



## FoodOmics as a new frontier to reveal microbial community and metabolic processes occurring on table olives fermentation

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### ABSTRACT

Table olives are considered the most widespread fermented food in the Mediterranean area and their consumption is expanding all over the world. This fermented vegetable can be considered as a natural functional food thanks to their high nutritional value and high content of bioactive compounds that contribute to the health and well-being of consumers. The presence of bioactive compounds is strongly influenced by a complex microbial consortium, traditionally exploited through culture-dependent approaches. Recently, the rapid spread of omics technologies has represented an important challenge to better understand the function, the adaptation and the exploitation of microbial diversity in different complex ecosystems, such as table olives. This review provides an overview of the potentiality of omics technologies to in depth investigate the microbial composition and the metabolic processes that drive the table olives fermentation, affecting both sensorial profile and safety properties of the final product. Finally, the review points out the role of omics approaches to raise at higher sophisticated level the investigations on microbial, gene, protein, and metabolite, with huge potential for the integration of table olives composition with functional assessments.

## 1. Introduction

### 1.1. Table olives: a fermented food with a complex microbial consortium

Fermented foods, such as table olives, bread, cheese, and wine have been prepared in rural households and small village communities for thousands of years and are strongly linked to culture and tradition (Botta and Cocolin, 2012). At first, fermented foods were obtained through a spontaneous and unpredictable process, and over the years, many practices, such as back slopping, have been developed to improve the quality and the safety of the final product.

Table olives are considered the most largely diffused fermented vegetables in the Mediterranean area and their consumption is expanding worldwide thanks to the nutritional and functional value of drupes, related to the presence of polyphenols, vitamins, minerals, and fatty acids. The content of the latter compounds changes according to both olive drupe maturity and cultivar (Lavermicocca et al., 2005). Overall, the olive drupe contains a low concentration of sugar

(2.6–6.0%), a high oil content (12–30%) (Botta and Cocolin, 2012) and a polyphenols fraction, which is characterized by the presence of oleuropein, responsible for the intense bitter taste. During the fermentation, this compound is hydrolysed by the activity of the  $\beta$ -glucosidase enzyme of indigenous microorganisms, with the release of glucose and aglycones, which, in turn, are completely degraded by esterase in the no-bitter phenols hydroxytyrosol and elenolic acid (Bianchi, 2003). Hence, the presence of these compounds is strongly influenced by microbial consortium of table olives, which is strongly affected by both cultivar and technological process. Generally, table olives microbiota includes members of lactic acid bacteria (LAB) and yeasts, which are the dominant microbial groups throughout the fermentation, whereas *Enterobacteriaceae*, *Clostridium*, *Pseudomonas*, *Staphylococcus* strains and, occasionally, molds (Bonatsou et al., 2017) may occur at the beginning of the process (Panagou et al., 2003; Abriouel et al., 2011a, 2011b; Randazzo et al., 2012). Among LAB, members of the genera *Lactobacillus*, *Streptococcus*, *Leuconostoc*, and *Pediococcus* and of the new genera recently proposed by Zheng et al. (2020) were the main detected

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(Randazzo et al., 2012; Abriouel et al., 2012), playing a major role during the fermentation process (Abriouel et al., 2011a, 2011b; Corsetti et al., 2012). To large extent, LAB, by fermenting sugars to organic acids, decrease pH of brine and stabilize the final product. When olive drupes are subjected to lye treatment (2.0–3.5% of NaOH) LAB dominate at the end of the fermentation process. On the contrary, in directly brined olives, LAB occur during the whole process, but their dominance is subjected to the low sugars concentration and to the presence of molecules released from olive flesh. In addition, LAB development can be influenced by phenolic compounds releasing from drupe to brine as well as by both sodium chloride concentration and temperature of fermentation (Tassou et al., 2002; Bautista-Gallego et al., 2011a). In fact, when the fermentation is carried out at low temperature (under 18 °C) and in presence of high salt content (over than 8.0%), LAB are overpowered by yeasts (Tassou et al., 2002; Arroyo-López et al., 2008), which determine mild taste and less self-preservation of final products (Panagou et al., 2008). However, when yeasts are present in a balanced proportion with LAB, they contribute to improve flavour and texture of the final product (Arroyo-López et al., 2008). Hence, LAB and yeast population create a microbial consortium, which acts for the success of the fermentation process. The most frequent LAB, and yeast species detected in table olive are summarized in Tables 1 and 2, respectively. Among LAB, *Lactiplantibacillus plantarum*, *Lactiplantibacillus pentosus*, *Lacticaseibacillus casei*, *Levilactobacillus brevis* and *Leuconostoc mesenteroides* are the species most frequently isolated from different cultivars (Sánchez et al., 2001; Randazzo et al., 2004; Panagou et al., 2008), while *Wyckherhamomyces anomalus*, *Candida diddensiae*, *Candida boidinii*, *Debaromyces hansenii* and *Pichia membranifaciens* are the main yeast species (Campus et al., 2018).

During the last twenty years, food microbiologists have introduced considerable changes in the study of table olives microbial ecosystem, traditionally relied on cultivation, isolation and phenotypic and (or) genotypic characterization of the microbial isolates. In particular, the advent of the DNA-based approaches (such as single-strand conformation polymorphism, terminal-restriction fragment length polymorphism, denaturing gradient gel electrophoresis, temperature gradient gel electrophoresis, etc.) (Nocker et al., 2007), has enabled a clear picture of the microbiota of table olives, revealing microbial taxa previously overlooked. Thus, the application of culture-independent techniques has considerably changed the way to study food microbial ecology, leading to consider microbial populations as a consortium (Cocolin and Ercolini, 2015). Given the great importance of the microbiota in determining the quality of table olives, considerable efforts are being made to identify the microbial species and their dynamics deepening the composition and functionality of table olives microbiota, through the application of omics approach mainly consisting in high-throughput methods and sophisticated bioinformatics tools. The term omics encompasses a set of approaches, which include metagenetics, metagenomics, metatranscriptomics, metaproteomics and metabolomics. The omics techniques can be considered the most powerful tool to study biological systems in terms of composition, activity, and function.

The present review aims at illustrating the potentiality of omics approaches as a new frontier to deepen the knowledge about microorganisms, enzymes, and metabolites involved in table olives fermentation and to discover new biomarkers of olives fermentation.

### 1.2. Why do we need biomarkers for table olives fermentation?

Table olives fermentation involves the transformation of bitter inedible olives into an edible foodstuff. Numerous table olive processing methods are known, the choice of which mainly depends on olive variety, degree of ripeness, and on available process technology. The main fermentation processes are reported in Fig. 1. The fermentation of table olives is hard to control because the raw material cannot be thermally treated and abnormal phenomena could occur (Heperkan, 2013; Iorizzo

**Table 1**

Lactic acid bacteria species detected in fermented table olives of different cultivars.

