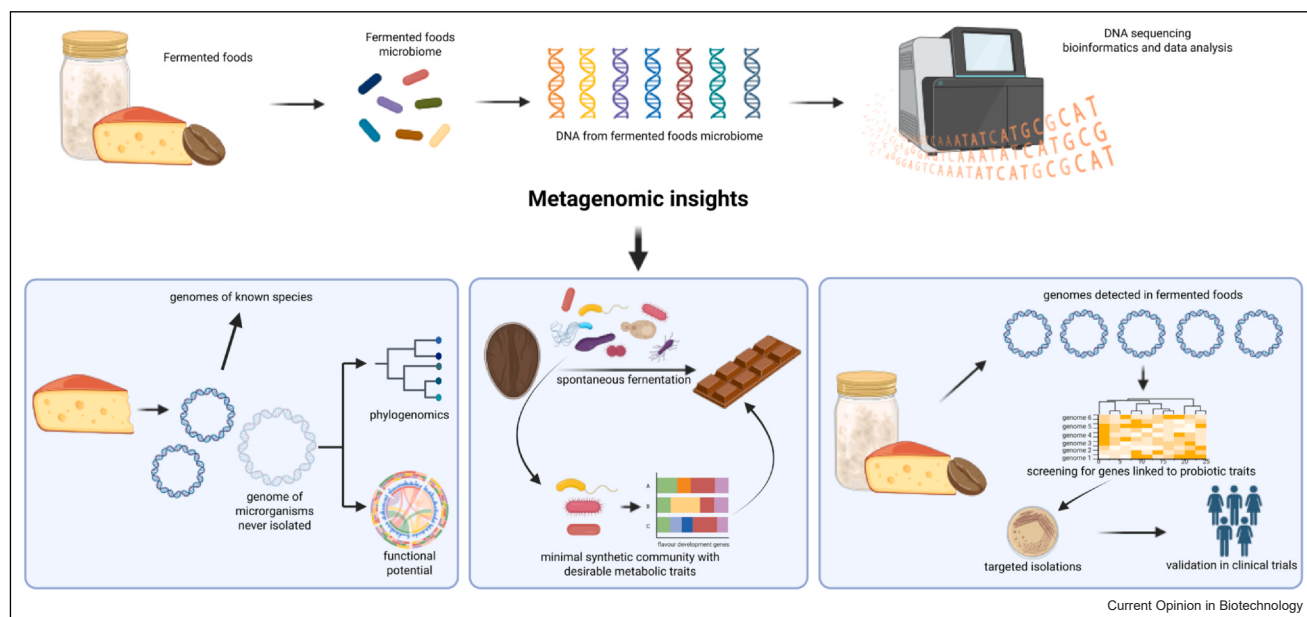
We have started studying microorganisms systematically roughly 150 years ago, and the understanding of the role of microorganisms in fermented foods is even more recent. However, the tools developed at the dawn of microbiology have changed the world, allowing researchers to discover, isolate, and intentionally propagate microbial strains relevant for the fermentation process and for human health. Over the decades, this has led to well-controlled fermentations, leading to the production of standardized products with predictable and defined sensory properties [7,8] and safety standards [9]. Nonetheless, cultivation of microorganisms has only unearthed a minor fraction of the total diversity of fermented foods microbial communities [10], suggesting that they host an unexplored microbial diversity with untapped potential applications. New insight into fermented foods has been made possible by a more recent cutting-edge technological approach, allowing for deep exploration of microbial communities, that is, metagenomics. In brief, metagenomics goes beyond isolation and propagation of microbes, rather focusing on the total genomic material derived from a particular ecological niche. By processing the genomic sequences of (virtually) all the microorganisms from an environment, metagenomic analyses have contributed to deepening our knowledge of the community's structure, activities, and dynamic shifts occurring at all stages of food fermentations.

Here we summarize what metagenomics has contributed to the knowledge of fermented foods (Figure 1) and highlight the further groundbreaking hypotheses that could be tested soon.

