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Review

Traditional cheeses: Rich and diverse microbiota with associated benefits



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ABSTRACT

The risks and benefits of traditional cheeses, mainly raw milk cheeses, are rarely set out objectively, whence the recurrent confused debate over their pros and cons. This review starts by emphasizing the particularities of the microbiota in traditional cheeses. It then describes the sensory, hygiene, and possible health benefits associated with traditional cheeses. The microbial diversity underlying the benefits of raw milk cheese depends on both the milk microbiota and on traditional practices, including inoculation practices. Traditional know-how from farming to cheese processing helps to maintain both the richness of the microbiota in individual cheeses and the diversity between cheeses throughout processing. All in all more than 400 species of lactic acid bacteria, Gram and catalase-positive bacteria, Gram-negative bacteria, yeasts and moulds have been detected in raw milk. This biodiversity decreases in cheese cores, where a small number of lactic acid bacteria species are numerically dominant, but persists on the cheese surfaces, which harbour numerous species of bacteria, yeasts and moulds. Diversity between cheeses is due particularly to wide variations in the dynamics of the same species in different cheeses. Flavour is more intense and rich in raw milk cheeses than in processed ones. This is mainly because an abundant native microbiota can express in raw milk cheeses, which is not the case in cheeses made from pasteurized or microfiltered milk. Compared to commercial strains, indigenous lactic acid bacteria isolated from milk/cheese, and surface bacteria and yeasts isolated from traditional brines, were associated with more complex volatile profiles and higher scores for some sensorial attributes. The ability of traditional cheeses to combat pathogens is related more to native antipathogenic strains or microbial consortia than to natural non-microbial inhibitor(s) from milk. Quite different native microbiota can protect against *Listeria monocytogenes* in cheeses (in both core and surface) and on the wooden surfaces of traditional equipment. The inhibition seems to be associated with their qualitative and quantitative composition rather than with their degree of diversity. The inhibitory mechanisms are not well elucidated. Both cross-sectional and cohort studies have evidenced a strong association of raw-milk consumption with protection against allergic/atopic diseases; further studies are needed to determine whether such association extends to traditional raw-milk cheese consumption. In the future, the use of meta-omics methods should help to decipher how traditional cheese ecosystems form and function, opening the way to new methods of risk-benefit management from farm to ripened cheese.

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Contents

1.	Introduction	137
2.	Transfer of microbial diversity from the environment to ripened cheeses	138
2.1.	Raw milk microbiota on the farm still hold secrets	138
2.2.	Microbial transfer from environmental sources to raw milk	138
2.2.1.	Direct microbial sources	138
2.2.2.	Indirect microbial sources	139

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2.3.	Conservation shifts the microbial balance of raw milk	140
2.4.	Enrichment of vat milk and/or cheese microbiota by traditional equipment and practices	140
2.5.	Microbial dynamics during cheese-making and ripening	140
2.5.1.	In cheese cores	140
2.5.2.	On cheese surfaces	141
3.	Microbial diversity: a key factor for sensory benefits	142
3.1.	Two approaches to cheese processing	142
3.2.	Sensory profiles altered by heat-treating milk	142
3.3.	Demonstration that microbial diversity in milk generates diversity in cheese sensory characteristics	142
3.4.	Functional diversity of microbial communities in the cheese ecosystem	143
3.4.1.	Role of lactic acid bacteria in the cheese core	143
3.4.2.	Role of other microbial species in the cheese core	143
3.4.3.	Role of the cheese surface microbiota	144
3.4.4.	Role of Gram negative bacteria	144
4.	Raw milk: a bulwark against pathogens	144
4.1.	Potential benefits of natural non microbial inhibitors	144
4.2.	Microbial diversity to combat pathogens	144
4.2.1.	Raw milk cheeses as a source of strains antagonistic to pathogens	144
4.2.2.	Efficiency of microbiota against <i>L. monocytogenes</i>	145
5.	Potential human health benefits associated with the consumption of traditional cheeses	146
5.1.	Positive impact of the consumption of raw milk cheeses on the enteric microbiota	146
5.2.	Limited milk processing in raw milk cheeses: a potential benefit for health	146
5.3.	The balance of unsaturated lipids beneficial to health is better in traditional cheeses	147
6.	Conclusion	147
	Acknowledgement	147
	References	147

1. Introduction

Guerrero et al. (2009), analysing European consumers' perceptions, defined a traditional food product as "a product frequently consumed or associated with specific celebrations and/or seasons, normally transmitted from one generation to another, made accurately in a specific way according to the gastronomic heritage, with little or no processing/manipulation, distinguished and known because of its sensorial properties and associated with a certain local area, region or country". Raw milk PDO cheeses (an estimated 70% of all traditional cheeses in France) fit this definition perfectly as each one is produced in a specifically defined geographical area using specific know-how and skills and with little or no prior processing of the milk. To some extent, however, the "traditional cheese" label can also be applied to cheeses made on-farm or at small dairies using thermized or pasteurized milk inoculated with various starter combinations and allowing the growth and expression of ripening microbiota. Makers of traditional cheeses adapt their manufacturing practices to the characteristics of the vat milk day by day. Moreover, traditional cheeses are recognized for their diverse and distinctive sensory properties.

Few of the risks and benefits claimed for traditional cheeses have been objectively and clearly set out, owing to the scattered data and large number of cheese varieties. All the focus has been on the recurrent debate over the pros and cons of raw milk cheeses. Anthropologists and sociologists, especially in the USA, have examined it from the standpoints of microbiopolitics (Paxson, 2008; Mendelson, 2011) and consumer fears (West, 2008). Microbiologists debate how best to handle microorganisms. Defenders of pasteurization advocate managing the pathogen risk by applying heat to reduce the microbial load on equipment and in milk and inputs, and standardising production by inoculating a few selected strains into milk. The raw milk sector also focuses its battles against pathogenic bacteria on the process upstream of the vat milk (review Claeys et al., 2013) and then in the cheese (Brooks et al., 2012). Herd certification programs, adapted Hazard Analysis Critical Control Point (HACCP) systems and systematic microbiological quality control throughout the supply chain (EFSA, 2010; European regulation EC853/2004) have been developed to guarantee the safety of

unpasteurized cheeses, including raw milk cheeses. In industrialized countries, successful management of the pathogen risk is reflected in the relative small number of food-borne outbreaks due to dairy products (1–5%), including unpasteurized cheeses (De Buyser et al., 2001; Kousta et al., 2010; EFSA European Food Safety Authority, 2011, 2012). *Salmonella* outbreaks have been scarce since 2000; only fifteen outbreaks have been reported in the last two decades (De Buyser et al., 2005; Jourdan-Da Silva and Le Hello, 2012). Outbreaks of shigatoxin-producing *Escherichia coli* (O157:H7, O26:H11) have been linked to raw milk and to cheeses made with both pasteurized and unpasteurized milk, due to defective pasteurization and/or post processing contamination (Farrock et al., 2013).

Listeriosis connected with the cheese consumption is very rare (Majjala et al., 2001; Goulet et al., 2006; Antal et al., 2007; EFSA, 2010) even though it has become the emblematic example of severe illness transmitted by raw milk products. Contamination by *Listeria monocytogenes* is not specific to raw milk cheeses; cheeses made from pasteurized milk can be contaminated (Rudolf and Scherer, 2001; EFSA, 2012; Pini and Gilbert, 1988) due to improper pasteurization or post-pasteurization contamination (De Buyser et al., 2001; Donnelly, 2001).

Defenders of traditional cheeses recommend maintaining high taxonomic diversity in indigenous cheese microbial communities and diverse cheese-making practices. Their arguments rely on the fact that a high diversity of microbial activities, combined with particular cheese manufacturing methods, is the key for allowing traditional cheeses to develop their particular characteristics, including low pathogen risk and diversification of gustatory characteristics. The raw milk microbiota is an important part of the microbiota of many traditional cheeses. This review first considers the sources of this microbiota and the particular practices that further enrich microbiota in the cheese. It then reports on the taxonomic composition and dynamics of cheese microbiota, which have been extensively documented for raw milk cheeses over the last decade, encouraged by the arrival of accurate molecular taxonomic methods. The main objective of this review is to assess the sensory, hygiene and potential health benefits of traditional cheeses. It does not set out to analyse the risks.

2. Transfer of microbial diversity from the environment to ripened cheeses

This section describes the richness and variability of microbial dynamics from raw milk to ripened traditional cheese, and considers the transfer of microflora from the environment to ripened cheese.

Knowledge of the microbial diversity of dairy products and the reservoirs involved was at first derived from culture-dependent methods using different media. It has been dramatically enhanced by an increasingly refined taxonomy and the use of molecular methods (reviewed in Quigley et al., 2011; Ndoye et al., 2011), of which the most recent is pyrosequencing (Alegria et al., 2012; Masoud et al., 2011, 2012; Quigley et al., 2012), to complement the traditional culture-dependent methods. However, the diversity of the methods applied sometimes makes it difficult to quantitatively compare microbiota from one study to another.

2.1. Raw milk microbiota on the farm still hold secrets

Raw milk can act either as a direct source, providing the vat milk with its microbiota, or as an indirect source, enriching the microbiota of the cheese making environment, whey cultures, wood vat/shelves and old smear (§ 2.4).

Orders of magnitude of culturable counts of the main microbial groups commonly investigated in cow, ewe and goat milk in industrialised countries are shown in Table 1. Regardless of animal species, bacterial counts are far higher than fungal counts. The predominant groups are *Staphylococcus* sp. and coryneform bacteria. Co-dominant groups are *Pseudomonas* sp. in refrigerated raw cow's milk, and lactic acid bacteria and *Enterobacteriaceae* in sheep and goat milk. For all microbial groups, inter-farm variability is wide while intra-farm variability is generally much lower except from season to season (Desmaures and Guéguen, 1997; Michel et al., 2001). In industrialized countries since the 1980s, practices such as cold storage of milk and udder-cleaning and teat-disinfecting procedures have improved the hygienic quality of raw milk and concomitantly decreased its microbial load (Beuquier and Buchin, 2004). The loads of most microbial groups have remained stable in raw cow's milk since the mid 1990s (Mallet et al., 2012) and standard plate counts (SPC) currently range from $5 \cdot 10^3$ to 10^4 colony forming units per mL (cfu/mL). Despite this low SPC, raw milk still exhibits substantial microbial diversity, with SPC levels varying significantly according to farm practices.

