Bacteriophage ecology of fermented foods: anything new under the sun?

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Abstract

Bacteriophage ecology has raised an increasing attention over the last few years, thanks to the improvement and contributions of microscopy, comparative genomics and viral metagenomics methods. Fermented foods host dense and diverse microbial communities and, therefore, represent an ideal biotope for bacteriophages. If their occurrence in such environments has been demonstrated decades ago, data highlighting their impact on mixed communities and their ecological roles are scarce when compared to other microbial ecosystems. This review summarizes most recent knowledge into the bacteriophage diversity of fermented foods and stress evidences suggesting the impact of these entities on the dynamics of food microbial communities. The main ecological roles played by bacteriophages in microbial ecosystems are also addressed. Understanding the impact of bacteriophages in fermented foods will further help in designing adapted microbial consortia and thus providing a better control of the food fermentations.

Key-words: fermented foods; bacteriophages; microbial ecology; population dynamics.

Introduction

Fermented foods are widely consumed worldwide and encompass diverse types of products including fermented dairy products, meats, fishes, cereals, legumes, vegetables, seeds, roots and also alcoholic and non-alcoholic beverages [1]. Initially developed with the objective of extending the raw products shelf-life, they are currently also appreciated for their typical sensory properties, nutritional value and potential health benefits [2,3]. Food fermentation relies on the conversion of substrates present in the raw material (e.g. sugars, proteins, lipids) into simpler products such as lactic acid, acetic acid, alcohol, carbon dioxide, ammonia and free fatty acids, through the specific activity of microorganisms.

Fermented foods are dynamic microbial ecosystems, where the succession of several microbial groups occur in a short time, usually from days to weeks or months. This period varies according to the nutrients available in the raw material, abiotic parameters such as temperature, humidity, oxygen and osmotic pressure, and microbial interactions as well [4]. Huge efforts have been performed by the scientific community during the past decades to describe the composition and functioning of food microbial communities, helped by the recent development of several meta-omics tools [5]. It is now well-established that microbial communities of fermented foods are generally dense (*e.g.* $>10^9$ cells per gram of cheese [6]) and have a low diversity when compared to other microbial ecosystems such as soils [7] or oceans [8]. Bacteria from diverse phyla, *e.g. Firmicutes* (which includes lactic acid bacteria), *Actinobacteria*, *Proteobacteria* and *Bacteroidetes*, yeasts and filamentous fungi constitute the main microbial groups involved in food fermentation [9]. Through this fermentative activity, they contribute to the quality of the food products in several ways, *i.e.* by preventing the development of pathogens, modifying the texture, releasing aroma compounds or degrading anti-nutritional factors.

Bacteriophages (phages), viruses that infect bacterial cells, are considered as key ecological drivers in the functioning of microbial ecosystems [10]. Indeed, phage-bacterial interactions can potentially affect the balance between the different functional groups of microbes and then (re-)shape microbial communities. In the human gut, where phage particles probably do not outnumber bacteria, phages could play a transitory role in the homeostasis or the evolution of the microbiota [11]*. In food fermentations, although the presence of bacteriophages has been demonstrated around one century ago [12], only few examples of deep inventory of their diversity are available and the literature about their ecological role is even rarer.

The present review summarizes the current knowledge on the occurrence and diversity of bacteriophages in fermented foods, especially in light of the recent discoveries resulting from the analysis of viral metagenomics data, and discuss the possible ecological roles played by these biological entities in the context of this peculiar ecosystem which, ultimately, may impact the success of the fermentation process.

Current knowledge on bacteriophages' occurrence and diversity in fermented foods

Several experimental approaches have been used for enumerating bacteriophages in microbial ecosystems and exploring their diversity. Some of them require the isolation of phages, which implies as first steps to identify and cultivate susceptible bacterial hosts, while others can be applied directly on environmental samples (Figure 1).

Culture-dependent approaches

The presence of bacteriophages in fermented foods was frequently investigated by culture-dependent approaches. In practice, the main technic consists in collecting phages from a liquid sample obtained from the food product, or from a suspected reservoir in the manufacturing environment, and putting them into contact with a sensitive bacterial strain on a double-layer agar plate (for a detailed protocol, see [13]). It is also possible to directly enumerate phages to determine their initial level in food products [14], or to enrich them before isolation to enhance the probability of recovery [15].