The hidden microbes

Throughout the years, isolation and characterization of microorganisms from fermented foods have indicated Lactic Acid Bacteria (LAB) as the main players in food fermentations. Several excellent reviews are available on this topic [11,12], also highlighting the probiotic potential of multiple LAB strains isolated from fermented foods. Different LAB species are determinant to the development of functional and sensory properties of fermented foods obtained from a wide range of

Figure 1



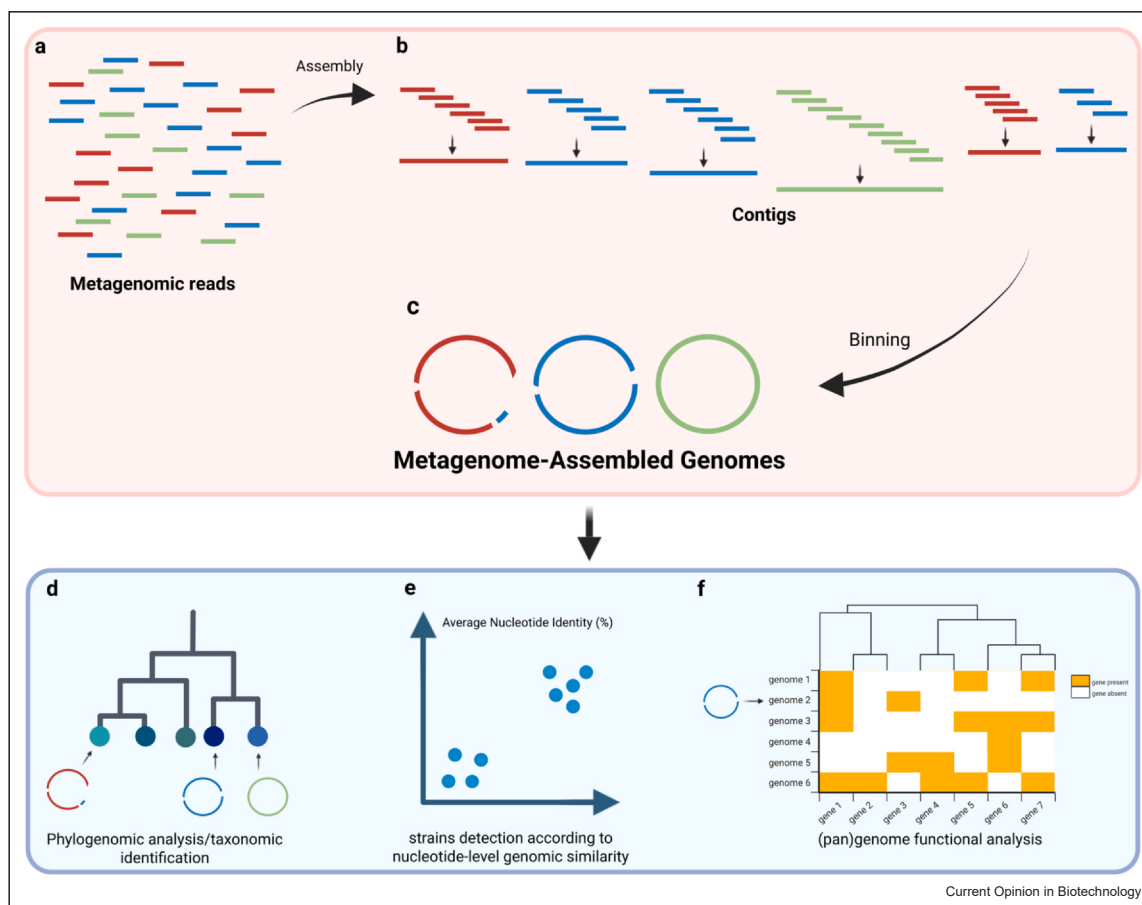
Metagenomics to unearth the fermented foods microbiome. Upon total microbial DNA extraction and whole metagenome sequencing, metagenomic data can provide comprehensive insights into the structure and functional potential of fermented foods' microbiomes. The approach has led to the discovery of novel species with possible key roles in determining the product's characteristics. In addition, metagenomics has been applied to disentangle the ecologic dynamics of spontaneous fermentation, leading to the development of synthetic communities. Finally, innovative tools to mine probiotic strains from metagenomic data are under development. Created in Biorender.

ingredients (e.g. dairy, vegetables), thanks to their overall diverse and versatile metabolic adaptation deriving from evolutionary pathways [13,14], some of which are still occurring [15].

Thanks to these relevant efforts, roughly >300 LAB species have been discovered and described so far [16,17], most of which are relevant to the production of fermented foods. However, extensive use of metagenomics to explore the microbiome of fermented foods has captured genetic signals that are not attributable to any of the currently known microbial species. Indeed, processing of metagenomic reads with specific tools and pipelines allows to detect genomes (i.e. Metagenome-Assembled Genomes; Figure 2) from both known and unknown species, helping to disclose the microbial diversity of complex microbial communities [18]. This approach has also successfully unraveled unknown microorganisms residing in fermented foods. A key example is the discovery of a putative novel *Oenococcus* species in water kefir [19] encoding for β -glucosidase and mannitol dehydrogenases, which release fructose and reduce it into mannitol, a key compound of this fermented beverage [20,21]. Similarly, a meta-analysis by Walsh et al. [22] focusing on cheese microbiomes detected several novel species spanning different genera with the metabolic potential to produce flavor-enhancing metabolites. These pioneering studies on the