More than 100 genera and 400 microbial species have been detected in raw milk (Tables 2 and 3). They are mainly Gram negative bacteria (>90 species), Gram positive and catalase positive bacteria (>90 species), lactic acid bacteria (LAB) (>60 species), yeasts (>70 species),

Table 1

Order of magnitude of counts (cfu/mL) of the main microbial groups usually investigated in raw milks from bulk tanks (based on Casalta et al., 2009; Gaya et al., 1987; Mallet et al., 2012; Masoud et al., 2011; Michel et al., 2001; Muehlherr et al., 2003; Sevi et al., 2004; Tormo et al., 2011).

Presumed microbial groups	Cow's milk	Goat's milk	Ewe's milk
<i>Staphylococcus</i> sp. and coryneform bacteria	10^2 – 10^3	10^3	10^2 – 10^4
<i>Lactococcus</i> sp.	10^1 – 10^2	10^2 – 10^3	10^4
<i>Lactobacillus</i> sp.	10^1 – 10^2	10^2	10^3 – 10^4
<i>Leuconostoc</i> sp.	10^1 – 10^2	10^2 – 10^3	10^4 – 10^5
<i>Enterococcus</i> sp.	10^1 – 10^2	10^1 – 10^3	10^3 – 10^5
Propionic acid bacteria	10^1 – 10^2	ND	ND
<i>Enterobacteriaceae</i>	10^1	10^2 – 10^6	10^2 – 10^4
<i>Pseudomonas</i> sp.	10^2 – 10^{3*}	10^1 – 10^2	10^2 – 10^4
Yeasts	10^1 – 10^2	10^1 – 10^2	10^2 – 10^4
Moulds	<10	<10	
Aerobic spores	<10	<10	
Coliform bacteria	<10	10^2 – 10^3	

and moulds (>40 species) (exhaustive list in Table S1). For historical and technological reasons, most studies focus on LAB often regarded as the main bacteria in raw milk. Recent techniques such as molecular inventories have made it possible to detect many more species besides LAB. Raw milk microbiota proves to be very rich, containing, for example, a wide diversity of halophilic and/or alcalophilic Gram-positive or -negative bacteria and yeasts (Table S1). A single milk sample can contain as many as 36 dominant microbial species (Callon et al., 2007; Fricker et al., 2011; Saubusse et al., 2007). It is difficult to evaluate changes in milk microbial diversity over recent decades owing to the enormous progress made in investigation methods.

Strain diversity in raw milk is also substantial but varies between species and between farms. Up to 43 genotypes of *Lactococcus lactis* have been described in raw milk in France, with 1 to 11 genotypes per farm (six farms studied by Corrolier et al., 1998; one farm by Dalmaso et al., 2008; 32 farms by Feutry et al., 2012a). Some strains remain at a farm for months (Corrolier et al., 1998), thereby linking a particular milk microbiota to a particular farm (D'Amico and Donnelly, 2010).

2.2. Microbial transfer from environmental sources to raw milk

The milk in the upper part of the udder of a healthy lactating female is often considered as sterile. The composition of the milk microbiota depends directly on the composition of the microbiota of sources directly in contact with the milk: the animal's teat and dairy equipment such as milking machine, milk line and tank. It also depends on the composition of the microbiota from indirect sources (feed, litter, drinking and washing water, stable and milking parlour air, milker) that may contribute to that of the direct sources. Indeed, the closer the environmental source is to the milk during a production step, the greater the similarity in microbiological composition. Indirect and direct sources act as microflora reservoirs. The milk microbiota is obviously strongly influenced by the overall management system of the farm, which makes it difficult to identify the influence of a single practice. But with regard to direct sources, teat care and washing, as well as disinfection of the milking equipment are of primary importance (Julien et al., 2008; Mallet et al., 2012; Michel et al., 2001; Tormo et al., 2011; Verdier-Metz et al., 2009). In cows, aseptic milking leads to very low SPC in the milk (<150 cfu/mL) (Kleter and De Vries, 1974).

2.2.1. Direct microbial sources

The teat canal can be a direct source of microorganisms for the initially sterile milk (Table S2). The predominant phyla are Actinobacteria and Firmicutes (*Clostridiaceae*, *Staphylococcaceae* and less frequently *Lactobacillaceae*, *Enterococcaceae*) followed by Proteobacteria (Gill et al., 2006).

The teat surface is the next potential direct source of microorganisms for farm milk, but not all species of teat surface microbiota are found in raw milk (Verdier-Metz et al., 2012). Teat surface microbiota have been found to be dominated by coagulase negative staphylococci and coryneform bacteria, *Enterobacteriaceae*, spoilage bacteria (e.g. butyric acid spores), lactic acid bacteria e.g. *Lactococcus lactis*, and non-fermenting Gram negative bacteria such as *Pseudomonas*. Finally, biofilms on stainless steel, rubber, silicone, glass and/or plastic milking equipment can be a direct source of micro-organisms for farm milk (Marchand et al., 2012). They can increase the microbial load of the raw milk by 3500–5000 cfu/mL (McKinnon et al., 1990). Rinsing water from milking machines or bulk tanks harbours most of the microbial groups found in raw milk (Table S2): LAB as well as *Staphylococcus* sp. and coryneform bacteria (*Micrococcus* sp.), Gram negative bacteria (*Pseudomonas* sp. and *Hafnia alvei*) and yeasts (Desmaures, 1995; Gelsomino et al., 2002; Kagkli et al., 2007a, 2007b; Laithier et al., 2005; Michel et al., 2001).

Table 2

Bacterial richness (number of species) from milk to cheese according to the bibliographic data compiled in Table S1. In addition, a single species represents each of the 14 families (*Alcaligenaceae*, *Deinococcaceae*, *Erysipelotrichaceae*, *Gordoniaceae*, *Hahellaceae*, *Leptotrichiaceae*, *Phyllobacteriaceae*, *Planococcaceae*, *Promicromonosporaceae*, *Rhodocyclaceae*, *Rikenellaceae*, *Sanguibacteraceae*, *Streptomyetaceae*, and *Thermaceae*) detected in milk only, as well as each of the three families (*Ruminococcaceae*, *Bacteroidaceae*, and *Bifidobacteriaceae*) detected in both milk and cheese core, and one family (*Peptostreptococcaceae*) detected on cheese surface only.

Gram-positive bacteria	Milk	Core	Surface	Gram-negative bacteria	Milk	Core	Surface
Lactic acid bacteria (<i>Firmicutes</i>)				Proteobacteria			
<i>Aerococcaceae</i>	4	0	1	<i>Aeromonadaceae</i>	4		
<i>Carnobacteriaceae</i>	4	3	4	<i>Alcaligenaceae</i>			3
<i>Enterococcaceae</i>	11	13	6	<i>Bradyrhizobiaceae</i>	3		
<i>Lactobacillaceae</i>	20	24	15	<i>Brucellaceae</i>	2		
<i>Leuconostocaceae</i>	10	13	4	<i>Burkholderiaceae</i>	2		
<i>Streptococcaceae</i>	16	13	4	<i>Caulobacteraceae</i>	6		
	65	66	34	<i>Comamonadaceae</i>	3		
Ripening bacteria (<i>Actinobacteria</i> + <i>Firmicutes</i>)				<i>Enterobacteriaceae</i>	23	14	16
<i>Brevibacteriaceae</i>	3	2	6	<i>Halomonadaceae</i>	1	1	4
<i>Corynebacteriaceae</i>	17	6	6	<i>Methylobacteriaceae</i>	2	1	0
<i>Microbacteriaceae</i>	20	1	9	<i>Moraxellaceae</i>	14	3	4
<i>Micrococcaceae</i>	17	4	11	<i>Oxalobacteraceae</i>	2	1	
<i>Nocardiaceae</i>	5		1	<i>Oceanospirillaceae</i>	1		1
<i>Propionibacteriaceae</i>	5	1	1	<i>Pseudoalteromonadaceae</i>	1	1	1
<i>Staphylococcaceae</i>	27	18	17	<i>Pseudomonadaceae</i>	16	4	3
	94	32	51	<i>Rhizobiaceae</i>	2		
<i>Listeriaceae</i>	5	6	3	<i>Rhodobacteriaceae</i>	2		
<i>Clostridiaceae</i>	8	5	0	<i>Sphingobacteriaceae</i>	2		
Unknown functions				<i>Vibrionaceae</i>		1	2
<i>Bacillaceae</i>	9	1	3	<i>Xanthomonadaceae</i>	5	1	
<i>Paenibacillaceae</i>	2		1	Total Gram—	94	26	35
<i>Dermabacteraceae</i>	8	2	3	Total	300	142	130
<i>Dietziaceae</i>	2						
<i>Intrasporangiaceae</i>	3						
	24	3	7				
Bacterioidetes							
<i>Flavobacteriaceae</i>	13	3	1				
<i>Prevotellaceae</i>		1	1				

2.2.2. Indirect microbial sources

Feed (grassland, silage and hay) may be an indirect source of microorganisms for farm milk (Verdier-Metz et al., 2012). Grassland contains high levels of Gram negative bacteria like *Enterobacteriaceae*, staphylococci, coryneform bacteria such as *Curtobacterium* sp., and yeasts, but low levels of *Lactococcus lactis* ssp. *lactis* (<1.6 log) (Denis et al., 2004). Silage can harbour various LAB, including *Pediococcus pentosaceus*, lactobacilli but no enterococci, *Pseudomonas* sp. (Desmaures, 1995), coliform bacteria, yeasts (Baroiller and Schmidt, 1990), and moulds and mould-like filamentous bacteria (Reboux et al., 2006).

Table 3

Yeast richness (number of species) from milk to cheese according to the bibliographic data compiled in Table S1.

Yeast genera	Milk	Core	Surface
<i>Candida</i>	17	20	9
<i>Debaryomyces</i>	2	2	2
<i>Dipodascus capitatus</i>	1		
<i>Geotrichum</i>	3	2	1
<i>Hyphopichia</i>	1	1	1
<i>Pichia</i>	3	6	4
<i>Kluyveromyces</i>	3	2	2
<i>Saccharomyces</i>	3	3	2
<i>Torulaspota</i>	1	1	1
<i>Wickerhamomyces</i>	1		
<i>Yarrowia</i>	1		1
<i>Zygosaccharomyces rouxii</i>	1		
<i>Cryptococcus</i>	14	1	2
<i>Kazachstania</i>	1	1	1
<i>Malassezia</i>	2		1
<i>Meyerozyma</i>	1	1	
<i>Rhodotorula</i>	4	4	2
<i>Trichosporon</i>	12	5	2
	71	49	31

Fungal genera such as *Eurotium* sp., mesophilic and thermophilic *Actinomycetaceae*, and Gram positive (*Curtobacterium* sp., *Bacillus* and *Paenibacillus* sp.) and Gram negative rods (*Pantoea* and *Pseudomonas* sp.) have been found in hay (Vacheyrou et al., 2011).