Once isolated, phages can be further identified and characterized by applying a variety of downstream analysis. The historical classification of bacterial viruses is based on electron microscopy (EM) observations [16], and it is now progressively moving to a molecular classification. In Philippe et *al*., the authors used EM for the morphological characterization of phage GC1 isolated from wine musts [17]. They observed tail-less icosahedral particles, meaning that this phage did not belong to *Caudovirales* order. A further characterisation of its genomic properties determined that GC1 belongs to the *Tectiviridae* family.

In most recent articles, genome sequencing and comparative genomics were also applied to phages isolated from fermented foods. De Melo et *al*., made comparative genomics on 18 *Brevibacterium aurantiacum* phages isolated from cheese [18]**. They were classified into 7 distinct genomic groups based on the number of DNA tandem repeats (TRs) in each genome. They also found that 85% of phages in databases possessed such TRs. Similarly, Cheng et *al*., classified 7 *Propionibacterium freudenreichii* phages into two clusters, based on the nucleotide identity and coverage percentage between each genomes [15].

In most cases, such a culture-dependent approach also gives clues as to whether the isolated phage is temperate or virulent, by confronting the aspect of plaques (turbid for temperate, and usually clear for virulent [19]) and the genetic analysis of the complete genome (which usually contains an integrase when the phage is temperate).

As summarized in Table 1, both virulent and temperate phages were isolated from many fermented foods. However, surprisingly, no filamentous phages were retrieved from this type of products to date. Most of them are *Siphoviridae* and *Myoviridae* but *Podoviridae* and *Tectiviridae* were also isolated occasionally [14,17,20]. The hosts are usually members of the dominant species present in the corresponding food, such as *Leuconostoc mesenteroides* in Sauerkraut [21] or *Oenococcus oeni* in Wine [22]. For the particular case of cheese, where an abundant literature regarding phages infecting Lactic Acid Bacteria (LAB) starter cultures is

available, as reviewed previously [23,24], only a few studies described the isolation of phages infecting other important bacteria such as *Propionibacterium freudenreichii* [15], the bacteria responsible for the production of holes in Emmental-type cheese, *Brevibacterium aurantiacum* [18], a surface ripening culture used in many cheese varieties and *Enterococcus faecalis* [25,26]*.

However, in the perspective of understanding the bacteriophage ecology in fermented foods, single phage isolation suffer from the major limitation of the culture-dependent approach that is the need of a susceptible host. By definition such approach cannot accurately reflect neither the bacterial and viral diversity present in fermented foods, nor their relative abundance. It is however very efficient from a technological point of view, for example in the case where a phage is suspected to be responsible of a fermentation failure and needs to be quickly identified.

Direct detection approaches

An alternative is to detect and/or quantify phages directly in food samples or in a viral fraction extracted from food samples without *a priori* on the bacterial host(s). Several techniques are available to count or observe viruses directly in complex samples [27], such as flow cytometry [28], epifluorescence microscopy [29], nanoparticle tracking analysis [30], interferometric light microscopy [31] and electron microscopy including Scanning Electron Microscopy (SEM) [32], Transmission Electron Microscopy (TEM) [33] and cryo Electron Microscopy (cryo-EM) [34].

Only few studies used such direct approaches to characterize the phage communities of fermented foods. Dugat-Bony et *al*., used interferometric light microscopy to determine the phage concentration on the surface of three cheese varieties and found that it ranged from 1×10^{9} to 4×10^{10} particles per gram at least [35]*. They also observed different morphotypes on Epoisses cheese with TEM, giving first indications about the complexity of phage communities present on the cheese surface.

As a complement to their metagenomic study, Park et *al*., used TEM on samples from shrimps, sauerkraut and kimchi, after a cesium chloride (CsCl) density gradient purification step [36]. They were able to characterize various phages morphologies, mainly *Sipho*- and *Myoviridae*.

To summarize, in the context of fermented foods, direct detection approaches can provide rapidly important ecological information such as total phage's concentration and rough elements about their diversity. However, since many bacteriophages can share similar morphological traits, techniques offering more precision are desirable to properly describe the composition of phage communities in fermented foods.

New contributions of whole metagenome sequencing and viral metagenomics

Two main categories of metagenomics approaches can be used to detect viral signals from environmental samples.