Species detected	Table olives cultivar	Country	References
<i>Lactiplantibacillus plantarum</i>	Aloreña	Spain	Abriouel et al. (2011a), 2011b, Benítez-Cabello et al. (2019a), Bautista-Gallego et al. (2013).
	Arbequina	Spain	Hurtado et al. (2008), 2009, 2010.
	Bella di Cerignola	Italy	Bevilacqua et al. (2010), De Bellis et al. (2010).
	Conservolea	Greece	Tassou et al. (2002), Bleve et al. (2015), Argyri et al. (2013), Doulgeraki et al. (2013).
	Edincik black olives	Turkey	Borcakli et al. (1993).
	Gemlik black olives	Turkey	Borcakli et al. (1993).
	Halkidiki	Greece	Argyri et al. (2013), Doulgeraki et al. (2013).
	Kalamata	Greece	Bleve et al. (2015), Doulgeraki et al. (2013).
	Galega	Portugal	van den Berg et al. (1993), Oliveira et al. (2004).
	Giarraffa	Italy	Randazzo et al. (2012).
	Gordal	Spain	Benítez-Cabello et al. (2019a), Bautista-Gallego et al. (2013).
	Grossa di Spagna	Italy	Randazzo et al. (2012).
	Jijelian black olives	Algeria	Idoui et al. (2009).
	Leccino	Italy	Ercolini et al. (2006).
	Manzanilla	Spain	Benítez-Cabello et al. (2019a), Bautista-Gallego et al. (2013).
	Moroccan table olives	Morocco	Abouloifa et al. (2019).
	<i>Lactiplantibacillus pentosus</i>	Nocellara del Belice	Italy
Nocellara Etna		Italy	Pino et al. (2018), 2019, Botta et al. (2014), Randazzo et al. (2018).
Oblica table olives		Croatia	Kulišić et al. (2004).
Picholine		Morocco	Asehraou et al. (2002), Ghabbour et al. (2011).
Aloreña		Spain	(2012), Benítez-Cabello et al. (2019a), Bautista-Gallego et al. (2013), López-López et al. (2018)
Arbequina		Spain	Hurtado et al. (2008), 2009, 2010.
Bella di Cerignola		Italy	De Bellis et al. (2010), Campaniello et al. (2005).
Conservolea		Greece	Tassou et al. (2002), Panagou et al. (2008), Argyri et al. (2013), Doulgeraki et al. (2013).
Gordal		Spain	Benítez-Cabello et al. (2015), 2019a, Bautista-Gallego et al. (2013), Ghabbour et al., 2011, Domínguez-Manzano et al. (2012).
Halkidiki		Greece	Argyri et al. (2013), Doulgeraki et al. (2013).
Kalamata	Greece	Doulgeraki et al. (2013).	
Manzanilla	Spain	Benítez-Cabello et al. (2019a), Bautista-Gallego et al. (2013), López-López et al. (2018), Arroyo-López et al. (2012).	
Moroccan green olives	Morocco	Abouloifa et al. (2019).	

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Table 1 (continued)

Species detected	Table olives cultivar	Country	References
<i>Lactocaseibacillus paracasei</i>	Nocellara del Belice	Italy	Guantario et al. (2018), Aponte et al. (2012).
	Nocellara Etnea	Italy	Pino et al. (2018), 2019, Botta et al. (2014).
	Picholine	Morocco	Ghabbour et al. (2011).
	Aloreña	Spain	Bautista-Gallego et al. (2013).
	Arbequina	Spain	Hurtado et al. (2008), 2009.
	Conservolea	Greece	Doulgeraki et al. (2013).
	Gordal	Spain	Bautista-Gallego et al. (2013).
	Halkidiki	Greece	Doulgeraki et al. (2013).
	Kalamata	Greece	Doulgeraki et al. (2013).
	<i>Lactocaseibacillus casei</i>	Bella di Cerignola	Italy
Jijelian black olives		Algeria	Idoui et al. (2009).
Nocellara Etnea		Italy	Pino et al. (2018), Asehraou et al. (2002), Randazzo et al. (2018).
Sigoise		Algeria	Mourad and Nour-Eddine (2006).
<i>Lactocaseibacillus rhamnosus</i>	Bella di Cerignola	Italy	De Bellis et al. (2010).
	Nocellara Etnea	Italy	Kulišić et al. (2004).
	Sigoise	Algeria	Mourad and Nour-Eddine (2006).
	Conservolea	Greece	Tassou et al. (2002).
<i>Levilactobacillus brevis</i>	Gemlik	Turkey	Kumral et al. (2009).
	Jijelian	Algeria	Idoui et al. (2009).
	Moroccan green olives	Morocco	Abouloifa et al. (2019).
<i>Lactococcus lactis</i>	Picholine	Morocco	Ghabbour et al. (2011).
	Bella di Cerignola	Italy	De Bellis et al. (2010).
	Sigoise	Algeria	Mourad and Nour-Eddine (2006).
<i>Leuconostoc mesenteroides</i>	Conservolea	Greece and Italy	Tassou et al. (2002), Bleve et al. (2015), Argyri et al. (2013), Doulgeraki et al. (2013).
	Halkidiki	Greece	Argyri et al. (2013), Doulgeraki et al. (2013).
	Kalamata	Greece and Italy	Bleve et al. (2015), Doulgeraki et al. (2013).
<i>Enterococcus faecium</i>	Nocellara del Belice	Italy	Guantario et al. (2018).
	Nocellara Etnea	Italy	Botta et al. (2014).
	Cypriot	Cyprus	Anagnostopoulos et al. (2018).
	Sigoise	Algeria	Mourad and Nour-Eddine (2006).
	natural green olives		

et al., 2016; Bonatsou et al., 2017). For this reason, salt is added in order to reduce the water activity, prevent the growth of spoilage microorganisms, and improve taste and textures of the final product (Bautista-Gallego et al., 2013). Recently, according to World Health Organization (WHO, 2012) which recommends to reduce the daily salt intake (5 g salt per day), several authors proposed the partial substitution of NaCl with calcium and potassium salts, such as KCl, CaCl<sub>2</sub>, and ZnCl<sub>2</sub> (Bautista-Gallego et al., 2010, 2011b; 2013; Ambra et al., 2017; Zinno et al., 2017; Mateus et al., 2016). Nevertheless, the replacement affected the microbiota of table olives (Mateus et al., 2016) modifying the sensorial quality of the final product (Zinno et al., 2017). Recently, Pino and co-workers (2018, 2019) demonstrated that the reduction of NaCl content, without the addition of other salts, resulted in a successful fermentation of Nocellara Etnea table olives, suggesting the possibility to formulate low salt table olives.

The use of starter cultures is largely applied to Spanish-style fermentation, where their addition is still considered a useful

Table 2

Yeasts species detected in fermented table olives of different cultivars.