The watering place may also be a source of yeasts, *Pseudomonas* sp. and coliform bacteria (Baroiller and Schmidt, 1990; Desmaures, 1995; Gelsomino et al., 2002).

Milking parlour and stable may also be indirect sources of microorganisms via rinsing water (Leriche and Fayolle, 2012), aerosols or biofilm formation (Table S2). In the bioaerosol of small farms (<65 dairy cows), *Microbacteriaceae*, *Staphylococcaceae*, *Bacillus*, *Streptomyces* and moulds such as *Eurotium* sp. and *Aspergillus* sp. predominate while LAB and Gram negative bacteria subdominate (Vacheyrou et al., 2011). Such aerosolized micro-organisms may originate mainly from the dairy females themselves and from plant particles (Vacheyrou et al., 2011). In bioaerosols in dairies with large herds (>800 dairy cows), Proteobacteria were the most abundant microflora (Dungan, 2012; Ravva et al., 2011).

At all stages, faeces may be indirect sources of *Enterobacteriaceae*, spoilage bacteria (e.g. butyric acid bacteria spores) (Rasmussen et al., 1991), yeasts (e.g. *Candida lambica* and *Saccharomyces exiguus*) (Baroiller and Schmidt, 1990; Desmaures, 1995), *Bifidobacterium* (Beerens et al., 2000), and various LAB (*Aerococcus viridans*, *Enterococcus hirae*, *Lactobacillus mucosae*, *Lactobacillus brevis*, and *Lactobacillus plantarum*) (Gelsomino et al., 2001; Kagkli et al., 2007b). Washing cows' teats before milking limits contamination of the teat tip.

Microbial transfers from reservoirs to farm milk need to be demonstrated at strain level. Such transfers are at present only suggested, as several microbial groups and species are found in milking parlour air, hay and raw milk as well as on teat surfaces (Vacheyrou et al., 2011). Using molecular typing, Denis et al. (2004) and Kagkli et al. (2007a,b) showed that only a few strains were common to raw milk and its farm environment (Table 4). However, thorough comparative genomic

Table 4

Sources of LAB species as assessed by strain typing from milk-producing females and their environment to raw milk.

Sources	Micro-organisms	References
Milking machine, bulk tank including after chlorination	<i>Enterococcus casseliflavus</i>	Kagkli et al. (2007a)
Cows faeces, cows teats, milker's hands, bulk tank, milking machine	<i>Enterococcus casseliflavus</i>	Kagkli et al. (2007a)
Cows faeces, silage, milking machine	<i>Lactobacillus parabuchneri/kefiri</i>	Kagkli et al. (2007a)
Teat cups	<i>Lactobacillus</i>	Bouton et al. (2007)
Milking machine	<i>Lactococcus lactis</i>	Mallet (2012)

analyses by whole-genome sequencing may provide new insights into gene flows and metabolic adaptation of strains from various reservoirs to raw milk (Price et al., 2012).

2.3. Conservation shifts the microbial balance of raw milk

Raw milk is often conserved at refrigeration temperature before cheesemaking, especially when it is not processed directly at the farm. Psychrotrophic bacteria are naturally present in milk, where they can reach counts of up to 10^5 cfu/mL (Ercolini et al., 2009). Most of these are Gram-negative bacteria. *Pseudomonas* spp. are the most commonly-occurring psychrotrophs in raw milk, along with *Acinetobacter* spp. and *Enterobacteriaceae* such as *H. alvei* (Ercolini et al., 2009; Hantsis-Zacharov and Halpern, 2007; Martins et al., 2006). They are recognized as a cause of milk spoilage, which may be due to their proteolytic and lipolytic activities (Hantsis-Zacharov and Halpern, 2007). Storage of milk at refrigeration temperature alters milk microbial balance, as shown by changes in the DGGE and TGGE banding patterns of bacterial communities after milk incubation at 4 °C for 24 h (Lafarge et al., 2004). Counts of culturable psychrotrophic bacteria in milk increased by more than 3 log cfu/mL within 3 days of storage at 8 °C and after 7 days at 4 °C (Rasolof et al., 2010). Different storage temperatures and durations led to different species balances in farm and dairy tanks. Upon refrigeration at 4 °C for at least 70 h, dominance in dairy tank milk populations shifted from Gram positive (*Macrococcus*) to Gram negative bacteria (*Pseudomonas*, *Acinetobacter*, *Chryseobacterium*) (Fricker et al., 2011; Raats et al., 2011; Rasolof et al., 2010).

2.4. Enrichment of vat milk and/or cheese microbiota by traditional equipment and practices

Dairy equipment and practices used in making many traditional cheeses (wooden vats and ripening shelves, whey cultures and old-young smearing) enrich the raw vat milk or the cheese during manufacture with certain microbial populations that are active during the process.

The wooden surfaces of the vats used to produce PDO Salers and PDO Ragusano cheeses are a reservoir of microorganisms, active acidifying LAB in particular. The group/species composition of a biofilm was found to be stable over several seasons once it had become established on a vat surface, but varied widely between vats (Didienne et al., 2012; Licitra et al., 2007). Wooden vats can increase microfloral levels in the milk compared to those in milk before pouring into the vat (Didienne et al., 2012; Lortal et al., 2009; Settanni et al., 2012). Both strain and species richness of the LAB dominating a raw milk increased by 50% after a few minutes in the wooden vat (Settanni et al., 2012).

For some traditional cheese, whey drained from previous days' curds is routinely used to culture LAB before their inoculation into raw milks to carry out the acidification step. Sometimes, selected LAB strains are added to the whey. At the end of culturing intended for making hard cooked and pasta filata cheeses, thermophilic LAB dominated (author's list in Table S3). The relative abundance of LAB strains/species remains difficult to assess (Bottari et al., 2010; Rossetti et al., 2008) as it varies widely between dairies and within one dairy over the year (de Candia et al., 2007; Ercolini et al., 2008; Gatti et al., 2003; Rossetti et al., 2008; Rossi et al., 2012).

Wooden ripening shelves are a reservoir of surface microflora that can be transferred directly to cheese surface. Yeasts, moulds and coryneform bacteria dominate in succession on the surface of Reblochon de Savoie, a raw milk PDO cheese, and also dominate the biofilms of shelves used for ripening (Mariani et al., 2007; Oulahal et al., 2009). These biofilms, which do not change with season or shelf age, are a possible source of surface microflora for smear cheeses, often not deliberately inoculated with surface microorganisms.

The microbial composition of smear brines obtained by old-young smearing have been poorly investigated. Seiler and Busse (1990) identify more than 15 yeast species in brines of soft, hard, and semi-hard cheese. Brine microbiota serve to inoculate the surface of many raw milk cheeses and in most cases optimize the ripening process (Goerges et al., 2008).

The microbiota of these biofilms, brines and cultures are often complex and vary between dairies. As a result they have not been fully described, especially at strain level and for subdominant populations. Strain tracking is required to illustrate not only microbial transfer from these biofilms, brines and cultures to the cheeses but also transfer from environmental sources to the biofilms, brines and cultures.

2.5. Microbial dynamics during cheese-making and ripening

Certain of the strains/species present in vat milk (indigenous and/or starter and/or adjuncts strains) can grow, survive and even become dominant during the cheese process. This depends on the microorganisms' metabolic potential and the expression of that potential, which both depend on environmental conditions and are species- or even strain-specific. The environmental conditions encountered by the microbiota are first the biochemical composition of vat milks, then that of the curd matrix as modified by the acidifying starters and technological factors (rennet addition, temperature..), and finally the technology applied during ripening (salting; smoking; temperature 2 °C to 17 °C; relative humidity, 85% to 97%; gas composition of cheese environment; etc.) (Callon et al., 2011a). This results in dramatic and continuous changes in the microbial balance during cheese making and ripening, but also in different microbial dynamics depending on the cheese technology applied. Microbial dynamics in the cores and on the surfaces of traditional cheeses have been extensively described. They vary between cheese varieties and, within a variety, between dairies and time periods. They are impacted by a complex and poorly understood network of interactions involving biotic factors (microbiota composition at species and strain levels, population counts and balances, etc.) and abiotic factors (physico-chemical composition and structure of cheese matrix – such as pH, a_w , redox potential, NaCl, CO₂, anaerobiosis, (un)dissociated acids, amino-acid, fatty acid and products of their catabolism, small peptide and carbon sources content, physicochemistry of cheese environment) (Callon et al., 2011a, 2011b; Charlet et al., 2009; Irlinger and Mounier, 2009; Pelaez and Requena, 2005).

2.5.1. In cheese cores

When changes in the species richness of the dominant bacteria from milk to ripened traditional cheese (core and surface) are monitored, estimated as the number of species detected in 80 recent studies (species listed in Table S4), LAB diversity increases only in the core because LAB are well adapted to the conditions prevailing there (low pH, high NaCl,

anaerobiosis, lack of fermentable carbohydrate...) (Table 2). Non-starter LAB are abundant in almost all cheese varieties, whether traditional or not. Mesophilic lactobacilli are among the most common non-starter LAB. Their relative abundance during the ripening of raw milk cheeses varies according to the type of technology (soft, semi-hard, hard) (Quigley et al., 2012) and the length of ripening (Depouilly et al., 2004; Gatti et al., 2008). Within a cheese variety or for cheeses made from the same raw milk, it also varies according to whether or not a starter is used and the composition of the starter if used (Feutry et al., 2012a; Henri-Dubernet et al., 2008; Masoud et al., 2011).