First, whole metagenome sequencing, which generates simultaneously sequences from both microbial cells and viruses, can be used to identify abundant phages present in microbial ecosystems using dedicated bioinformatic tools [37,38]. Regarding fermented foods, only two articles refer to the use of such approach for studying the composition of phage communities. In kimchi [39], the authors identified four putative phage contigs with sequence similarity with the genome of LAB-phages. In kinema, a fermented soybean product, the viral community was dominated by phages infecting *Bacillus* species. Their identity was further confirmed by taxonomic analysis, and they all had one or several well-characterized host(s) [40].

Second, viral metagenomics, or "viromics", consist in extracting and sequencing the genomic material of the viral community selectively purified from an environmental sample (*e.g.* food products, natural environment, host-associated) [41]. This approach is designed to obtain a deep overview of the composition of the phage community present in a given ecosystem. Generally, only dsDNA phages are sequenced, letting a grey area regarding RNA and ssDNA phages, whose quantities and diversity are probably underestimated thus far [42]. In natural ecosystems such as ocean, or soils, numerous viral metagenomic studies targeting phages have been carried out (respectively, [43] and [44,45]). However, they are scarce when it comes to fermented foods or fermented beverages, as reviewed in [46].

Park et al. firstly analysed the metavirome of fermented shrimp, kimchi and sauerkraut [36]. Viral particles were recovered and concentrated from the food samples by using filtration and ultracentrifugation prior to viral DNA extraction and pyrosequencing. The results revealed an important diversity in phage sequences, most of which showing no significant hits in public databases, and 6 to 27 contigs >5 Kb per food sample were assembled. Major discrepancies were observed between predicted hosts and the actual bacterial diversity detected in kimchi and fermented shrimp, reflecting the fact that viral genomes of these fermented foods were poorly represented in public databases at the time of the study, so that host predictions probably failed. On the contrary, phage host predictions in sauerkraut were reliable, thanks to the availability of several phage genomes isolated in previous work [21].

The viral community from ten samples representative of Korean and Chinese kimchi was also investigated [47]. Viral concentrates were obtained through filtration and Polyethylene Glycol (PEG) concentration, and DNA was sequenced providing several thousands of contigs >500 bp per sample, and revealing a very high diversity. The phage host prediction was consistent with the bacterial diversity and, interestingly, viral community profiling was found to outperform bacterial community profiling for predicting the geographical origin of kimchi.

Recently, the first metavirome of the cheese surface was described [35] using Epoisses cheese as an example. The viral fraction was obtained according to an optimized protocol involving filtration, PEG concentration and chloroform treatment. DNA sequences were assembled into 124 viral contigs from 2.5 to 122 kb, highlighting the presence of an unexpected viral diversity in this ecosystem. The authors were able to predict a bacterial host for the most abundant ones, *e.g. Glutamicibacter*, *Lactococcus*, *Psychrobacter*, *Vibrio*,

Leuconostoc and *Halomonas*, which were previously detected as dominant bacterial genera in Epoisses cheese [48].

Overall, available data suggest that fermented foods host dense and complex phage communities, at least as diverse as bacterial ones. However, despite the growing descriptive data available regarding bacteriophages occurrence and diversity in fermented foods, there is still a gap before demonstrating that these entities play an ecological role in this environment and can impact food fermentations.

Relationships between viral and bacterial dynamics

The first step would be to determine if a relationship exists between the levels of viral and bacterial populations during the fermentation cycle. For fermented foods, few studies demonstrated such correlation.

In kimchi [39], the monitoring of the composition of bacterial and phage populations during 29 days of fermentation was achieved by using a whole metagenome sequencing approach. The relative abundance of the four putative phage contigs identified increased during the fermentation cycle, reaching ~7% of the total metagenomics sequences after 25 days. This large number of sequences was correlated to the decrease of bacterial population observed after 25 days suggesting that bacteriophages may influence the microbial community dynamics in this product.

Recently, Kong and Park used a culture media made from sterilized supernatant of dongchimi kimchi (a watery kimchi made from radish, green onions, garlic, ginger and salt) to perform co-culture of the main LAB species involved in the fermentation of this product, *i.e. Leuconostoc citreum, L. mesenteroides* and *Weissella cibaria* [49]*. They used different combinations of strains, sensitive to phages or not, and followed the dynamic of both bacterial and phage populations by culture-dependent methods over 10 days. They observed a negative relationship between the abundance of phages and the viability of their hosts, independently of the pH of the medium, demonstrating the impact of bacteriophages on the succession of LAB species during dongchimi kimchi fermentation.