Species detected	Table olives cultivar	Country	References
<i>Candida boidinii</i>	Aloreña	Spain	Arroyo-López et al. (2006).
	Arbequina	Spain	Hurtado et al. (2008).
	Bosana	Italy	Porru et al. (2018).
	Galega	Portugal	Pereira et al. (2008).
	Hojiblanca	Spain	Arroyo-López et al. (2006).
	Kalamata	Greece	Bonatsou et al. (2018).
	Manzanilla	Portugal	Alves et al. (2011).
	Negrinha de Freixo	Portugal	Pereira et al. (2015).
	Nocellara Etnea	Italy	Pino et al. (2019).
	Nocellara Messinese	Italy	Sidari et al. (2019).
<i>Candida diddensiae</i>	Aloreña	Spain	Arroyo-López et al. (2006), Bautista-Gallego et al. (2011a).
	Arbequina	Spain	Hurtado et al. (2008), Romo-Sánchez et al. (2010).
	Cornicabra	Spain	Romo-Sánchez et al. (2010).
	Gordal	Spain	Bautista-Gallego et al. (2011a).
	Hojiblanca	Spain	Porru et al. (2018).
	Leccino	Greece	Doulgeraki et al. (2013).
	Manzanilla	Portugal	Bautista-Gallego et al. (2011a), Alves et al. (2011).
	Nocellara Etnea	Italy	Pino et al. (2019).
	Aloreña	Spain	Bautista-Gallego et al. (2011a).
	Ascolana	Spain	Ruiz-Moyano et al. (2019).
<i>Wickerhamomyces anomalus</i>	Azeitera	Spain	Ruiz-Moyano et al. (2019).
	Bella di Cerignola	Italy	Bevilacqua et al. (2013).
	Bosana	Italy	Porru et al. (2018).
	Gordal	Spain	Bautista-Gallego et al. (2011a), Ruiz-Moyano et al. (2019).
	Leccino	Italy	Ciafardini et al. (2019).
	Nocellara Etnea	Italy	Pino et al. (2019).
	Nocellara Messinese	Italy	Sidari et al. (2019).
	Aloreña	Spain	Arroyo-López et al. (2006).
	Arbequina	Spain	Romo-Sánchez et al. (2010).
	Ascolana	Spain	Ruiz-Moyano et al. (2019).
<i>Saccharomyces cerevisiae</i>	Azeitera	Spain	Ruiz-Moyano et al. (2019).
	Bosana	Italy	Porru et al. (2018).
	Conservolea	Italy	Bleve et al. (2015).
	Cornicabra	Spain	Romo-Sánchez et al. (2010).
	Gemlik	Turkey	Mujdeci et al. (2018).
	Gordal	Spain	Ruiz-Moyano et al. (2019).
	Kalamata	Greece	Bonatsou et al. (2018), Bleve et al. (2015).
	Manzanilla	Portugal	Alves et al. (2011), Hernández et al. (2007).
	Negrinha de Freixo	Portugal	Pereira et al. (2015).
	Nocellara Messinese	Italy	Sidari et al. (2019).
<i>Debaryomyces hansenii</i>	Manzanilla	Spain	Hernández et al. (2007).
	Thassos	Greece	Panagou et al. (2002).
	Arbequina	Spain	Hurtado et al. (2008).
<i>Pichia kluyveri</i>	Nocellara Etnea	Italy	Pino et al. (2018).
	Manzanilla	Spain	Arroyo-López et al. (2012).
	Arbequina	Spain	Hurtado et al. (2008).
<i>Pichia galeiformis</i>	Ascolana	Spain	Ruiz-Moyano et al. (2019).
	Azeitera	Spain	Ruiz-Moyano et al. (2019).

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Table 2 (continued)

Species detected	Table olives cultivar	Country	References
	Conservolea	Greece and Italy	Nisiotou et al. (2010), Bleve et al. (2015).
	Gordal	Spain	Benítez-Cabello et al. (2015).
	Negrinha de Freixo	Portugal	Pereira et al. (2015).

biotechnological strategy in order to prevent the development of pathogenic and/or spoilage bacteria, accelerating the brine acidification (Romeo, 2012). The use of starter cultures has been the subject of many studies and nowadays the interest in multifunctional starters, with adequate technological properties, has strongly increased (Ciardini and Zullo, 2019). Many studies have recently demonstrated the synergic effects between LAB and yeast starters, with a significant improvement of sensory quality of the final products (Benítez-Cabello et al., 2019a). However, further efforts are needed to appropriately select and design the starter inoculum in a cultivar dependent manner, including functional and sensorial profiles, and to elucidate the role of different table olives microbial populations and their relationship with specific metabolites.

The exploitation of a specific microbiota and how its metabolism impacts on sensorial traits of table olives could help to identify biomarkers linked to certain table olives flavours, texture, and bioactive metabolites with potential effects on human health.

Another reason to identify biomarkers is related to the development of a technology able to guarantee the reproducibility of table olives fermentation, achieving a final product with unique characteristics related to cultivar, process and geographical origin.

## 2. Omics-based approach for molecular profiling of table olives microbial consortium

It has been already established that in food ecosystems, omics technologies have revolutionized our understanding of complex

microbial population composition and functions, underlying what the microbial community is doing in terms of gene expression, protein production, and metabolism (Turnbaugh and Gordon, 2008). As reported in Table 3, only metagenetics, metabolomics and proteomics approaches have been applied to table olives ecosystem and, overall, the number of the cultivars that have been studied is still limited. The majority (64%) of the studies reported in Table 3 was focused on the characterization of the metabolite produced during the fermentation process; others (28%) revealed table olives microbial composition; only few available studies (8%) have explored the proteomic profile of indigenous LAB. Zooming in each omics approach, the cultivars of table olives investigated, expressed as percentage, are shown in Fig. 2. Manzanilla and Hojiblanca were the main cultivars studied through metabolomics; Aloreña de Malaga, Manzanilla and Nocellara Etna cultivars through metagenetics and only two studies on Aloreña de Malaga applied a proteomic approach (Fig. 2).

### 2.1. Metagenetics

The metagenetics approach is based on the analysis of a single gene such as the 16 S rRNA encoding gene, which is the most powerful marker for the identification of phylogenetic studies and bacterial species identification. The development and the application of metagenetics approach, by capturing a broad range of bacterial population, have deepened the knowledge about the composition and the dynamics of food ecosystems revealing greater microbial richness than expected.

In the field of table olives fermentation, the metagenetics approach has been used to gain information on communities less explored by classical cultural methods revealing the complexity of the LAB and yeast microbial consortium (Ferrocino and Cocolin, 2017). Evaluating the literature, we can assert that overall metagenetics approach has been more in depth exploited for studying bacterial community than yeast-/fungal ones. Presumably, this could be due to an overall lower interest in the yeast composition by the researchers or to (i) the lack of an inclusive, reliable public reference data set; (ii) the lack of means to refer to fungal species, for which no Latin name is available in a standardized stable way and (iii) to a non-standard workflow associated with yeast