In the cores of traditional raw milk cooked hard cheeses and pasta filata cheeses (also made from raw milk), LAB largely dominate at all stages of the cheese process, together with propionic acid bacteria in cheeses with eyes (Swiss-type cheeses). Thermophilic starter LAB are the dominant viable microflora from the beginning of cheese-making to at least six months of ripening (Grappin et al., 1999; Table S3), despite partial lysis (Gatti et al., 2008) and partial unculturability from the first days of processing (Gala et al., 2008; Gatti et al., 2008; Rossi et al., 2012). Levels of \log_{10} 8–9 may persist, as shown in experimental Swiss-type cheese (Falentin et al., 2012). The main thermophilic LAB species are *Lactobacillus delbrueckii* and/or *Streptococcus thermophilus*, and/or *Lactobacillus helveticus*, and/or *Lactobacillus fermentum*, varying even within one cheese variety. *L. helveticus* levels decline more rapidly than those of *L. delbrueckii* as ripening progresses (Bouton et al., 2002; Gatti et al., 2008). Thermophilic LAB originate from whey cultures or wooden vats and/or the raw milk (Tables S1 and S2). *L. delbrueckii* from milk dominate only during ripening. Mesophilic viable/cultivable non-starter LAB, mostly *Lactobacillus paracasei*, but also *Lactobacillus rhamnosus* (Grappin et al., 1999; Table S3), originating from raw milk (Berthier et al., 2001; Casey et al., 2006), often become dominant; but they predominate over viable thermophilic lactobacilli only after 10 to 30 months of ripening (Gala et al., 2008; Gatti et al., 2008; Rossi et al., 2012). Microbial growth and the balance between cultivable LAB vary from just under the surface to the centre of the core (Monfredini et al., 2012) and according to the nature and initial levels of the strains (Charlet et al., 2009). Microbial interactions occur as early as the pressing step, as shown in experimental cooked hard cheeses made from raw milk (Charlet et al., 2009), and during ripening (Fröhlich-Wyder et al., 2002). Psychrotrophic microflora and strictly mesophilic microflora are never detected in cheese cores. Viable *Macrocooccus caseolyticus*, *Rothia* spp., *Leuconostoc lactis*, *Lactococcus lactis* and psychrotrophic bacteria (*Chryseobacterium* spp., *Pseudomonas* spp.) disappear once the curd temperature has reached 47–48 °C (Giannino et al., 2009). Yeasts, Gram positive catalase positive bacteria, enterococci and pediococci are subdominant (Demarigny et al., 1997; Rossi et al., 2012). Variation in active cell numbers, species balance and strain composition between cheeses of the same variety, according to dairy and period, is related firstly to differences between vat raw milk batches and/or between whey cultures (Table S3), and secondly to differences in ripening conditions (Berthier et al., 2001). Several strains of *S. thermophilus*, *L. paracasei* and/or *L. delbrueckii* can co-exist in Caciocavallo, Gruyère and Comté PDO cheeses (Berthier et al., 2001; Bouton et al., 2002; Casey et al., 2006; Depouilly et al., 2004; Settanni et al., 2012). The dominant strains of *Lactobacillus casei* in cheese cores are often different from those found in raw milks, suggesting that selective conditions arise during the cheese process.

In the cores of uncooked pressed and ripened cheeses, the balance of dominant species varies with time and between cheese varieties. Indeed, the physico-chemical composition and the structure of cheese cores are largely variable, as shown for the moisture content (42%–55%). However, LAB are the dominant microbial group, usually reaching counts above 9 log cfu/g within the first day of cheese making and remaining dominant to the end of ripening, despite variations in the species balance as ripening progresses. At least 21 different LAB species, spanning 7 genera, can be found (author list in Table S4). The most widespread and most frequently dominant are *Lactococcus lactis*,

S. thermophilus, *Leuconostoc mesenteroides*, *L. plantarum*, *L. casei*, *Enterococcus faecalis* and *Enterococcus faecium*. In addition, intra-species genomic heterogeneity in non-starter LAB is wide within and between cheeses of different origins (Callon et al., 2004; Feutry et al., 2012a, 2012b). Staphylococci rank second among the Firmicutes groups in these cheeses, with at least four species, at counts of up to 5 log cfu/g (Delbès et al., 2007; Quigley et al., 2012), followed by *Clostridiales* (Quigley et al., 2012). Proteobacteria can reach counts as high as 8 log cfu/g in cheese cores (Delbès-Paus et al., 2012; Tornadizo et al., 2001). They span at least 9 genera, mainly *Enterobacteria* genera such as *Enterobacter* and *Klebsiella*, but also other *Gammaproteobacteria* such as *Pseudomonas*, *Stenotrophomonas* and *Psychrobacter* (Delbès et al., 2007; Quigley et al., 2012). Subdominant populations of Actinobacteria have also been detected (up to 4 log cfu/g). They belong to at least 7 genera, the most often reported being *Corynebacterium* (*Corynebacterium flavescens*, *Corynebacterium variabile*), *Arthrobacter* (*Arthrobacter arilaitensis*) and *Brevibacterium* (*Brevibacterium linens*) (Delbès et al., 2007; Duthoit et al., 2003; Quigley et al., 2012). Finally, minor populations of Bacteroidetes such as *Chryseobacterium* and *Prevotella* have occasionally been reported (Delbès et al., 2007; Quigley et al., 2012).

Data are scarce for other traditional cheeses. LAB were the most abundant bacterial groups in scalded–smoked cheese (Alegria et al., 2012) and fresh or ripened cheeses (Alessandria et al., 2010; Edalatian et al., 2012; Martin-Platero et al., 2008, 2009) made from sheep or goat milk without starter. Of note in these cheeses is the recurring report of *Lactococcus garvieae* (Alegria et al., 2012; Alessandria et al., 2010; Edalatian et al., 2012) and of wild strains of *S. thermophilus* (Alegria et al., 2012; Edalatian et al., 2012). Proteobacteria (*Enterobacteria*), Actinobacteria (*Kocuria*, *Propionibacteria*) as well as salt-tolerant bacteria found in marine environments and assigned to *Flavobacteriaceae* have been detected sporadically in cheese (Ercolini et al., 2012). Proteobacteria counts decreased between the curd stage and the smoked cheese, while those of *Lactococcus lactis*, *Lactobacillus* and *Enterococcus* increased (Alegria et al., 2012; Edalatian et al., 2012). So did lactobacilli in Camembert cheese during ripening – particularly *L. paracasei*, which also showed wide intra-species diversity (Henri-Dubernet et al., 2008). In the cores of raw milk blue cheeses, *Lactococcus lactis* was dominant from curd stage to the end of ripening, whereas lactobacilli increased during ripening, as did moulds (Florez and Mayo, 2006). Subdominant populations of *Leuconostoc* have also been detected. Interestingly, most uncooked cheeses harbour a wide diversity of yeast species from 13 genera, mainly *Candida*, *Pichia*, *Saccharomyces*, *Rhodotorula*, and *Trichosporon* (Table 3).

2.5.2. On cheese surfaces

Cheese surface is a more open ecosystem than the core and a very different one (Bockelmann et al., 2005; Law, 2010). Yeasts, moulds and aerobic bacteria such as *Corynebacteriaceae* and *Micrococcaceae* develop mainly on cheese surface, where O_2 is more readily available than in the core (Table S4).

Cheese surfaces exhibit specific microbial dynamics. On the surfaces of smear-ripened and mould-ripened cheeses, bacterial populations (mainly starter LAB in the earliest stages) dominate numerically throughout ripening. Microbial growth is initially due to budding yeast populations followed closely by the arthroconidial yeast *Geotrichum candidum*, when present. Yeast counts range around 6–8 log cfu/cm² within 2–7 days; they then remain fairly constant until the end of ripening, with variations in species balance. The yeast growth leads to an increase pH values and then bacterial growth occurs. From day 10 (for Reblochon, Gubbeen) or days 14–20 (for Camembert, Limburger, Raclette-type cheese, Saint-Nectaire, Tilsit) and until the end of the ripening process, various bacteria grow on the cheese surface, reaching counts of 8–11 log cfu/cm². On the surface of mould-ripened cheeses, yeast growth is followed by mould growth. For example, on Saint-Nectaire type cheese *Mucor* sp. starts to grow on day 4 and *Fusarium*

domesticum on day 20 of ripening while on Camembert, *Penicillium camemberti* ssp. *caseicum* starts to grow on days 6–7 of ripening and covers the surface by days 10–12.

Cheese surfaces exhibit a high species and genus diversity for both eukaryotes and prokaryotes. At least 30 different yeast species, compared to 48 in the cores, spanning 14 genera can be found (Tables 3, S4), the main species being *Debaryomyces hansenii*, *G. candidum*, *Candida catenulata*, *Kluyveromyces lactis* and *Yarrowia lipolytica*. Sohler et al. (2009) found that *D. hansenii* and *Kluyveromyces marxianus* strains isolated from French traditional cheeses were genetically diverse. Firmicutes, Actinobacteria and Proteobacteria (Quigley et al., 2012) are by far the most commonly co-dominant bacterial populations, their balance varying with cheese variety. Among Firmicutes, and apart from starter LAB, marine lactic acid bacteria (*Alkalibacterium*, *Marinilactibacillus*) (Roth et al., 2010) and *Staphylococcaceae* are reported on cheese surface, with at least 17 species. For Actinobacteria at least 11 genera are reported; as in the cores, the most commonly reported are *Arthrobacter* (*A. arilaitensis*), *Corynebacterium* (*Corynebacterium casei*, *C. variabile*), *Brevibacterium* (*Brevibacterium aurantiacum*), and *Microbacterium gubbeenense* (Brennan et al., 2002; Eliskases-Lechner and Ginzinger, 1995a; Larpin-Laborde et al., 2011; Marcellino and Benson, 1992; Mounier et al., 2009). Proteobacteria can reach counts as high as those of Actinobacteria on the surfaces of some smear cheeses (Larpin-Laborde et al., 2011). They span at least 10 families, and are mainly *Enterobacteriaceae* (*Hafnia* and *Proteus*), *Moraxellaceae* (*Psychrobacter*), *Halomonadaceae* (*Halomonas*), *Alcaligenes* (Table 2) (Coton et al., 2012; Larpin-Laborde et al., 2011; Maoz et al., 2003; Mounier et al., 2009; Quigley et al., 2012).