Finally, Erkus et al. studied an undefined complex cheese starter culture, composed of several strains of *Lactococcus lactis* and *Leuconostoc mesenteroides* grouped in eight different genetic lineages, some of which carrying active prophages [50]. In one of the described experiment, they propagated *in vitro* the culture daily in milk during several weeks, mimicking the back-slopping procedure used in the dairy industry, and followed temperate phage population by titration and the different bacterial lineages by qPCR. The results indicated that although some strains can undergo dramatic decrease in abundance at certain stages of propagation, due to the increase in a particular phage population in the medium, the effect on the relative abundance of the genetic lineage they belong to was very limited, ensuring an overall stability of the community structure, both regarding genes and functionalities.

To summarize, there are increasing evidences that bacteriophages affect the dynamics of food microbial communities during fermentation. The impact of phage attacks on the overall structure and function of microbial communities is thought to depend on the complexity of the studied system and microdiversity seems to play an important role in the overall stability of microbial communities in fermented foods.

Ecological roles of bacteriophages

Studies elucidating the ecological roles of bacteriophages occurring in fermented foods are scarce. Thus, this section summarizes the main roles attributed to these entities regardless of the microbial ecosystem of origin. It is likely that major results observed within natural ecosystems are transferable to fermented products.

Direct regulation of bacterial populations

Bacteriophages may have several types of behaviours toward their bacterial hosts (Box 1). They can directly impact the population levels of their hosts in different ways and, consequently, the whole community structure.

First, phages performing a lytic cycle, which encompass professionally lytic, virulent mutant (or ex-temperate, see [51]) and temperate phages entering a lytic cycle, foster a prey-predator relationship with their host. Since bacteriophages are non-motile entities, the probability of encountering a host cell and starting infection strongly depends on the host's density. In mixed microbial communities, this means that bacteriophages kill the sensitive bacterial strain(s) with the highest density, as theorized in the Kill-the-Winner [52] and seed-bank models [53,54], while having a little impact on the total microbial biomass. This direct effect also promotes bacterial diversity since several bacterial populations sharing the same ecological niche can coexist [55] and grow in a sequential manner. Finally, it also favours the optimal utilisation of all resources present in the ecosystem, as a single dominant bacteria wouldn't have all the necessary enzymatic equipment to exploit all the available nutrients [56].

Second, temperate phages can also affect the fitness of their host when entering a lysogenic cycle. When integrated as prophages into the bacterial host genome, they can develop either a parasitic or a mutualistic interaction with their host. In complex cheese starter culture, Alexeeva et al. [57]* demonstrated the competitive advantage of *Lactococcus lactis* lysogens compared to their prophage-cured derivatives but the mechanism behind this observation was not identified. Similarly, Costantini et al. [22] observed that, among sixteen *Oenococcus oeni* strains used for malolactic fermentation in wine, the ones integrating one or several prophages in their genomes were more resistant to the predation by other oenophages.

Finally, bacteriophages which cannot enter a lysogenic cycle and are producing virions in a chronic fashion without cell lysis interact with their host through a parasitic relationship. In this case, the main expected effect would be a lower fitness of the host caused by the

energy cost required for the bacteriophage's replication but this was not studied in the context of fermented foods to our knowledge.

In addition to the regulation of the population level of their hosts, bacteriophages can also prompt substantial modifications of the bacterial transcriptome and proteome and, hence, affect their metabolism [58].

Indirect effects on non-host populations

Bacterial lysis mediated by bacteriophages is responsible for the release of organic matter into the environment. In ecology, this phenomenon is known as the "viral shunt" and it affects trophic webs by lowering bacterial biomass before it is assimilated at higher trophic levels [59]*. Bacterial lysis provides an important source of free nutrients which can support and promote the growth of other microorganisms. It has thus a large impact on microbial dynamics and densities.

For example, Fazzino et al. studied the effect of virulent bacteriophages on the mutualistic interaction between *Escherichia coli* and *Salmonella enterica* [60]**. In such cross-feeding model community, phages can have extensive indirect effects affecting the bacterial community dynamics. One of those indirect effect was the release of organic matter since the growth of *S. enterica* was stimulated by the lysis of *E. coli* by phage T7.