unexplored microbiome of fermented foods have stimulated further large-scale investigations, as well as the creation of public databases that can be easily accessed to delve more into the phylogeny and functional diversity of uncultured (fermented) foods-associated species. As such, one of the most relevant outputs has been an integrated metagenomic analysis of >2500 food metagenomes, including a large proportion of fermented foods [23]. Through this strategy, the authors highlighted the existence of an unexpected number of uncharacterized microbial species with a cumulative impressive functional diversity, possibly impacting food properties. Interestingly, the study detected about 300 novel species exclusively found in foods, with more than half phylogenetically distant from any currently known genus but spanning across *Bacillota*, *Pseudomonadota*, *Actinomycetota* and *Bacteroidota* phyla. In addition, roughly the totality (98 %) of unknown species was well adapted to specific (fermented) foods, including fermented vegetables, seeds, and dairy products, suggesting a relevant yet undisclosed role in defining their properties. Collectively, these large-scale explorations of uncultured species inhabiting fermented foods not only widen our understanding of the microbial diversity and of the functional assembly of fermented foods microbiomes, but might result in a practical advancement for the food industry, possibly driving next efforts toward development of culturomics approaches well suited for

Figure 2



Genomes reconstruction from metagenomes. **(a)** Upon removal of low-quality nucleotides and fragments from the host genome, reads from a complex microbial community are assembled into contigs, **(b)** representing longer consensus fragments belonging to a single organism. **(c)** Through the binning process, contigs that show nucleotide-level signatures and have similar depth are grouped together into Metagenome-Assembled Genomes, which are quality-assessed through estimation of genome completeness and contamination with fragments from other organisms. Upon exclusion of MAGs showing low completeness and/or high contamination, downstream applications are possible, for example, **(d)** taxonomic identification through phylogenomic analyses; **(e)** strain-level resolution based on average nucleotide identity with other genomes from the same species (either reference genomes or MAGs); **(f)** (pan)genome functional analysis to unearth the metabolic potential of microorganisms detected *in silico*.

the isolation of currently unknown species [24] and understanding of optimal growth parameters for these novel species, that might ultimately result in novel and more effective starter cultures.

Deciphering and optimizing spontaneous fermentation

Most of the traditional fermented foods are produced through spontaneous fermentation, that is, relying on indigenous microorganisms naturally present in the food matrix that prevail and start the fermentation in specific environmental conditions [25]. Other types of traditional fermented foods are obtained through inoculation of undefined starter cultures from previous successful production batches, that is, back-slopping [26]. In both cases, the exact species- and strain-level composition of

the starter community is unknown, albeit fundamental to induce desirable transformations in the food matrix [27], which are often stable and mostly reproducible. However, metagenomics has the potential to fully disclose the contribution of microbial strains from undefined starter cultures, even when isolates are lacking. Deciphering the dynamics in natural starters and in spontaneous fermentations will guide researchers to fine-tune synthetic consortia, preserving the traditional sensory and nutritive properties of fermented foods while minimizing the risks of unsuccessful production batches, with a reduction of food waste.

The use of metagenomics to discern the composition and function of communities involved in spontaneous fermentation has already been tested for some

traditional fermented foods, and successful applications have been published so far. For example, Gopaulchan and colleagues [28] uncovered the main actors involved in the development of chocolate flavor during cocoa fermentation. Traditionally, cocoa seeds are fermented spontaneously in wooden boxes or baskets immediately after harvesting, and the fermentation not only leads to decay of mucilage surrounding the seeds, but also contributes to develop the sensory profile of chocolate [29]. Although previous works have revealed the taxonomic composition involved in cocoa fermentation [30], their metabolic contribution has been undisclosed for a long time. Also, batch-to-batch variability in terms of taxonomic communities often leads to failure of the fermentation or to inconsistencies and instability in flavor development [31]. However, *in silico* detection of genomes from metagenomes and their functional characterization allowed Gopaulchan and collaborators to link each species to a specific metabolic profile, and to select only those taxa harboring enzymes and pathways relevant to the production of desirable cocoa flavor, identifying a minimal synthetic community. Since isolates from the taxa selected *in silico* were available, the research group tested the effectiveness of the synthetic community through a controlled fermentation of cocoa seeds. Intriguingly, the fermented product fully reproduced the sensory properties of the spontaneously fermented seeds, providing the first evidence of a minimum synthetic community needed to produce cocoa with a high succession rate. Similarly, a multi-omics approach integrating metagenomics and metatranscriptomics allowed Calabrese and colleagues [32] to identify the microbial strains essential to fully reproduce the metabolic activities observed in the spontaneous sourdoughs. Upon identification of the strains harboring the core microbial traits needed for the sourdough reproduction, the resulting synthetic community was validated through metabolomics and strain profiling in a dough, fully reproducing the sensory properties of the original sourdoughs. Importantly, the authors outlined that gene redundancy across the strains is needed to ensure sourdough stability and efficiency. These brilliant experiments confirm metagenomics as a game-changer in the understanding of spontaneous fermentation dynamics, providing a remarkable tool to identify unneeded and detrimental strains that can be excluded from synthetic consortia. The same approach could be applied to other spontaneously fermented food products, upon validation and standardization of pipelines and procedures. Development of minimal synthetic communities and fine-tuning of fermentation through metagenomics will drastically reduce the environmental impact of food chains by reducing food waste, further contributing to reaching the United Nations Sustainable Development Goals, particularly SDG 2 — Zero Hunger, and SDG 12 — Responsible Consumption and Production.