Some species seem to be characteristic of particular cheese varieties, e.g. *Mycetocola reblochoni* on Reblochon (Bora et al., 2008) and *Leucobacter* sp. on surfaces of Saint-Nectaire, Danish farmhouse, and Livarot cheeses (Callon et al., 2014; Gori et al., 2013; Mounier et al., 2009; Larpin-Laborde et al., 2011). Some are mainly associated with a specific ripening stage. Among yeasts, *D. hansenii* and *K. lactis* are particularly present at early ripening stage, while *G. candidum*, when present, is present throughout ripening and *Y. lipolytica* is mainly detected in ripened cheeses. Regarding moulds, Panelli et al. (2012) found that *Penicillium commune* dominated on the surface of PDO Taleggio cheese, but also detected *Cladosporium* sp. and *Aureobasidium pullulans*.

Yeast–yeast and yeast–bacterium interactions condition the establishment of the cheese surface ecosystem (Lessard et al., 2012; Mounier et al., 2009). Yeasts, and moulds when present, metabolize lactic acid and produce NH₃, so raising the surface pH (from 4.8–5.2 to up to 6–8.2) and allowing salt-tolerant and acid-sensitive bacteria to grow. Population levels and balance during cheese ripening can be affected by deliberate inoculation of exogenous species in large quantities into the milk or curd or onto the surface (Irlinger et al., 2012), but surface ecosystems respond differently to the addition of such species according to their microbial composition (Feurer et al., 2004b; Goerges et al., 2008). Resident microbiota from the milk or from the cheese-making environment, e.g. halophilic bacteria (Ishikawa et al., 2007) possibly originating from salt or brine, may adapt to the cheese ecosystem (Monnet et al., 2010b; Suzzi, 2011) and outcompete adjunct strains (Goerges et al., 2008; Gori et al., 2013).

3. Microbial diversity: a key factor for sensory benefits

3.1. Two approaches to cheese processing

Over the centuries, cheese makers have domesticated fermentation processes empirically, without a deep understanding of the multiple biochemical reactions governing the sensory qualities of their cheeses. They have managed the microbial ecosystem by adopting undefined blends, home-made cultures and cheese process parameters on the basis of personal experience and empirical observation (Bérard and Montel, 2012; Bertoni et al., 2001; Scott et al., 1998). In traditional

cheese processing, diversity in herd management, cheese making and cheese ripening practices, often in small-scale production, has generated the diversity of characteristics in ripened cheeses that still exists in traditionally-made cheeses today. Raw milk cheeses are processed by traditional methods because raw milk requires appropriate practices, such as the traditional short supply chain and small dairy units. This helps to maintain both the richness (intra-sample diversity) and variability (inter-sample diversity) of microbial consortia in cheese. By contrast, industrial cheese production processes, often applied on a large scale, are designed to standardize the ripened cheese, reducing variability at the end of the chain by reducing variability in milk matrix characteristics and the cheese-making practices (Bachmann et al., 2011). Pasteurization is one method commonly used to standardize microbial composition and improve the microbial safety of milk by reducing its microbial load and biodiversity. It can necessitate the adoption of new practices throughout the production chain, as Bachmann et al. (2011) have shown for Camembert and Emmental.

3.2. Sensory profiles altered by heat-treating milk

The sensory characteristics of cheeses made with raw milk were positively perceived by consumers compared to pasteurized cheeses, which were considered to “lack flavour” (Chambers et al., 2010; Colonna et al., 2011). Moreover, consumers who like raw milk cheeses appreciate the varied flavour nuances they find within a given cheese type.

Raw milk cheeses ripen faster and acquire richer, more intense flavours than pasteurized or microfiltered milk cheeses (review in Bachmann et al., 2011; Beuvier and Buchin, 2004; Grappin and Beuvier, 1997; Van Hekken, 2012). This has been observed in cheeses as diverse as hard cooked cheeses (Swiss-type, Emmental, Bergkäse, Reggiano), hard uncooked cow's milk cheeses (Cheddar, Gouda, Raclette, Morbier-type, Cantal-type), and sheep or goat milk cheeses (Manchego, Idiazabal, Roncal, Canestrato pugliese) (Alonso et al., 2013; Ballesteros et al., 2006; Beuvier and Buchin, 2004; Cornu et al., 2009; Velez et al., 2010). Raw milk cheeses generally have larger amounts of most aromatic compounds (acids, aldehydes, alcohols, esters and sulphur compounds), with the exception of some ketones. The effects of raw milk microflora on texture differ according to cheese variety and processing conditions (Beuvier and Buchin, 2004). The flavour and texture of raw milk cheeses seem to be affected more than those of pasteurized ones by factors that modify the physico-chemical composition of the milk. Changes in flavour of experimental Cantal cheeses according to animal diet (Verdier-Metz et al., 2002) or in texture of Chihuahua Queso according to season (Tunick et al., 2007) were observed in raw milk cheeses but not in pasteurized ones. The link between ruminant management and the characteristics of traditional cheeses has been extensively reviewed (Coulon et al., 2004; Martin et al., 2009).

Pasteurization denatures milk enzymes such as proteases or lipases (Hayes et al., 2001; Hickey et al., 2007) and dramatically reduces the levels of milk natural microflora and associated enzymes, all of which are involved in the formation of raw milk cheese characteristics. It also affects bitterness, but differently depending on cheese variety. It probably does this by changing the balance between production and degradation of bitter peptides (Beuvier et al., 1997).

3.3. Demonstration that microbial diversity in milk generates diversity in cheese sensory characteristics

Variations in the sensory characteristics of cheeses manufactured with different native milk microbial consortia have been poorly investigated. Three studies performed with experimental cheeses produced under the same manufacturing and ripening conditions using re-constituted raw milk batches highlight the role of the raw milk microflora's abundance and diversity (§1.1.1). In hard cooked cheeses, the composition of native microbiota from different raw milk samples,

inoculated at similar levels (2.10^4 to 7.10^4 cfu/mL) into vat microfiltered milk (10^3 cfu/mL), affected the flavour and texture attributes of the cheeses (firm, grainy, salty, acid, pungent, animal, toasted, milky etc.). The dynamics and balances of volatile compounds (acids, aldehydes, alcohols, ketones, esters, and sulphur compounds) in the cheeses were found to differ (Buchin et al., 2004; Demarigny et al., 1997). These differences were associated with differences in the dynamics of the microbial populations present in the milk consortia, mainly non-starter LAB and propionic acid bacteria. In the same way, experimental PDO Salers type cheeses manufactured from three different raw milk microbial communities differed in their relative levels of butter, cream, hazelnut, caramel and sweet aromas versus sour cream, chemical, rancid, bitter, spicy and alliaceous or citrus-fruity flavours (Callon et al., 2005). They also differed in their balances of aromatic compounds (acids, alcohols and aldehydes). Microbial diversity generated sensory diversity, but correlation between microbial counts and sensory attributes has been difficult to establish. Nevertheless, each sensory attribute was associated with several microbial groups identified on 16SrDNA Single Strand Conformation Polymorphism profiles of ripened cheeses (Duthoit et al., 2005).

3.4. Functional diversity of microbial communities in the cheese ecosystem

The diversity of sensory characteristics of cheeses results from diversity in the balance of aromatic compounds arising from many metabolic pathways (sugars, citrate, lactate, amino-acid and fatty acid catabolisms, casein breakdown and lipolysis). Oxidative pathways occur on the surface, whereas fermentative pathways occur in the core. Several species may cooperate in a metabolic pathway, as observed for branched amino-acid catabolism (Smit et al., 2005) and for thioester formation (Arfi et al., 2002) in defined media. The different microbial populations mentioned above (§ 1.5) can be extensively involved in these pathways, as suggested by their multiple and varied potential enzymatic activities compiled in Table S5 from many reviews. However, the compiled data do not explain how a complex cheese ecosystem functions. They do not indicate the expression of the enzymatic potential, microbial or not, in cheese (Brennan et al., 2004; Corsetti et al., 2001; Irlinger and Mounier, 2009; Mounier et al., 2005, 2008) and they do not enable us to link this expression to the cheese microbiota's dynamics (§ 1.5) and environment (extrinsic and intrinsic cheese factors). In particular, the numerous microbial interactions involved in microbiota dynamics, especially complex in traditional cheeses due to the complex composition of the microbiota, are far from being elucidated. They determine and at the same time are governed by factors intrinsic to the cheese (availability of substrates and co-factors, presence of inhibitor/activator compounds, pH and redox potential) and extrinsic factors (oxygen availability, temperature, relative humidity). The cheesemaking and ripening processes drive all the dynamics in cheese ecosystems.

3.4.1. Role of lactic acid bacteria in the cheese core

Non-starter LAB (§ 1.5.1), mainly mesophilic lactobacilli but also leuconostocs, enterococci and pediococci for some cheese varieties, are dominant in the cores of most type of cheese. Present in raw milk, their predominance in natural cheese microbiota is attributed to their numerous enzymatic systems, which enable them to use milk nutrients efficiently (Peterson and Marshall, 1990). They are also tolerant to selective values of pH (as low as 4.9), salt (6% NaCl/water), moisture (<50%) and a wide range of temperature (2 °C–53 °C) conditions (Gobbetti et al., 2007; Wouters et al., 2002). Their occurrence – at lower counts – in pasteurized milk cheeses is probably due both to a partial resistance to heat treatment and to contamination by the factory environment after pasteurization (Banks and Williams, 2004; Beresford et al., 2001; Peterson and Marshall, 1990). Their functions (fermenting lactose, lactate, citrate, amino-sugars, glycerol and catabolising peptides and amino-acids) vary widely between species, but also between strains of the same species (Table S5). They are decisive for cheese

quality such as flavour. For example, in the cores of uncooked experimental cheeses made from pasteurized milk, volatile compound contents were associated with mesophilic lactobacilli but not with other microbial populations that develop to a lesser extent during ripening (Callon et al., 2011b). In the cores of ripened experimental hard cooked cheeses made from microfiltered milk inoculated or not with facultatively heterofermentative lactobacilli and/or enterococci, volatile profiles were affected only by lactobacilli, which reached higher counts than enterococci (Bouton et al., 2009).

Among the microorganisms interacting within cheese cores, special mention should be made of the acidifying starters, which rapidly reach high counts (10^9 – 10^{10} cfu/g of cheese at day 1). By their diverse metabolic activities (Table S5) and major modifications of cheese matrix (e.g. curd acidification, decrease in redox potential, proteolysis) they directly produce aromatic compounds, provide substrates that can be further degraded by other microbial populations, and regulate the early growth of the cheese microbiota. In the core, the more active the acidifying starters during the first day of manufacture, the more the expression of the other internal microflora will be repressed or delayed. Acidifying starters selected for a given traditional cheese variety are composed of a few strains, compared to traditional starters (§ traditional starters); they are increasingly used to limit major taste and aroma defects by normalizing acidification kinetics (O'Sullivan et al., 2013). But by reducing the inter-starter variability observed with traditional practices (§ 1.4), they may reduce the variability of sensory characteristics between ripened cheeses (Pereira et al., 2009). Not all traditional cheese-makers use selected acidifying strains, but they may need to do so because farm hygiene practices have reduced microbial population levels in raw milk, including acidifying populations.