In fermented foods, such phenomenon is likely to occur. However, contrary to other natural ecosystems, the trophic chain is short and there is generally no upper trophic level above heterotrophic microorganisms. In this case, the role of the viral shunt encompasses probably only the release of cellular debris and intra-cellular compounds, providing additional resources for non-hosts species. In line with this suspected role, Kong & Park experimentally evidenced that a bacteriophage lysate of *Weissella cibaria* can promote the growth of *L. citreum* in kimchi fermentation [49].

Phages as bacterial evolution drivers

Bacterial viruses represent a continuous selective pressure on bacteria, driving them to evolve by selecting antiphage defence mechanisms [61]*. In response, phages adopt strategies to overcome host defence systems. This antagonistic co-evolution is a kind of perpetual arms race, referred to as the Red Queen dynamics [62]. This is due to the extremely rapid evolution and turnover of phage particles [63], increasing mutation rates in their host(s) [64], driving neither the predator nor the prey to extinction. The most prominent outcome of this interaction is ecological speciation, resulting in a high microdiversity of both hosts and phages.

Horizontal gene transfer (HGT), which refers to the incorporation by an organism of genetic material from another organism without mating, contributes to the microbial genome evolution [65]. Bacterial lysis due to the phage progeny release is accompanied by the release of intra-cellular components into the environment and especially pieces of DNA that could be acquired by other bacteria through natural transformation [66]. HGT can also happen through transduction (generalized or specialized [67]), when a bacteriophage accidentally packages bacterial DNA and transfers it to another host.

Lysogeny has been suggested as a survival strategy when the environment contains low host densities [68]. Prophages integrated in a host bacteria are usually in a dormant state, as they don't actively replicate their genomes, while regulating bacterial genes. If some phages have evolved to insert only in highly conserved sites [69], others as transposable phages integrate themselves randomly in the host genome, possibly inactivating genes coding for essential functions and having therefore a detrimental effect on host fitness [70]. Some phages are also able to display "active lysogeny", acting as regulatory switches, as they turn off the gene by integrating in its sequence [71].

Phages can stay in lysogenic cycle for several generations. However, they are not totally inactive since the bacterial cell expresses moron genes (for "more DNA") that are not necessary for the phage cycle, and expressed during lysogeny [72,73]. A well-known example is the *stx* gene coding for shigatoxin, which is acquired by bacterial strains through lysogenic conversion, meaning the acquisition of a *stx*-positive prophage [74]. These morons are far from being all characterized, but they probably enhance bacterial fitness and expand the environmental niche of the host [75].

Conclusions

Fermented foods represent undoubtedly suitable ecosystems for the development of bacteriophages. The isolation of a large set of bacteriophages and the first viral metagenomics data shed light into the viral diversity of this type of products. However, the question of the impact of this diversity on the composition and functioning of microbial communities still remains underexplored.

The continuous improvement of sequencing techniques, with in particular the first applications of long-read sequencing for the description of metaviromes [76]**, makes it possible to envisage both the description and the monitoring of the composition of viral communities in fermented foods more easily and in a more comprehensive way.

Furthermore, synthetic microbial ecosystems offer new perspectives for investigating individual to ecosystem level microbial interactions [77]. The viral dimension of food microbial ecosystems should therefore be considered for the future design of synthetic ecology experiments with the objective of characterizing the role of bacteriophages in fermented foods.

The exploitation of this knowledge should help the food industry facing numerous challenges such as controlling phage contamination to reduce the risk of fermentation failure. Main applications are the biocontrol of pathogens [78] and spoilage bacteria [25]* but new developments could lead to finely modulate the composition of microbial communities in order to reach the desired technological properties in fermented products.

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Declaration of interest. None.

Tables

Table 1. Selected examples describing the isolation of phages directly from fermented foods.