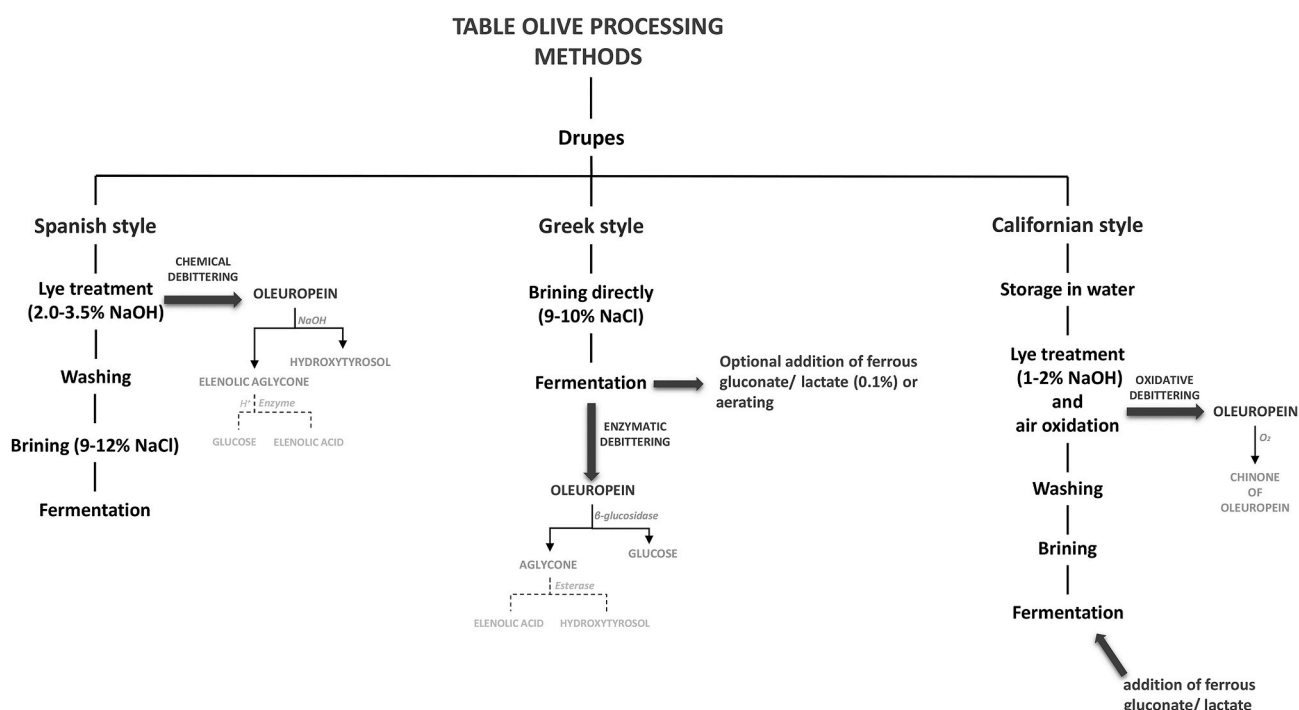


Fig. 1. Table olives fermentation processes.



Table 3

Omics approaches and methodology to reveal genera, volatile organic compounds (VOCs) and proteins on table olives of different cultivars.

Omics	Methodology	Olive Variety	Techniques	Genera/Compounds	References
Metagenetics	OTUs, QUIIME and SILVA 108 database, $\alpha$ -diversity estimator, ANOVA Tukey-Kramer <i>post hoc</i> test (STATISTICA 7.1 software).	Aloreña de Malaga	Illumina	<i>Lactobacillus</i> <sup>a</sup> , <i>Pediococcus</i> , <i>Marinilactibacillus</i> , <i>Celerinatantimonas</i> , <i>Salinicola</i> , <i>Marinobacter</i> , <i>Pseudomonas</i> , and <i>Vibrio</i>	Rodríguez-Gómez et al. (2017).
	OTUs, QUIIME and SILVA 108 database, $\alpha$ and $\beta$ -diversity indexes, <i>t</i> -test (999 Monte Carlo permutations) Krona hierarchical data browser, PCoA (KiNG graphic program).	Aloreña	Pyrosequencing	<i>Celerinatantimonas</i> , <i>Pseudomonas</i> , <i>Propionibacterium</i> , <i>Salinibacter</i> , <i>Staphylococcus</i> , <i>Rhodovibrio</i> , <i>Streptococcus</i> , and <i>Alicyclobacillus</i>	Medina et al. (2016).
	OTUs, QUIIME, USEARCH, $\alpha$ and $\beta$ -diversity indexes, rarefaction analysis, nonparametric two sample <i>t</i> -test with Monte Carlo permutations, PCoA (R, KiNG graphics program)	Aloreña de Malaga	Pyrosequencing	<i>Penicillium</i> , <i>Cladosporium</i> , <i>Malassezia</i> , <i>Candida</i> <i>Zygorulasporea</i> , <i>Pichia</i> , <i>Debaryomyces</i> , <i>Saccharomyces</i> , and <i>Citeromyces</i>	Arroyo-López et al. (2016).
	OTUs, QUIIME, USEARCH, $\alpha$ and $\beta$ -diversity indexes and RDP (RDP v10.28, STATISTICA 7.0 software)	Bella di Cerignola	FLX pyrosequencing	<i>Hafnia</i> , <i>Methylobacterium</i> , <i>Clostridium</i> , <i>Propionibacterium</i> , <i>Lactiplantibacillus</i> , <i>Loigolactobacillus</i> , <i>Levilactobacillus</i> , <i>Lacticaseibacillus</i> , <i>Secundilactobacillus</i> , <i>Paucilactobacillus</i> , <i>Lactococcus</i>	De Angelis et al. (2015).
	OTUs, RDP, UNITE Fungal Classification database, $\alpha$ -diversity estimator, (ad-hoc pipeline RStatistics and STATISTICA 7.0 software).	Manzanilla and Hojiblanca	Miseq Illumina	<i>Pichia</i> , <i>Kregervanrija</i> , <i>Acetobacter</i> , <i>Lactobacillus</i> <sup>a</sup> , <i>Oenococcus</i> , <i>Enterococcus</i> , <i>Lactococcus</i> , <i>Weissella</i> , <i>Pseudoalteromonas</i> , <i>Alteromonas</i> , <i>Marinomonas</i> ,	Medina et al. (2018).
	OTUs, ad-hoc pipeline RStatistics, RDP, UNITE Fungal Classification database, $\alpha$ -diversity estimator, PCA (XLSTAT v.2016 software)	Manzanilla and Gordal	Miseq Illumina	<i>Suttonella</i> , <i>Dekkera</i> , <i>Ruminococcus</i> , <i>Pichia</i> , <i>Candida</i> ,	De Castro et al. (2018).
	OTUs, QUIIME, USEARCH, $\alpha$ and $\beta$ -diversity indexes (STATISTICA 7.1 software).	Nocellara Etna	Pyrosequencing	<i>Marinilactibacillus</i> , <i>Halomonas</i> , <i>Chromohalobacter</i> , <i>Lactiplantibacillus</i>	Cocolin et al. (2013).
OTUs, QUIIME, UPGMA, $\alpha$ and $\beta$ -diversity indexes (PMG software and	Nocellara Etna	Ion Torrent PGM sequencing	<i>Secundilactobacillus</i> , <i>Ligilactobacillus</i> , <i>Pediococcus</i>	Randazzo et al. (2017)	
Metabolomics	Compounds identification.	Black-ripe. Table olives	GC-MS	Aldehydes, alcohols, esters, ketones, phenols, terpenes, norisoprenoids, pyridines, $\beta$ -damascenone, nonanal, (E)-dec-2-enal, 3-methylbutanal, ethyl benzoate, octanal, 2-methoxyphenols, 2-methylbutanal and 2-methoxy-4-methylphenol.	Sansone-Land et al. (2014).
	ANOVA (Duncan <i>post-hoc</i> test); PCA (STATISTICA 7.0 software).	Conservolea and Kalamata	HS-SPME-GC/MS	Ethanol, citric acid, phenol, aldehydes, ketones, esters, alcohols, terpenes, guaiacol, styrene.	Bleve et al. (2015).
	ANOVA (Duncan <i>post-hoc</i> test); PCA (STATISTICA 7.0 software).	Cellina di Nardò and Leccino	HS-SPME-GC/MS	Aldehydes, alcohols (2-methyl-1-propanol, 3-methyl-1-butanol), styrene, o-cymene, acetate esters	Bleve et al. (2014).
	ANOVA (Duncan <i>post-hoc</i> test); PCA (XLSTAT PRO 5.7 software).	Giarraffa and Grossa di Spagna	SPME-GC-MS	Ethanol, isoamylalcohol, phenylethyl alcohol, esters, phenols, ethyl-acetate, ethylbutanoate, propionic acid, aldehydes, 3-octanal, 3-octanone.	Randazzo et al. (2014).
	ANOVA (Tukey HSD <i>post-hoc</i> test); PCA, biplot (STATISTICA 7.0 software).	Kalamata, Picual and Manzanilla	HPLC and HS-SPME-GC/MS	Esters, alcohols, acids, hydrocarbons, terpenes and volatile phenol.	Tufariello et al. (2019).
	ANOVA (Fisher's LSD <i>post-hoc</i> test), PLS analysis, biplot and bicluster graph (XLSTAT v2018 and R package Multiplot v2018 software).	Manzanilla	GC-MS	Acetic acid, geraniol, 2-dodenal, 1,4-dimethoxybenzene, 4,8-dimethyl-1,3,7-nonatriene, ketones, alcohols, aldehydes, volatile phenols.	Benítez-Cabello et al. (2019b)
	Variation array; tertiary graph; biplots; codadendrogram; Cluster and PCA (CoDaPack v.2.01.14 and XLSTAT, 2014 software).	Manzanilla and Hojiblanca	GC-MS	Propionic acid, 1-propanol, isopropanol, 2-heptenal, propyl acetate, (E)-2-decenal, methyl hexanoate, 1-heptanol, isobutanol, 1-butanol.	Garrido-Fernández et al. (2017)
	ANOVA (test of Student-Newman-Keuls; Duncan <i>post hoc</i> test) Levene test; Shapiro-Wilk test; Welch test and Games-Howell <i>post hoc</i> test); HCA; PCA; PLS regression model (Microsoft Excel, 2010 and Statistica 7.0 software; XLSTAT v.2016 and SIMCA 14.1 software; Microsoft Excel and SPSS v.23.0 software).	Manzanilla, Gordal and Hojiblanca	SPME-GC-MS	Esters, alcohols, terpenes, aldehydes, phenols, hydrocarbons, sulphur compounds, ketones and lactone, carbonyl compounds, (E)-2-decenal and (E,E)-2,4-decadienol.	Cortés-Delgado et al. (2016), López-López et al. (2018), Sánchez et al. (2018).
	Compounds identification	Moroccan	GC-MS	Guaiacol, 3-methylthiopropionaldehyde, $\alpha$ -farnesene, <i>trans</i> -nerolidol, nerol acetate, limonene, $\alpha$ - $\beta$ - $\gamma$ -terpineol, linalool and $\beta$ -myrcene	Montaño et al. (1990)
	Compounds identification		GC-MS		