The use of wild strains of *Lactobacillus*, *Lactococcus*, *Leuconostoc*, and *Enterococcus* as acidifying and/or flavouring starters is promising (Wouters et al., 2002). In experimental pasteurized milk cheeses, inoculation of milk with wild strains of *Lactobacillus*, singly or in combination, resulted in adequate but milder acidification and higher scores for sensory attributes, due to more complex volatile profiles than with commercial strains. This has been observed in a number of cheese varieties: Cheddar (Wouters et al., 2002), Roncal (Ortigosa et al., 2005), Manchego (Cabezas et al., 2007; Gomez-Ruiz et al., 2008; Poveda et al., 2003), Corsican Venaco and Tenerife goat's milk cheeses (Casalta and Zennaro, 1997 and Gonzalez and Zarate, 2012, respectively), Greek Feta (Foulquié Moreno et al., 2006; Sarantinopoulos et al., 2002), and Pecorino Siciliano (Randazzo et al., 2008). Overall, compared to commercial strains, wild lactococci are less acidifying, less sensitive to phages and lysis, and have greater enzyme capability for citrate and amino acid metabolism (Wouters et al., 2002). Wild strains produce larger amounts of branched compounds from amino acid catabolism, and this may enhance cheese flavour. However, if produced too abundantly, such compounds may be a source of off-flavour such as chocolate or malty tastes in some cheeses (Wouters et al., 2002). Intensive use also results in numerous subcultures in milk; in the process, the wild strains may lose some of their initial functions and gain new ones, as observed for lactococci (Bachmann et al., 2012).

3.4.2. Role of other microbial species in the cheese core

For some hard cooked cheeses, flavour is also significantly impacted by propionic acid bacteria that originate from raw milk for some PDO cheeses (PDO Comté) and which are localized in the core. These bacteria produce acetic acid, propionic acid and CO₂ from lactate, branched compounds from leucine and isoleucine (Table S5), and have lipase and esterase activities (Table S5). Their interactions with thermophilic starters and NSLAB may also participate to variability in the final characteristics of such cheeses (Baer and Ryba, 1999; Bouton et al., 1996; Chamba, 2000; Jimeno et al., 1995; Kerjean et al., 2000; Piveteau et al., 2002).

Pasteurized PDO Stilton cow's milk blue cheeses made in different dairies differed in the ketone/alcohol/aldehyde balance produced by *P. roquefortii* in their inner blue part (Gkatzionis et al., 2009).

3.4.3. Role of the cheese surface microbiota

The potential of surface microorganisms for producing volatile compounds, singly or in combination (usually combinations of two) has been described in culture media (Arfi et al., 2002; Lecocq and Guéguen, 1994; Spinnler et al., 2001; Mansour et al., 2009), in cheese-based medium (Arfi et al., 2004) and on cheese surface (Brennan et al., 2004; Sorensen et al., 2011; Wouters et al., 2002). Numerous enzymatic potentialities (Table S5), as well as numerous metabolic interactions among surface microorganisms, have been described (Corsetti et al., 2001). For soft surface-ripened cheeses, microbial activity on the surface during ripening is crucial, as the surface microbiota constitutes a large part of cheese microbiota.

Ripening bacteria and yeasts/moulds are naturally present in brine and in the smear solutions traditionally used for “old–young” smear cheese (§ 1.5) (Bockelmann et al., 2005). The positive or negative role of many yeast species present on surface (Table S4) remains to be determined. To protect against undesirable microorganisms, selected inocula are commercially available for adding to brine or smear, or for spreading directly onto the cheese surface (Bockelmann, 2010). However, the fitness of natural cheese microbiota and their impact on sensory characteristics are generally greater than those of inocula of *Brevibacterium* alone (Brennan et al., 2002; Mounier et al., 2005) or of selected smearing species (Feurer et al., 2004b; Goerges et al., 2008). In particular, with a semi-soft smeared cheese Tilsit, a culture composed of *D. hansenii*, *Staphylococcus equorum*, *B. linens*, *M. gubbeenense* or *Arthrobacter nicotianae*, and *C. casei* was able to normally deacidify to pH 7.0 at one week, and gave a similar appearance to that achieved by old–young smearing (Bockelmann et al., 2005), but the typical sulphur flavour was delayed (Bockelmann and Hoppe-Seyler, 2001).

Boutrou and Guéguen (2005) reported the use of adjunct cultures of the yeast *G. candidum* to produce pasteurized soft and semi-hard cheeses with taste and aroma close to those of raw milk cheeses. *G. candidum* produces many volatile compounds important for flavour (phenyl compounds, NH₃, lactones, esters and volatile sulphur compounds) (Table S5).

Penicillium species are decisive for the flavour and texture of whitemould-ripened cheeses owing to their lipolytic and oxidative activities, leading to high production of aromatic ketones and alcohols (Molimard and Spinnler, 1996). They are added as ripening cultures to both raw and pasteurized milks. The use of a limited number of commercial strains, often at high levels, has standardized cheese sensory characteristics. To achieve in Camembert made from pasteurized milk the sensory characteristics of raw milk Camembert, *P. camemberti* must be associated in the right proportions with *G. candidum*, other yeasts, and coryneform bacteria (Bockelmann, 2010; Spinnler and Gripon, 2004). Its flavour results from interactions between all these microorganisms (Molimard et al., 1997); in particular, by its aminopeptidasic activities, *G. candidum* reduced the bitterness that can be produced by *P. camemberti* proteolytic activity (Molimard et al., 1994) in the range of 4.2 to 11.5 g peptides/kg. Compared to the extensive use of *Penicillium*, other mould species (Table S4) are rarely used as ripening cultures in traditional cheeses (Ropars et al., 2012).

However, the sensory differences between surface-ripened cheeses made from raw and processed milk lie not only in the nature and quantities of their surface microorganisms at the beginning of ripening, but also to the entire processing chain as exemplified for Camembert (Bachmann et al., 2011; Spinnler and Gripon, 2004). For example acidifying starters, acidifying kinetics and matrix mineralization all differ, affecting the microbial and other dynamics during ripening and the quality of the ripened cheese.

3.4.4. Role of Gram negative bacteria

Although Gram negative bacteria are abundant and highly diverse in raw milk and traditional cheeses (Tables 2 and S4), the functional potentialities of only a few species have been studied; cheese-makers

talk of a flavouring role mainly in cheeses for which surface ripening is crucial. *Enterobacteriaceae* have a high aromatic potential as they can catabolize citrate, lipids and proteins (Chaves-Lopez et al., 2006; Zago et al., 2007). On the surface of a model soft smear cheese, *Proteus vulgaris* inoculated at 10⁵ cfu/g and reaching 10⁹ cfu/g after ripening, increased levels of ketones and branched compounds (aldehydes, alcohols and esters), but not sulphur compounds in the presence of yeasts (Deetae et al., 2009). On a similar model cheese inoculated with eleven microbial species representative of the diversity of that cheese, Irlinger et al. (2012) inoculated *Psychrobacter celer* separately at 10⁶ cfu/g. It reached more than 10⁹ cfu/g during ripening and reduced the microbial biodiversity of the cheese. Directly or indirectly (by acting on other microbial populations), *P. celer* promoted aromatic complexity due to the production of aldehydes from amino acids and of ketones from fatty acid oxidation and thioesters (Irlinger et al., 2012). In the same model cheeses *H. alvei*, inoculated at similar levels, enhanced volatile sulphur compounds (Irlinger et al., 2012). In the contrary, inoculating Gram negative bacteria into the cores of model semi-hard cheeses did not change core flavour, the inoculated bacteria reaching no more than 10⁶ cfu/g (Delbès-Paus et al., 2012). Nevertheless *H. alvei* is commonly used as a flavouring adjunct (Bourdichon et al., 2012). Gram negative bacteria can produce biogenic amines (Maifreni et al., 2013; Marino et al., 2000, 2008; Martuscelli et al., 2005), and may have spoilage potential (Dogan and Boor, 2003; Franciosi et al., 2011).

4. Raw milk: a bulwark against pathogens

4.1. Potential benefits of natural non microbial inhibitors

Protection against pathogen growth in milk and cheese can be provided by antimicrobial agents such as lactoferrin (Farnaud and Evans, 2003; Wakabayashi et al., 2006), lactoperoxidase system (LPS) (Seifu et al., 2005), lysozyme (Vincenzetti et al., 2008), immunoglobulins and some free fatty acids present in milk. These agents are more or less inactivated by heat treatment (Claeys et al., 2013). Heat treatment at less than 85 °C–10 min did not affect the antibacterial activity of lactoferrin in culture medium (Conesa et al., 2010). But milk pasteurization may partially denature lactoferrin, making it more sensitive to cheese proteases (Dupont et al., 2006) and therefore more rapidly inactivated during ripening. Lactoperoxidase activity was intact after pasteurization at 63 °C for 30 min or at 72 °C for 15 s, but was completely inactivated in cow's milk by heating at 78 °C for 15 s. Heating at 75 °C for 28 s reduced it by between 39% and 53% depending on animal species. Sheep milk lactoperoxidase was less resistant to thermal denaturation than either goat or cow milk lactoperoxidases (Dumitraşcu et al., 2012; Lorenzen et al., 2010). The fact that *E. coli* and *Staphylococcus aureus* grow better in pasteurized than unpasteurized human milk can be partly explained by reduced concentrations and activity of immunologic compounds with bactericidal and bacteriostatic properties, and by the denaturing of milk lipases leading to lower output of fatty acids with antagonistic properties (Van Gysel et al., 2012).

4.2. Microbial diversity to combat pathogens

Undoubtedly, cheeses are safer than unfermented milk because fermentation (involving pH decrease in the core due to acid production, redox potential reduction, nutrient depletion and antagonistic metabolite production), combined with a decrease in a_w and a ripening temperature often below 15 °C, creates environmental conditions that are more or less hostile to pathogens depending on manufacturing and ripening process.