Fermented food	References	Phage families	Type	Host
Cheese*	[15]	7 *Siphoviridae*	Virulent	*Propionibacterium freudenreichii*
	[18]	16 *Siphoviridae*	Virulent	*Brevibacterium aurantiacum*
	[25]	1 *Myoviridae*	Virulent	*Enterococcus faecalis*
	[26]	1 *Siphoviridae*	Virulent	*Enterococcus faecalis*
Fermented Cucumber	[79]	1 *Siphoviridae*	Virulent	*Lactobacillus plantarum*
	[80]	3 *Siphoviridae* and 3 *Myoviridae*	N.D	*Lactobacillus brevis, Lactobacillus plantarum, Weissella paramesenteroides, Weissella cibaria*
	[81]	1 *Siphoviridae*	Virulent	*Pediococcus* sp.
Fermented Soybean	[82]	N.D	Virulent and temperate	*Bacillus subtilis*
	[83]	16 *Siphoviridae*	N.D	*Bacillus cereus*
	[84]	1 *Myoviridae*	N.D	*Bacillus cereus*
	[85]	1 *Siphoviridae* and 1 *Myoviridae*	N.D	*Pediococcus halophilus*
Kefir	[86]	2 *Siphoviridae*	N.D	*Lactobacillus plantarum*
Kimchi	[20]	1 *Podoviridae*	N.D	*Weissella cibaria*
	[49]	N.D	N.D	*Weissella cibaria, Leuconostoc citreum*
	[87]	1 *Siphoviridae*	N.D	*Lactobacillus plantarum*
Salami	[88]	2 *Podoviridae*	N.D	*Staphylococcus carnosus*
Sauerkraut	[89]	3 *Siphoviridae* and 3 *Myoviridae*	N.D	*Leuconostoc fallax*
	[90]	5 *Siphoviridae* and 3 *Myoviridae*	N.D	*Leuconostoc pseudomesenteroides, Leuconostoc mesenteroides, Leuconostoc citreum, Leuconostoc fallax, Weissella* sp., *Lactobacillus plantarum, Lactobacillus brevis*
	[21]	1 *Siphoviridae*	Virulent	*Leuconostoc mesenteroides*

	[91]	2 phages	N.D	*Leuconostoc mesenteroides*
	[92]	2 *Myoviridae* 'type 1', 5 *Myoviridae* 'type 2' and 2 *Siphoviridae*	N.D	*Leuconostoc mesenteroides, Lactobacillus plantarum*
Sourdough bread	[93]	9 *Siphoviridae*	3 virulent and 6 temperate	*Lactobacillus fermentum*
	[94]	1 *Siphoviridae*	Virulent	*Lactobacillus sanfranciscensis*
Wine	[95]	11 *Siphoviridae*	N.D	*Oenococcus oeni*
	[14]	*Siphoviridae, Myoviridae, Tectiviridae*	N.D	*Lactobacillus plantarum, Lactobacillus hilgardii, Oenococcus oeni*
	[22]	15 *Siphoviridae*	Temperate	*Oenococcus oeni*
	[96]	4 *Siphoviridae*	N.D	*Oenococcus oeni*
	[97]	2 *Siphoviridae*	N.D	*Oenococcus oeni*
	[98]	1 *Siphoviridae*	Virulent	*Oenococcus oeni*
	[99]	17 *Siphoviridae*	N.D	*Oenococcus oeni*
	[17]	1 *Tectiviridae*	Temperate	*Gluconobacter cerinus*
	[100]	17 *Siphoviridae*	Temperate	*Oenococcus oeni*

N.D = Not Documented.

*For cheese, no example describing the isolation of phages infecting LAB starter culture is listed since the literature on such phages is extremely abundant and already reviewed [23,24].

Figure captions

Figure 1: General methods for the study of bacteriophages in fermented foods.

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Box1: definitions of the different bacteriophage types according to (Hobbs & Abedon, 2016).

Professionally lytic: Phage that is both obligately lytic and not recently descended from a temperate ancestor

Virulent mutant (ex-temperate): Clear temperate phage mutant that can form plaques even on lysogens (i.e. bacteria hosting a prophage) formed by the phage wild-type parent

Temperate phage: Description of a phage that is able to display lysogenic cycles (under the form of a prophage) or lytic cycle according to specific environmental and host parameters.

Filamentous phage: Phage whose productive infection is chronic (may or may not be a temperate phage)

Authors declare no conflict of interest.