Metagenomic-driven isolation of and characterization of probiotics

Although a recent meta-analysis concluded that no recommendation for the preventive intake of probiotics can currently be published [33], research is showing the benefits of several probiotic strains, some of which have contributed to counteract diseases and infections successfully [33,34], particularly acting as adjuvants in adults [35].

According to the International Scientific Association for Probiotics and Prebiotics, probiotics are live organisms that confer a health benefit to the host when administered in adequate amounts [36]. To confer health benefits, probiotics must stay alive throughout the gastrointestinal tract transit. Therefore, the ability to overcome hurdles from the host's gastrointestinal tract (e.g. low stomach pH, presence of bile salts) is an imperative trait that candidate probiotics must have [37]. There is no consensus on the methods to test the strains resistance to gastrointestinal tract transit [38], and different protocols, stressors, and parameters to monitor have been reported. However, all of them require *in vitro* testing of the strain, and when large-scale screening for probiotics is set up, high quantities of consumables and lab work are needed to investigate the strain's resistance and probiotic potential, sometimes making the whole experiment difficult to implement. This limitation hinders the detection of novel probiotic strains.

Given that clinical trials are necessary to provide evidence of the health-promoting properties of a candidate probiotic strain, (meta)genomics approaches can ease the discovery of interesting strains from complex communities and their functional characterization, moving from the traditional top-down (e.g. isolation of species enriched in healthy people or fermented foods [39]) to a 'purpose-driven' approach, that is, focusing on the characterization of strains with potentially desirable functional properties. Metagenomics-driven isolation of probiotics might also make large-scale screening from fermented foods more feasible. Indeed, extensive databases of genes linked to probiotic traits (either encoding gut engraftment and health-promoting properties) have been developed [40,41], which can facilitate the screening of both genomes from isolates and metagenome-assembled genomes (MAGs), while other curated repositories and tools can be used to predict the absence of virulence factors and antimicrobial resistance genes in candidate strains [42–45]. In this vein, Wu and colleagues published metaProbiotics — a bioinformatics tool that uses machine learning trained on genomes of known probiotic strains to identify candidates among MAGs [46]. These approaches could speed up and increase the efficiency of the screening of probiotics from fermented foods, potentially also uncovering the health-promoting potential of species not commonly associated with

probiotics [47]. Preliminary attempts to detect potential probiotic genomes from fermented foods metagenomes have been published already, suggesting several Acetic Acid Bacteria (including *Gluconobacter* spp. [48]), as interesting for future probiotics-oriented investigations.

However, it should be noted that *in silico* screening for probiotics from food microbiomes through ‘probiotics-mining’ tools is still at developmentary stages, and more robust pipelines and studies validating the approaches currently available are needed.

Conclusions and future perspectives

Fermented foods are an exciting source of (novel) microorganisms with potential applications in various fields, and metagenomics has the power to help their thorough detection. The presence of some food-specific species has already been highlighted and applied in some proof-of-concept studies to produce synthetic communities from highly diverse communities involved in spontaneous fermentations. However, there’s still a need for standardized computational pipelines and well-defined approaches to extract meaningful information from metagenomic data. Overcoming these limitations, particularly through the adoption of integrated multi-omics approaches, will represent a key step toward a deeper, systems-level understanding of fermented food microbiomes and the beneficial microbes therein.

CRediT authorship contribution statement

Vincenzo Valentino: Conceptualization, Investigation, Writing – original draft. **Francesca De Filippis:** Writing – review & editing. **Daniilo Ercolini:** Conceptualization, Writing – review & editing

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Data Availability

No data were used for the research described in the article.

Declaration of Competing Interest

The authors declare no conflict of interest.

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