4.2.1. Raw milk cheeses as a source of strains antagonistic to pathogens

Raw milk cheeses are valuable sources of bioprotective cultures. They harbour lactic acid bacteria that are the first and primary agents in the biopreservation of cheese, producing a wide range of

antimicrobial substances, depleting fermentable sugars and/or lowering pH. There is an extensive literature describing strains of LAB from traditional dairy products able to inhibit the most important cheese pathogens (*L. monocytogenes*, *S. aureus*, *Klebsiella pneumoniae*, *Salmonella typhimurium*, *Bacillus subtilis*, and *Pseudomonas aeruginosa*) in laboratory media (Dal Bello et al., 2010; Diop et al., 2007; Ortolani et al., 2010). Some of these authors show that LAB strains have the genetic potential to produce bacteriocins, or that they produce them in vitro. Only a few studies mention antagonistic action in cheese. Single strains of *L. garvieae* and *Lactococcus lactis* inhibited *S. aureus* early in a cheese matrix (Alomar et al., 2008; Cretenet et al., 2011). *H. alvei* inhibited shigatoxin-producing *E. coli* O26: H11 in the core of uncooked pressed cheeses and microbial consortia may enhance this inhibition (Delbès-Paus et al., 2012).

The gap between inhibition in vitro and in cheese may be attributed to the weak antagonistic effect of bacteriocins in cheeses. This may be due to their interactions with the cheese matrix (degradation, adsorption, uneven distribution), with native microflora or starter culture, and with an unfavourable physicochemical environment (Deegan et al., 2006; Grattepanche et al., 2007; Sobrino-López and Martín-Belloso, 2008). The risk of developing resistant strains among target pathogens is also a major concern (Gravesen et al., 2002).

4.2.2. Efficiency of microbiota against *L. monocytogenes*

Natural cheese microbiota of various microbial compositions and degrees of diversity (Table 5) can protect cheeses against *L. monocytogenes*. Several multispecies consortia with antilisterial properties have been identified on red smear cheese surfaces (Eppert et al., 1997; Imran et al., 2010; Maoz et al., 2003), on raclette (Roth et al., 2010), on Saint-Nectaire surfaces (Retureau et al., 2010) and in Saint-Nectaire cores (Millet et al., 2006; Saubusse et al., 2007). The degree of biodiversity and the species composition of consortia are not necessarily associated with their ability or not to inhibit *L. monocytogenes*; this has been shown for natural consortia from the surfaces of red smear cheeses (Bleicher et al., 2010a) and for several reconstituted ones from a Livarot surface consortium (Imran et al., 2010).

Even after changing the microbial composition of antilisterial consortia by simplification, successive reconstitution, propagation, and modification of extrinsic factors during ripening, it is not easy to identify which microbial combination is necessary for the inhibition. Three microbial ripening consortia (RI, RII, and KII) in the surfaces of red smear cheeses ripened at a constant temperature of 13 °C for 13 days had quite different compositions (Table 5) but similar antilisterial activities. For both RI and RII, ripening at 16 °C for 13 days and then at 12 °C for 7 days did not affect their antilisterial properties despite significant changes in their coryneform bacteria composition (coryneforms remained the dominant population) (Mayr et al., 2004). For KII, this change in the ripening temperature increased the dominance of Gram positive and catalase negative bacteria and of *Marinilactibacillus psychrotolerans*, and led to a decline in antilisterial properties. In one study, after the fourth application of a red smear consortium to a model cheese, the proportion of the *Vagococcus*–*Carnobacterium*–*Enterococcus* group increased and antilisterial activity increased concomitantly, suggesting that this group was involved in inhibiting *L. innocua* (Monnet et al., 2010a). Elsewhere, the growth of three facultative anaerobic halophilic and alkaliphilic species (*Alkalibacterium kapii*, *M. psychrotolerans* and *Faklamia tabacinensis*) on the surface of Raclette-type cheese early in the ripening phase was shown to be associated with the inhibition of *Listeria* (Roth et al., 2011). In another study consortia were reconstituted from a natural antilisterial consortium from Saint Nectaire cheese surface. The consortium that proved most inhibitory on cheese surface contained the highest proportion of LAB (*L. mesenteroides*, *Lactococcus lactis*) and included infrequent LAB species (*Carnobacterium maltaromicum*, *Vagococcus fluvialis*, *Enterococcus gilvus*) (Callon et al.,

2014) but *M. psychrotolerans* was not the most important species for the inhibition. Two combinations of five to six individual strains of yeast, Gram positive and Gram negative bacteria, one of them including species that are infrequent in cheeses (e.g. *Paenibacillus*) (Table 5), had similar inhibiting properties in a cheese microcosm to those of the smear from which they originated (Imran et al., 2010). With an initial microbial community of six members, changing the microbial balance by omitting one strain at a time had no significant effect on antilisterial activity (Imran et al., 2013).

A simplified bacterial community from a *Listeria*-inhibiting raw milk was still able to inhibit this bacterium in the cores of uncooked pressed cheeses (Millet et al., 2006; Saubusse et al., 2007). In a study by Callon et al. (2011a), *L. monocytogenes* was inhibited by a combination of LAB (*L. casei*, *L. plantarum*, *Lactobacillus farciminis*, *Lactobacillus curvatus*, *Leuconostoc citreum*, *Leuconostoc pseudomesenteroides*, *E. faecalis*, *E. hirae*) with Gram-positive and catalase-positive bacteria (*C. casei*, *C. flavescens*, *A. nicotiana*, *Staphylococcus saprophyticus*, *S. equorum*, *M. caseolyticus*, *Exiguobacterium* spp.), but more simplified consortia were not tested. The hypothesis that *Lactobacillus* plays a part in inhibition in the cores of uncooked pressed cheese is supported by the fact that inhibition of *L. monocytogenes* increased when the *Lactobacillus* population was increased by raising the temperature from 9 °C to 13 °C or reducing relative humidity (97 °C to 93 °C) during ripening (Callon et al., 2011b).

The mechanisms involved in *Listeria* inhibition are not well elucidated. Lactate or acetate concentrations were highest in the most inhibitory consortia of *L. monocytogenes* in the core of uncooked pressed cheeses but no causal effect was demonstrated (Callon et al., 2011a). Bacteriocins (heat stable non-proteinaceous molecules, probably produced by LAB) were detected in the cell-free supernatant of an antilisterial consortium from a red smear cheese (Munster) (Bleicher et al., 2010b). Inhibition associated with *F. tabacinensis*, *M. psychrotolerans* and *A. kapii* may be due to the production of antimicrobial compounds or to competition for nutrients (Roth et al., 2010). *L. monocytogenes* was in a stressed state when it was in contact with an antilisterial consortium from the surfaces of red smear cheeses (Maoz et al., 2003), as also shown by microarray experiments (Hain et al., 2007). Its transcriptome changed, with induction of genes involved in energy supply, stress response and cell wall synthesis.

Complex microbial biofilms on wooden surfaces can protect against pathogen implantation. *Salmonella*, *L. monocytogenes*, and *E. coli* O157: H7 were generally absent and *S. aureus* was rarely detected on the surface of wooden vats in which milk is curdled (vats called *gerle* used for PDO Salers, Didiene et al., 2012) and vats called *tina* used for Ragusano cheese (Lortal et al., 2009). On wooden shelves used for cheese ripening, neither *Listeria* nor *Salmonella* were detected and *S. aureus* and *E. coli* were below 10 cfu/cm² (Mariani et al., 2011).

The absence of pathogens on wood surfaces has also been observed after adding high levels of *Listeria* and *S. aureus* to milk (Didienne et al., 2012) and of *Listeria* to wooden shelves (Mariani et al., 2011). The microbial biofilms in the various cases were quite different in composition. The biofilm on the wooden shelves was dominated by micrococci, corynebacteria, moulds and yeasts (Mariani et al., 2007). Biofilm on the *tina* was dominated by thermophilic lactic acid bacteria, particularly *S. thermophilus* and lactobacilli, and sometimes *Enterococcus* (Licitra et al., 2007). The antilisterial biofilm on the *gerle* vat was dominated by mesophilic lactobacilli, *Lactococcus*, *Leuconostoc* and yeasts. The microbial interactions governing inhibition on wooden surfaces are still unknown. Low pH (4.7 < pH < 5.3) may contribute to the inhibition observed on wooden vats (Didienne et al., 2012; Lortal et al., 2009), but not to that observed on wooden shelves (7 < pH < 8) (Mariani et al., 2011). The *a_w* values (>0.93) of the wooden surface allowed the growth of *L. monocytogenes*. The dense colonization of wooden equipment by yeasts and bacteria may inhibit the pathogens by restricting nutrient supply (Guillier et al., 2008) and/or hindering adhesion (Habimana et al., 2009).

Table 5

Consortia composition and nature of consortia inhibition. Antilisteria consortia from cheeses (N) and simplified (S.). *Consortia are named as in the studies. Inhibitions were generally expressed by comparison of *L. monocytogenes* in the assay (in the presence of the consortium), in the control (in the presence of commercial starter or unique not inhibitory strains).