Figure 1

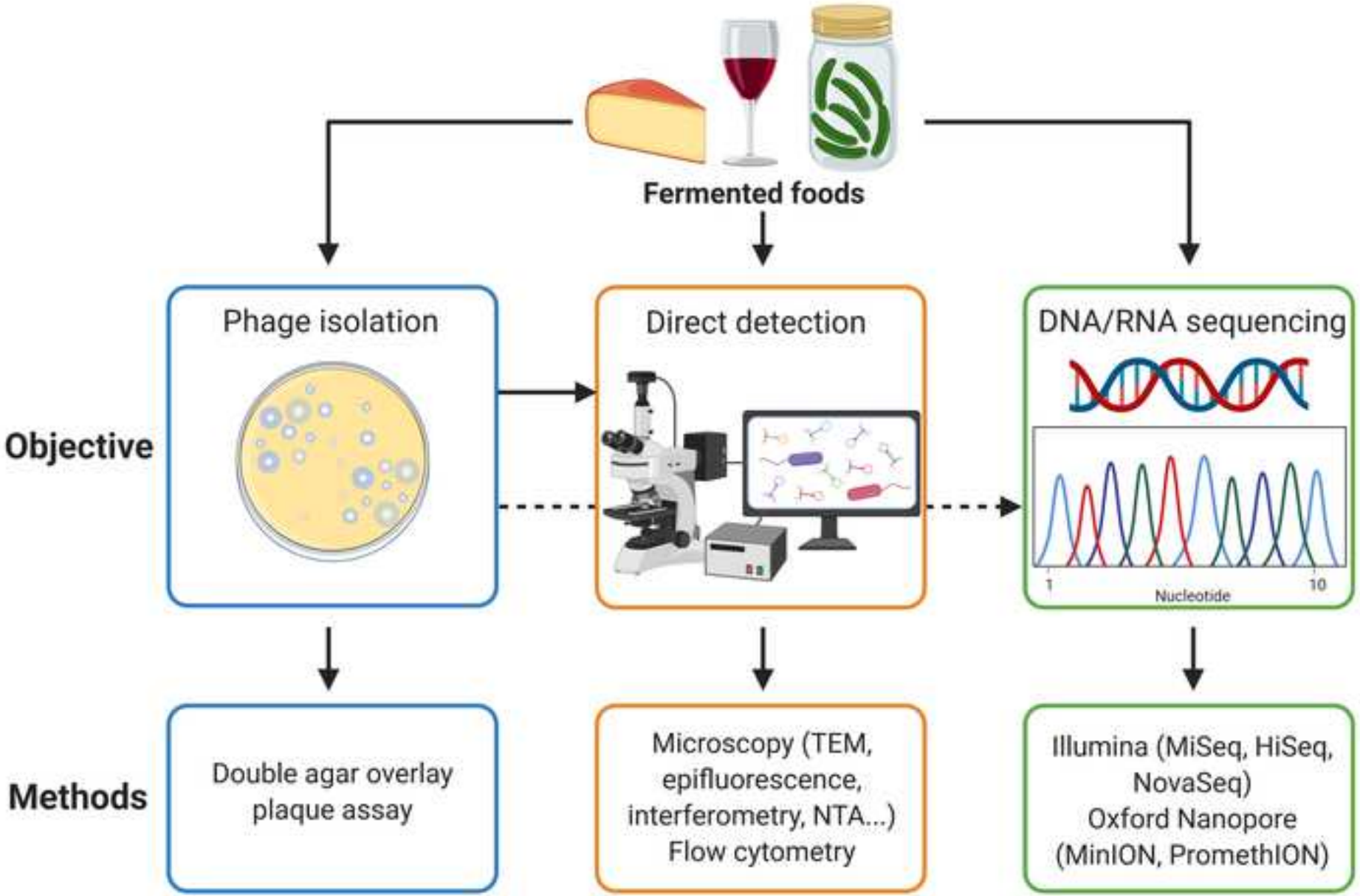

Table 1. Selected examples describing the isolation of phages directly from fermented foods.