(continued on next page)

Table 3 (continued)

Omics	Methodology	Olive Variety	Techniques	Genera/Compounds	References
		Nocellara del Belice		Ethanol, acetic acid, 2-butanol, 1-propanol, propyl-acetate, ethyl propanoate, ethyl acetate, propionic acid, <i>cis</i> -3-hexen1-ol, 2-butanone, 1-hexanol, isopentanol, 3-pentanol, 2-pentanol, ethyl propanoate, 2-butanone.	Sabatini and Marsilio (2008).
	GLM based on ANOVA (Tukey's <i>post hoc</i> test); HMCA (STATISTICA v.10 and XLSTAT 7.5.2 software)	Nocellara del Belice	HS-SPME-GC-MS	Homoguaiacol, 2-butanol, 4-ethylphenol, phenylethyl alcohol.	Martorana et al. (2017)
	ANOVA (Tukey's <i>post hoc</i> test), PCA, Permutation analysis (XLSTAT PRO 5.7, MATLAB, PermutMatrix software and STATISTICA 7.0; MATLAB and XLSTAT V.2016.1). PCA (SPSS 11.0)	Nocellara Etnea	SPME-GC-MS	Isoamyl and phenyl-ethyl alcohol, esters, ethyl acetate, butanoic-acid-2-methylester, nonanal and cresol.	Pino et al. (2018), 2019.
		Tunisian Meski, Picholine and Manzanilla	GC-MS	Aldehydes, ketones, alcohols and esters.	Dabbou et al. (2012).
Proteomics	PacBio RS II technology; PROKKA pipeline; BlastKOALA (KEGG tool)	Aloreña de Malaga	WGS and <i>in silico</i> analysis	Hexosyltransferases, pentosyltransferases, phosphotransferases, glycosylases (glycosyl hydrolases), isomerases.	Abriouel et al. (2017).
	PEAKS 8.0; FASTA format	Aloreña de Malaga	2-DE-gel electrophoresis and nanoLC-MS/MS	Phosphoglycerate mutase and glucosamine-6-phosphate deaminase, small heat shock protein, transcription elongation factor GreA.	Montoro et al. (2018).

<sup>a</sup> According to the taxonomic classification reported before the new description of the 23 genera, proposed by Zheng et al. (2020).

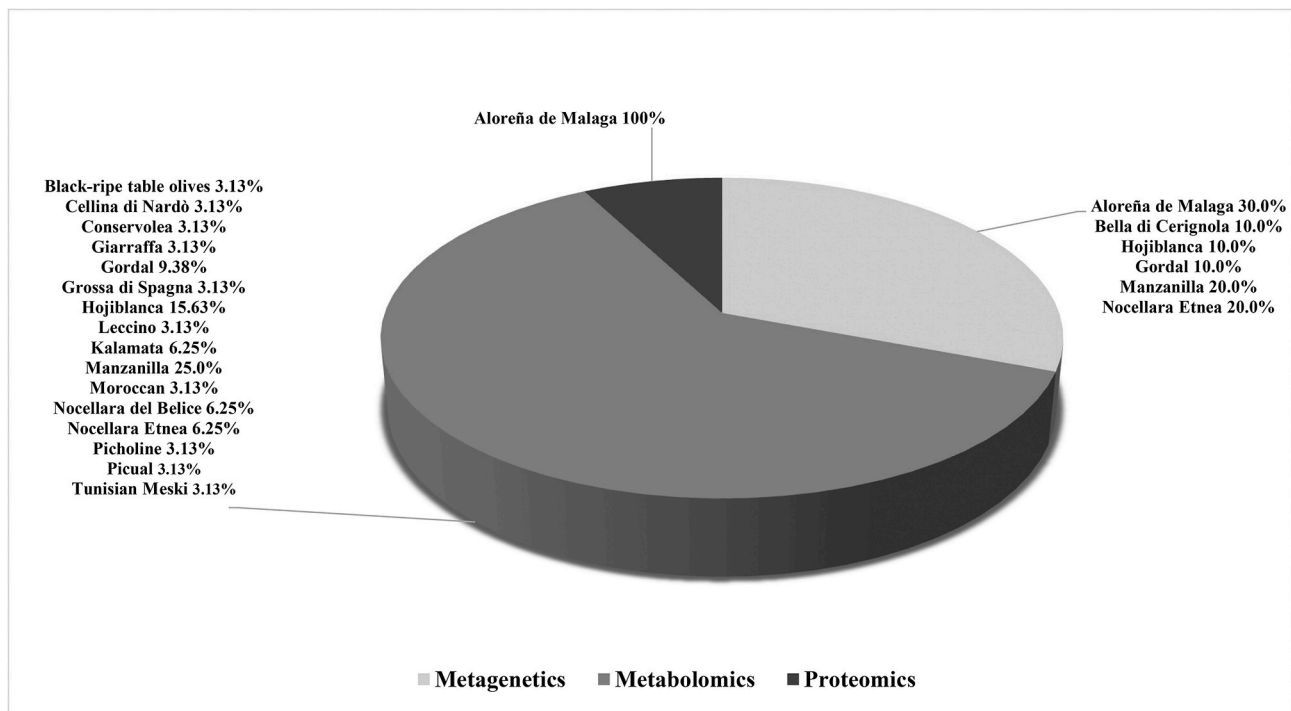


Fig. 2. Pie chart of omics techniques applied to table olives ecosystem.

metagenetic analysis.