Cheeses	Soft red smeared									Raclette		Saint-Nectaire		
	N.RI	N.RII	N.KII	N.6	N.11	N.24	S.FC12	S.Elm	S.Alm	S.ECF	S.ECFS	N.TR15	S.TR15	S.AB
Consortia name*														
Reference	Maoz et al. (2003), Mayr et al. (2004)			Bleicher et al. (2010a, 2010b)			Monnet et al. (2010a)	Imran et al. (2010, 2013)		Roth et al. (2010, 2011)		Retureau et al. (2010), Callon et al. (2014)		Callon et al. (2011b)
Composition										X				
<i>Agrococcus casei</i>														
<i>A. arilaitensis/nicotiana/protophormiae</i>	XX	X	XXX	XX	XXX	XXX		X	X			XX	XXX	
<i>Coryne. ammoniagenes/casei/variabilis/flavescens/mobile</i>	XXX	XXX		XX	X	X	(X)			X				X
<i>Brevibacterium linens</i>	XX	XX	X							X				
<i>B. arcticum/paraconglomeratum/tyrofermentans</i>			X	(X)						X			X	
<i>Microbacterium gubbeenense, Microbacterium sp.</i>	X	X								X				
<i>S. equorum/xylosus/saprophyticus/vitulinus</i>			XXX	X	XX				X	X				X
<i>Macrocooccus caseolyticus, Exiguobacterium spp.</i>														X
<i>Microcooccus luteus</i>			X											X
<i>Facklamia tabacinensis</i>										X	XXX			
<i>Leucobacter komagatae, Leucobacter ariodicallis</i>			X										X	
<i>Alkalibacterium kapii</i>										X	XXX			
<i>Paenibacillus sp.</i>									X					
<i>Vagococcus carniphilus/salmoninarum/fluvialis</i>	X	X				X	XXXX					XXX	XXX	
<i>Carnobacterium; Ca. maltaromaticum, Ca. mobile</i>			X					XXXX				XXX	XXX	
<i>Marinilactibacillus psychrotolerans</i>			X	XXX	XX	XX				X	XXX			
<i>Enterococcus sp., E. faecalis, E. hirae, E. gilvus</i>			X					XXXX				XXX	XXX	XXX
<i>Ln. citreum, Ln. pseudomesenteroides</i>														XXX
<i>Lactococcus lactis</i>														XXX
<i>Lb. casei, Lb. plantarum, Lb. farciminis, Lb. curvatus</i>														XXX
<i>Brochothrix thermosphacta</i>												XXX	XXX	
<i>Marinomonas sp.</i>									X	X				
Gram negative bacteria	X	X												
<i>Pseudomonads</i>			X	X					X			X	X	
Enterobacteria; <i>Serratia liquefaciens</i>			X	X				X		X				
<i>Psychrobacter</i>	XXX		XXX											
<i>Halomonas</i>	X	X	X											
<i>Candida natalensis</i>							(X)		XX					
<i>Debaryomyces hansenii</i>									X			XX		
<i>Geotrichum candidum</i>									X	X				
<i>Yarrowia lipolytica</i>							XXX					XX		
Hypothesis on nature of inhibition	nd		nd	Bact.			nd				Nut.	Nut.	Acids	Acids

A., *Arthrobacter*; B., *Brachy bacterium*; Ca., *Carnobacterium*; Coryne., *Corynebacterium*; E., *Enterococcus*; Lb., *Lactobacillus*; Ln., *Leuconostoc*; S., *Staphylococcus*; Bact, bacteriocins; Nutri Compet, nutritional competition; nd, non determined.

5. Potential human health benefits associated with the consumption of traditional cheeses

5.1. Positive impact of the consumption of raw milk cheeses on the enteric microbiota

Bertrand et al. (2007) investigated the effect of raw milk cheese consumption on the enteric microbiota. After amoxicillin-clavulanate was administered to human volunteers for five days, during the 42-day post-antibiotic period levels of amoxicillin-resistant intestinal enterococci fell significantly, from 6.2% to 0.03%, in volunteers consuming experimental raw milk hard-cooked cheeses instead of experimental pasteurized hard-cooked cheeses made from the same milk batches (Bertrand et al., 2007). This positive and perhaps transitory effect may be linked to the raw milk cheese's higher levels of mesophilic lactobacilli, propionibacteria and enterococci. Ingestion of large quantities of LAB (independently of milk products) may indeed have a positive effect on bowel movements during antibiotherapy and on the enteric microbiota in healthy volunteers (Koning et al., 2008; Madden et al., 2005; Plummer et al., 2005).

5.2. Limited milk processing in raw milk cheeses: a potential benefit for health

Health benefits associated with the consumption of traditional cheeses have not yet been investigated. In a first approach, however, it

is interesting to evoke the advances in epidemiological research about health benefits of raw milk consumption.

In cross sectional studies conducted in different countries, reviewed by Braun-Fahrländer and von Mutius (2011), an inverse association was observed between the consumption of unprocessed cow milk (farm milk) and occurrence of asthma and allergy in children/young adults. The association with atopic diseases was stronger when farm milk was raw, and it was independent from the mere fact of living on a dairy farm. Children whose mothers drank raw milk during pregnancy and who drank raw milk during their first year of life had a significantly lower prevalence of asthma, hay fever and atopic sensitization. The significant and independent association was confirmed by a cohort study of 1000 children living in 5 European countries and studied from their mother last trimester of pregnancy to 10 years of age (Pasture-EFRAIM cohort, von Mutius, 2012).

The underlying milk components (microbial, physico-chemical) are not known yet (von Mutius, 2012; Loss et al., 2011). Riedler et al., 2001 suggested that microbial components (lipopolysaccharides, endotoxines) in raw milk may play a role. But the studies from Pasture-EFRAIM cohort (Gehring et al., 2008; Loss et al., 2011) did not support this explanation as microbial content was not related to asthma and atopy. The beneficial milk components may derive from the non-microbial fraction of unprocessed milk. Protective factors against asthma may be associated with whey proteins, with proteins with immunological properties, such as lactoferrin and secretory immunoglobulins (Loss et al., 2011). The effect of milk pasteurization on bovine, ovine

and caprine milk proteins, as practised in cheese making is not known; the results on human milk (Chang et al., 2013; Christen et al., 2013) suggest that it would be dependent on pasteurization method.

Transforming growth factor-beta (TGF- β_1 and TGF- β_2 , cytokines crucial for both gut epithelium growth and immune tolerance mediated by regulatory T cells) was also found to be associated with asthma protection (Lluis et al., 2014). Levels of TGF- β were higher in unpasteurized, unboiled cow's milk than in commercial pasteurized or microfiltered milk (Peroni et al., 2009). Traditional cheeses made from raw milk are therefore more likely to harbour these protective factors if they are not lost in the whey or degraded during cheese-making.

Fat soluble vitamins (A, E) and carotenoids (mainly β -carotene) can be lost in the whey or degraded during cheese making (Lucas et al., 2006b; review in MacDonald et al., 2011). Thus they probably would not convey a special benefit in traditional cheeses made from raw milk (review in Claeys et al., 2013), even though they have been found at higher level in milk from grass-fed cows (Martin et al., 2004; Lucas et al., 2006a).

Changes in intestinal uptake of milk proteins after pasteurization have been shown in experimental studies (Roth-Walter et al., 2008). It is still debated whether the modification of fat globules caused by homogenization during the pasteurization process reduces the immunological effects of milk (Miller, 2013; Perkin, 2007).

5.3. The balance of unsaturated lipids beneficial to health is better in traditional cheeses

Fatty acid profile is of nutritional interest when the ratio is in favour of polyunsaturated fatty acids rather than saturated fatty acids. The positive effects of conjugated linoleic acids (CLAs) on human health (body composition, blood lipid profile, bone formation and immune system) are widely recognized (reviews in Terpstra, 2004; von Mutius, 2012). CLA may further exert their influence through breast milk, and diet supplementation with CLA-rich Alpine butter has been shown to modify fatty acid composition and CLA isomers in breast milk (Bertschi et al., 2005). Traditional cheeses benefit from the CLA naturally present in milk, as CLA content in cheese mainly depends on milk composition (Lucas et al., 2006a). Milk used to make traditional cheeses, whether raw or not, is rich in CLA because of the particular milk production methods involved: nowadays traditional cheeses are mainly made in areas where farming systems are based on summer grazing, especially in mountain. Compared to winter rations with high concentrate levels (65%) or based on corn silage, a summer diet of rich green pasture grass leads to a sharp decrease in saturated fatty acids in the milk and higher levels of polyunsaturated fatty acids, including C18:3n-3 and CLA particularly (Chilliard et al., 2007). The fatty acid profile of the milk is also affected by the maturity and botanical composition of the grass. C18:3n-3 and CLA content in milk decreases after several weeks of grazing on the same patch. Similarly, polyunsaturated fatty acid production rates are higher with mountain pasture grazing than with lowland pasture (review in Martin et al., 2009; Van Wijlen and Colombani, 2010).

6. Conclusion

This review highlights the fact that the benefits of traditional practices for the sensory characteristics of cheese cannot be dissociated from the diversity of their microbiota and microbial activities. The diversity of traditional practices at each of the many steps from milk production to cheese ripening, many of which are specific to one cheese type, results in a wide variety of microbiota and environments that affects microorganism activities. Were it possible to recreate such diversity this would be a major contribution to industrial production, but that seems beyond our reach. Since the beginning of the 20th century, industrial production of pasteurized or thermized milk cheeses has made use of only a small part of the microbial wealth of traditional cheese

diversity to reconstitute microbiota de novo in vat milk and on cheese surfaces. This has involved selecting strains from traditional cheeses, initially for acidification purposes but increasingly to diversify and enrich the flavour characteristics of the ripened cheese.

Nowadays, this selection is officially limited as only species recognized as safe can be used on an industrial scale. In Europe, traditional cheeses are not faced with this limitation as they benefit from their history of use. The safety status of many dairy microorganisms has been reviewed (see International Journal of Food Microbiology, special issue, 2006). The authoritative list of microorganisms "with technological beneficial use" has recently been published (Bourdichon et al., 2012), but it does not reflect the actual microbial diversity of traditional cheeses.

The main concern of traditional producers is to concomitantly preserve microbial diversity and exploit its benefits. Traditional cheese-makers have managed safety on an empirical basis, by day-to-day adjustments. Examples described in this review give evidence that some traditional practices (e.g. wooden equipment) and some raw milk cheese microbial consortia are especially efficient for managing cheese safety.

In the future, applying new molecular methods for describing microbiota, especially meta-omics methods, to milk, cheese and environmental samples, will certainly increase our knowledge of the source, nature and metabolic activities of cheese microbiota during the cheese process. These new methods will also lead to a better understanding of the numerous interactions between different microbial populations in cheeses. This will open up possible new ways to manage the risks and benefits from the farm to the ripened traditional cheese.

No conclusions can be drawn at present about the direct health benefits of consuming traditional cheeses, besides their recognized benefits in terms of consumer's pleasure. Theoretical and indirect arguments favour such health benefits. In particular, it should be firstly checked whether traditional cheese consumption is associated with protection against allergy/atopic diseases as observed for raw milk consumption and whether it can favour immunity protection against foodborne diseases. The relationship between consumption of traditional cheeses and the intestinal microbiota is a new and fruitful avenue of investigation. The enteric microflora homeostasis is the key step between external factors and intestine-mediated disorders (Feehley et al., 2012). Progress in metagenomic analysis should provide new data on the microbiota in cheese and in the intestine which, put together with data on non-microbial cheese compounds, intestinal immunological responses (systemic and local), and the prevalence of disorders and diseases, may allow the chain of connections between traditional cheese consumption and health to be elucidated.

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