Fermented food	References	Phage families	Type	Host
Cheese*	(Cheng *et al.*, 2018)	7 *Siphoviridae*	Virulent	*Propionibacterium freudenreichii*
	(De Melo *et al.*, 2020)	16 *Siphoviridae*	Virulent	*Brevibacterium aurantiacum*
	(Del Rio *et al.*, 2019)	1 *Myoviridae*	Virulent	*Enterococcus faecalis*
	(Ladero *et al.*, 2016)	1 *Siphoviridae*	Virulent	*Enterococcus faecalis*
Fermented Cucumber	(Lu *et al.*, 2003a)	1 *Siphoviridae*	Virulent	*Lactobacillus plantarum*
	(Lu *et al.*, 2012)	3 *Siphoviridae* and 3 *Myoviridae*	N.D	*Lactobacillus brevis, Lactobacillus plantarum, Weissella paramesenteroides, Weissella cibaria*
	(Yoon *et al.*, 2007)	1 *Siphoviridae*	Virulent	*Pediococcus* sp.
Fermented Soybean	(Nagai & Yamasaki, 2009)	N.D	Virulent and temperate	*Bacillus subtilis*
	(Oh *et al.*, 2017)	16 *Siphoviridae*	N.D	*Bacillus cereus*
	(Shin *et al.*, 2011)	1 *Myoviridae*	N.D	*Bacillus cereus*
	(Uchida & Kanbe, 1993)	1 *Siphoviridae* and 1 *Myoviridae*	N.D	*Pediococcus halophilus*
Kefir	(Antoni *et al.*, 2010)	2 *Siphoviridae*	N.D	*Lactobacillus plantarum*
Kimchi	(Kleppen *et al.*, 2012)	1 *Podoviridae*	N.D	*Weissella cibaria*
	(Kong & Park, 2019)	N.D	N.D	*Weissella cibaria, Leuconostoc citreum*
	(Yoon *et al.*, 2001)	1 *Siphoviridae*	N.D	*Lactobacillus plantarum*
Salami	(Bruttin *et al.*, 1992)	2 *Podoviridae*	N.D	*Staphylococcus carnosus*
Sauerkraut	(Barrangou *et al.*, 2002)	3 *Siphoviridae* and 3 *Myoviridae*	N.D	*Leuconostoc fallax*
	(Lu *et al.*, 2003b)	5 *Siphoviridae* and 3 *Myoviridae*	N.D	*Leuconostoc pseudomesenteroides, Leuconostoc mesenteroides, Leuconostoc citreum, Leuconostoc fallax, Weissella* sp.,

				Lactobacillus plantarum, Lactobacillus brevis
	(Lu *et al.*, 2010)	1 *Siphoviridae*	Virulent	*Leuconostoc mesenteroides*
	(Mudgal *et al.*, 2006)	2 phages	N.D	*Leuconostoc mesenteroides*
	(Yoon *et al.*, 2002)	2 *Myoviridae* 'type 1', 5 *Myoviridae* 'type 2' and 2 *Siphoviridae*	N.D	*Leuconostoc mesenteroides, Lactobacillus plantarum*
Sourdough bread	(Foschino *et al.*, 2001)	9 *Siphoviridae*	3 virulent and 6 temperate	*Lactobacillus fermentum*
	(Foschino *et al.*, 2005)	1 *Siphoviridae*	Virulent	*Lactobacillus sanfranciscensis*
Wine	(Arendt & Hammes, 1992)	11 *Siphoviridae*	N.D	*Oenococcus oeni*
	(Cordero-Bueso *et al.*, 2020)	*Siphoviridae, Myoviridae, Tectiviridae*	N.D	*Lactobacillus plantarum, Lactobacillus hilgardii, Oenococcus oeni*
	(Costantini *et al.*, 2017)	15 *Siphoviridae*	Temperate	*Oenococcus oeni*
	(Davis *et al.*, 1985)	4 *Siphoviridae*	N.D	*Oenococcus oeni*
	(Henick-Kling *et al.*, 1986)	2 *Siphoviridae*	N.D	*Oenococcus oeni*
	(Jaomanjaka *et al.*, 2016)	1 *Siphoviridae*	Virulent	*Oenococcus oeni*
	(Nel *et al.*, 1987)	17 *Siphoviridae*	N.D	*Oenococcus oeni*
	(Philippe *et al.*, 2018)	1 *Tectiviridae*	Temperate	*Gluconobacter cerinus*
	(Santos *et al.*, 1996)	17 *Siphoviridae*	Temperate	*Oenococcus oeni*

N.D = Not Documented.

*For cheese, no example describing the isolation of phages infecting LAB starter culture is listed since the literature on such phages is extremely abundant and already reviewed (Brüssow, 2001; Garneau & Moineau, 2011).

Highlights

- **Food fermentations are driven by microbial communities**
- **Bacteriophages have an impact on the dynamic of food microbial communities**
- **The precise roles of bacteriophages in fermented foods remain to be characterized**

Graphical Abstract