Although the ITS barcoding became a reliable taxonomical tool for fungal species identification, within the frame of a curated copy of the public fungal ITS sequences (Köljalg et al., 2013), the intrinsic multicopy nature of ITS regions may lead to erroneous attribution of the reads to the right species, especially in complex microbial mixtures, like table olives, if intra-genomic variability occurs within single individuals (Dakal et al., 2016; Colabella et al., 2018).

Table 3 summarizes the main genera and species detected through the metagenetics approach. Cocolin and co-workers (2013) applied for the first time a high-throughput sequencing approach to determine the bacterial ecology and dynamics occurring during the fermentation of

Nocellara Etnea table olives, subjected or not to NaOH treatment. The authors in-depth studied the microbiota composition of brine and olive samples confirming the selective effect of NaOH treatment on bacterial ecology. In particular, the halophilic population (such as *Marinilactibacillus*, *Halomonas* and *Chromohalobacter*) and *Enterobacteria* resulted dominant on olive surface of untreated and treated samples, respectively. Similarly, Medina and co-workers (2018), evaluating the microbial diversity of Spanish style olives darkened by oxidation, revealed, through MiSeq sequencing of the 16 S rRNA, the presence of *Pseudoalteromonas*, *Alteromonas*, *Marinomonas* and *Oenococcus* genera. In addition, investigating fungi population through ITS region sequencing, *Pichia membranifaciens*, *Magnusiomyces capitatus*, *Kregervanrija fluxum*,

*Dekkera anomala*, and *Dipodascaceae* spp. Were detected for the first time in Spanish-style table olives. De Castro and co-workers (2018), focusing on spoilage bacterial and fungal biota responsible for the unpleasant cheesy and zapatera odors, highlighted the presence of unexpected bacterial taxa, such as *Cardiobacteriaceae* and *Ruminococcus* families. The fungal community of raw material, brines and drupes, during the fermentation of natural Aloreña de Málaga table olives, was studied by Arroyo-López and co-workers (2016). Through high-throughput bar-coded pyrosequencing analysis of ITS1-5.8 S-ITS2 region, the authors highlighted the existence of a complex fungal consortium which included phytopathogenic, saprofitic, spoilage and fermentative genera. In particular, *Penicillium*, *Cladosporium*, *Malassezia*, and *Candida* were identified as the main important genera in raw material. After 4 months of fermentation, *Zygorulaspota* and *Pichia* were found predominant in brine whereas *Candida*, *Penicillium*, *Debaryomyces* and *Saccharomyces* were mainly detected in drupes. The fungal genera *Penicillium*, *Pichia*, and *Zygorulaspota* were considered as the core fungal population. The phylogenetic analysis of the ITS sequences allowed to assign the operational taxonomic units (OTUs) to *Pichia manshurica*, *Candida parapsilosis*/C. *tropicalis*, *Candida diddensiae*, and *Citeromyces nyonensis* clades (Arroyo-López et al., 2016).

For table olives fermentation, it is already established that the use of selected starter cultures comes out to be promising in order to standardize the process, to reduce the growth/survival of pathogenic and/or spoilage microorganisms, to accelerate the hydrolysis of bitter compounds, to improve the aroma and stabilize the final product. By adopting an “omics” approach, these effects have been pointed out on Greek-style Bella di Cerignola (De Angelis et al., 2015) and Sicilian-style Nocellara Etnea (Randazzo et al., 2017) table olives. The bacterial tag-encoded FLX amplicon pyrosequencing showed the dominance of *Hafnia alvei* and *Methylobacterium* in un-inoculated Bella di Cerignola samples at the first day of fermentation. Differently, after 90 days of fermentation the vast majority of the OTUs were identified as *Lactiplantibacillus plantarum* and *Lactiplantibacillus pentosus*, followed by *Loigolactobacillus coryniformis*, *Levilactobacillus brevis*, *Lacticaseibacillus paracasei*, *Secundilactobacillus paracollinoides*, *Paucilactobacillus vaccinoatercus* and *Lactococcus lactis* in all samples. On the contrary, *Proteobacteria*, including *Enterobacteriaceae*, *Lactococcus lactis*, *Propionibacterium acidipropionici* and *Clostridium*, showed low abundance (De Angelis et al., 2015). Similar results were obtained on Nocellara Etnea brine samples through Ion Torrent PGM Sequencing of V3 region of the 16 S rRNA gene (Randazzo et al., 2017). The dominance of starter was highlighted at the initial stage of fermentation in all brine samples. At the end of the process (60 and 120 days of fermentation), a turnover on bacterial ecology and an increase of biodiversity was observed in all samples, with the detection of *S. paracollinoides*, *Pediococcus parvulus* and *Ligilactobacillus acidipiscis*, not found by culturing. Despite the central role of *Lactobacillaceae* in table olives fermentation, their low abundance has been reported in directly brined Aloreña de Málaga olives by Medina and co-workers (2016), who investigated the bacterial biota composition and dynamic during fermentation through high-throughput bar-coded pyrosequencing analysis of the V2 and V3 regions of the 16 S rRNA gene. The authors revealed a high abundance of members of *Celerinatantimonas*, an undesirable genus, of spoilage microorganisms (*Pseudomonas* and *Propionibacterium*) and of halophilic bacteria (*Modestobacter*, *Rhodovibrio*, *Salinibacter*) during the whole fermentation, confirming the low presence of *Lactobacillaceae* and *Enterobacteriaceae*. These results were partially denied by a subsequent study conducted on heat-shocked Aloreña de Málaga table olives (Rodríguez-Gómez et al., 2017). In this case, the metagenomic analysis conducted at the end of the fermentation revealed the dominance of *Lactobacillus*, *Pediococcus*, and *Celerinatantimonas* genera.

The metagenetic studies above reported allowed to gain a comprehensive view of table olives microbiota at different taxonomic levels, revealing the presence of unexpected bacteria involved in table olives fermentation. However, the technique is not able to determine the

activity of the genetic elements sequenced, providing a static image of genes of interest. For this reason, a metagenomics analysis, studying the entire metagenome of a sample, could deepen knowledge and strengthen the available information about table olives microbiota and its function. Indeed, whole-metagenome sequencing could help us to understand the taxonomic and functional composition of the table olives microbial communities. This approach could predict which strains, from a complex population, are involved in the flavour formation and the conditions affecting their metabolic pathway, shedding light on the complementary interactions at the species or strain level. One limitation, by targeting DNA, is the overestimation of the active portion of the microbiota because the technique gives information on live and dead cells. Hence, the RNA-based methods provide a dynamic microbial snapshots by exploring the activation of pathways and regulatory systems along with detection of the expression of the main genes involved in the ecosystem (De Filippis et al., 2017).

### 2.1.1. Whole genome sequence of table olives isolates

Whole genome sequencing (WGS) has become an important tool to investigate the information contained in the genome sequence of bacteria and yeasts. Nowadays, sequencing cost and high-throughput data generation are no longer limiting factors and for these reasons the WGS is increasingly used to address various questions in microbiology (He, 2015). Indeed, as reported in Table 4, the complete genome sequence of few bacteria strains isolated from brine and table olives surface is now available. Overall, among bacteria the vast majority of the sequenced strains are ascribed to the *Lactiplantibacillus pentosus* showing total genome sizes ranging from 3,591,251 to 4,033,890 bp. Similar G + C content, which varied from 45.00% to 46.32%, was achieved. In addition, several plasmids per strain, ranging from 13 to 5, were found (Table 4). Based on our knowledge, no information about the genome sequence of yeasts isolated from table olives is now available.

### 2.2. Transcriptomics and metatranscriptomics

Transcriptomics is a cost-effective technology enabling the quantification of several thousands of defined mRNA species in a miniaturized presentation (Hegde et al., 2003). While transcriptomics reveals valuable information on bacterial activities, the metatranscriptomic approach, by using high-throughput sequencing technologies, allows to understand the active microbes and their gene expression under different environmental niches (Sirén et al., 2019). The first studies, adopting a metatranscriptomic approach, were focused on freshwater and marine microbial communities (Poretsky et al., 2005; Gilbert et al., 2008; Frias-Lopez et al., 2008) demonstrating that, similarly to DNA, the microbial RNA could represent a valuable target to profile community structure, function and diversity. Metatranscriptomics approach, focusing on sequencing the entire complementary DNA (cDNA) converted from messenger RNA (mRNA), has been applied to fermented food (Jung et al., 2013; De Filippis et al., 2016, 2017; Chen et al., 2017) to explore the complex interaction network among microbial communities. Studies conducted on cheeses, sourdough and wine, highlighted the usefulness of this approach in revealing microbial dynamics that could be applied for technological purposes (De Filippis et al., 2016; Weckx et al., 2018). Despite the increase of metatranscriptomic studies on different food matrices, table olives are still unexplored with high success potentiality for shedding light on cell growth and stress response fluctuation during the fermentation process. In addition, such approach could help to underline the mechanism driven the debittering process for reduced fermentation rate in naturally fermented table olives.

### 2.3. Proteomics and metaproteomics

Proteomics is defined as the study of the whole set of proteins encoded by a genome while the term metaproteomics is referred to the characterization of all proteins synthesized by a metagenome or present

**Table 4**  
Whole-genome sequencing of bacteria isolated from brine and table olives surface.

Species	Strain	Isolation source	Accession no.	Size (bp)	No. Of contigs	G + C content (%)	No. Of protein-coding genes	No. Of plasmids	No. Of tRNAs	No. Of rRNAs	References
<i>Lactiplantibacillus pentosus</i>	MP-10	Brines of naturally fermented Aloreña green table olives	GCA_900092635.1	3,698,214	108	46.32	3109	5	71	16	Abriouel et al. (2011a), 2011b; 2016
<i>Lactiplantibacillus pentosus</i>	BGM48	Sicilian-style green olive fermentation 118 days after the start of fermentation	PRJNA329412	3,591,251	NA	45.00	3179	5	81	NA	Golomb et al. (2013)
<i>Lactiplantibacillus plantarum</i>	S2T10D	Brine from table olives after 10 days of fermentation	MQNK00000000	3,165,258	92	44.48	2871	0	45	6	Botta et al. (2017)
	S11T3 E	Brine from table olives after 11 days of fermentation	MQNL00000000	3,168,693	58	44.49	2884	0	61	8	
	O2T60C	Surface of table olives after 60 days of fermentation	MPLC00000000	3,311,558	68	44.41	3005	0	65	11	
<i>Lactiplantibacillus pentosus</i>	IG2	Brines of traditional non-inoculated	PVOB00000000	4,033,890	460	45.70	3946	7	85	8	Calero-Delgado et al. (2018)
	IG3	Spanish-style green table olive	PVOA00000000	3,919,445	111	45.80	3639	13	92	3	
	IG4	olive	PVNZ00000000	3,806,728	166	45.97	3522	6	84	5	Calero-Delgado et al. (2019)
	IG5	Biofilms on the skin of traditional fermented olives	PVNY00000000	3,768,924	96	45.98	3449	10	88	3	
	IG6		PVNX00000000	3,882,104	187	45.79	3631	11	88	3	
	IG7		PVNW00000000	3,802,404	352	45.79	3675	10	92	8	
	IG8		RDCL00000000	3,791,593	99	45.91	3450	6	79	24	
	IG9		RDCK00000000	3,787,967	99	45.91	3447	6	81	16	
	IG10		RDCJ00000000	3,811,295	121	45.95	3432	7	78	12	
	IG11		RDCI00000000	3,790,820	107	45.91	3448	6	78	20	
	IG12		RDCH00000000	3,796,685	81	45.90	3459	6	80	16	

NA: data not available.

in an ecosystem in a given time (Wilmes and Bond, 2004). The metaproteomic approach provides information related to all the metabolic pathways that are active during a food process (Ferrocino and Coccolin, 2017) and allows the identification of new functions involved in complex biological pathways (Maron et al., 2007). Working on proteins, and more precisely on enzymes, involved in biotransformation processes, the proteomic and metaproteomic analyses can be used to characterize the dynamics of microbial functions linking, directly *in situ*, genotype to phenotype (Wilmes and Bond, 2006; Chen et al., 2017). The interpretation of proteomic data can be enough straightforward if the genome sequence or a partial genome sequence of an organism is available while it can be a challenge in the analysis of mixtures of organisms, as in fermented foods (Armengaud, 2016). Currently, based on our knowledge, no metaproteomic studies have been conducted on fermented table olives and the available data have focused on the proteomic profile of LAB (Pessione et al., 2015; Abriouel et al., 2017; Montoro et al., 2018). Pessione and co-workers (2015), through the two-dimensional gel electrophoresis (2-DE) and the matrix-assisted laser desorption ionization source and tandem time-of-flight (MALDI-TOF/TOF) mass spectrometry, characterized the extracellular proteomes of *L. plantarum* S11T3 E and *L. pentosus* S3T60C strains both isolated from fermented olives and brine samples. The applied approach allowed to identify different isoforms of six and seven proteins, with extracellular location, from *L. pentosus* S3T60C and *L. plantarum* S11T3 E, respectively. The majority of the identified proteins showed adhesive functions suggesting the strains' ability to adhere to the gut mucosa. Adhesion properties of *L. pentosus* strains, isolated from naturally fermented Aloreña green table olives, were also studied by Abriouel and co-workers (2017) and by Montoro and co-workers (2018). The *L. pentosus* MP-10 strain,

beyond the presence of several genes putatively involved in the adaptation to the human gastro-intestinal tract (such as those related to carbohydrate metabolism as well as proteins implicated in the interaction with host tissues), harbored enzymes related to carbohydrate modification and complex-carbohydrate metabolism. As reported by the authors, this layout influences the survival, the competitiveness, and the persistence of the MP-10 strain in the gastro-intestinal tract niche. In addition, the presence of genes encoding mucus-binding proteins and moonlighting proteins was also highlighted predicting the attractiveness of this bacterium as a potential probiotic for human and animal hosts. Montoro and co-workers (2018), by using an immobilized mucin model, studied the adhesion ability of thirty-one *L. pentosus* strains. Based on the exhibited mucus adhesion abilities, the strains were classified as highly adhesive (*L. pentosus* CF1-43 N, 73.49% of adhesion ability), moderately adhesive (*L. pentosus* CF1-37 N, 49.56% of adhesion ability) and poorly adhesive (*L. pentosus* CF2-20 P, 32.79% of adhesion ability). In addition, it was pointed up that the highly adhesive *L. pentosus* CF1-43 N strain overproduced four moonlighting proteins involved in the glycolytic pathway (phosphoglycerate mutase and glucosamine-6-phosphate deaminase), stress response (small heat shock protein) and transcription (transcription elongation factor GreA). Based on such evidence, the centrality of the metaproteomic approach to understand the link between microbial community composition and function is clearly highlighted. Nevertheless, the proteomic and metaproteomic approaches remain underexploited on table olives ecosystem, although they represent a valuable and efficient tool in strain typing.



## 2.4. Metabolomics

Over the past few years, headspace solid phase microextraction (HS-SPME) and gas chromatography–mass spectrometry (GC–MS) have been extensively used to in-depth study the metabolic profile of Spanish, Greek, Castelvetrano and Tunisian styles table olives. In addition, as showed in Table 3, several studies have been conducted to determine the volatile organic compounds (VOCs) profile of table olives differently treated (spontaneous or pilot fermented), as well as belonging to different cultivars. In this context, Sabatini and Marsilio (2008) studied, by GC-MS analysis, the VOCs profile of spontaneously fermented Nocellara del Belice table olives, processed according to Spanish, Greek and Castelvetrano styles. The results revealed that the applied process technologies and the fermentation time significantly affected the VOCs profile of table olives. The VOCs profile of Spanish-style Nocellara del Belice table olives, fermented by using the *L. pentosus* OM13 starter, was also evaluated by Martorana and co-workers (2017). Head Space followed by Gas Chromatography/Mass Spectrometry (HS-SPME/GC/MS) applied to table olives at the end of fermentation (195 days) allowed to identify twenty-seven VOCs. Homoguaiacol, 2-butanol, 4-ethylphenol, phenylethyl alcohol and 4-ethylphenol were the compounds detected at highest concentrations in all experimental trials. Among Spanish-style green table olives, the volatile profile of Manzanilla, Gordal and Hojiblanca was identified by SPME and GC–MS (Cortés-Delgado et al., 2016; López-López et al., 2018). The metabolomics approach revealed the presence of more than one-hundred VOCs, including esters, alcohols, terpenes, aldehydes, phenols, hydrocarbons, sulphur compounds, ketones, and lactone, as previously reported (Montaño et al., 1990, 1992; Iraqi et al., 2005; Sabatini and Marsilio, 2008; Cano-Lamadrid et al., 2015; Cortés-Delgado et al., 2016; Sánchez et al., 2017, 2018), highlighting that sampling time affects in a more pronounced way VOCs composition than olive cultivar. On the contrary, Garrido-Fernández and co-workers (2017), by GC-MS analysis, differentiated Spanish-style Manzanilla and Hojiblanca green table olives, from different parts of Spain, by VOCs profiles in relation to both cultivars and production area. Benítez-Cabello and co-workers (2019b) investigated, for the first time, the volatile profile of Manzanilla Spanish-style green table olives, fermented by different starter cultures. Based on the VOCs profile, the authors concluded that the use of LAB and yeast as starters, singularly or in mixture, improve the aromatic profile of the final product. The ability of starters to influence the volatile profile of fermented table olives was confirmed by Tufariello and co-workers (2019) who focused the attention on Kalamàta, Picual and Manzanilla Greek-style olives type. Twenty-one compounds belonging to esters, alcohols, acids, hydrocarbons, terpenes and volatile phenol were identified and the starter-fermented olives exhibited a more complex profile in esters, alcohols, and volatile phenols compared to non-inoculated samples. Similarly, even if in directly brined Sicilian table olives, Randazzo et al. (2014) and Pino et al. (2018, 2019) evaluating the influence of lactobacilli starter cultures on the volatile profile, demonstrated a significant change in the VOCs pattern. Greek-style fermented table olives were also investigated by Bleve and co-workers (2015) who found, between the natural fermented Conservolea and Kalamàta black olives, pronounced differences in the volatile profile. In addition, Bleve and co-workers (2014) characterized the volatile compounds generated during the fermentation process of Cellina di Nardò and Leccino cultivars. Through HS-SPME-GS/MS technique, the authors disclosed that, in both cultivars, aldehydes were closely related to the first stage of fermentation (30 days); alcohols (2-methyl-1-propanol and 3-methyl-1-butanol), styrene, and *o*-cymene to the middle stage (90 days) whereas acetate esters were linked to the final stage fermentation (180 days). Commercial black-ripe table olives processed in United States, Spain, Egypt and Morocco were analysed by GC–MS (Sansone-Land et al., 2014). A variety of aldehydes, alcohols, esters, ketones, phenols, terpenes, norisoprenoids, and pyridines were isolated and among these  $\beta$ -damascenone, nonanal, (E)-dec-2-enal, 3-methylbutanal,

ethyl benzoate, octanal, 2-methoxyphenol, 2-methylbutanal and 2-methoxy-4-methylphenol were identified as the major contributors to table olives' aroma. The metabolomics approach allowed to discriminate the imported olives from the domestic ones. Along with Spanish and Greek style, worthy of attention is the Tunisian-style olive processing, which was investigated by Dabbou and co-workers (2012). The authors evaluated the changes in VOCs using three different cultivars: the autochthonous Tunisian Meski cultivar and two introduced table Picholine and Manzanilla. Sixty-six volatile compounds were identified by GC with the dominance of aldehydes while the percentages of total ketones, alcohols, and esters differed according to the cultivar.

Table olives flavor develops by the combined metabolic activity of microbial community on drupes, carbohydrates, accompanied by further enzymatic and chemical conversions during fermentation. The identification of active VOCs compounds, using metabolomics, has led to create a library that can be used to associate desirable flavor or defects to specific molecules.

In addition, the integration of metagenetics and metabolomics can be considered a valuable approach to reveal the existence of positive and/or negative correlations between the microbiota composition and the produced microbial metabolites. In this context, De Angelis et al. (2015) revealed that lactobacilli and *W. anomalus* strains markedly affect the content of free fatty acids, phenolic compounds and VOCs in directly brined Bella di Cerignola table olives, highlighting differences between un-inoculated and inoculated samples. Randazzo and co-workers (2017) showed the influence of the microbiota on metabolic profile of Nocellara Etnea table olives during controlled and spontaneous fermentation. The authors observed that *Proteobacteria* were positively correlated to aldehydes and octanal, yeasts with alcohols and ethanol, *S. paracollinoides* with esters, and *L. acidispicis* with acetic acid. Similarly, as suggested by de Castro et al. (2019), the development of microbiota involved in olive spoilage is directly correlated to the development of VOCs responsible of off-odor. In particular, the genus *Propionibacterium* was positively correlated with acetic, propionic and succinic acids, and methyl propionate while the genus *Ruminococcus* showed significant positive correlation with propionic and butyric acids.

## 2.5. Data management and processing of information

Table 5 shown the applications, weakness, and challenges of omics techniques applied in table olives ecosystem, generating a vast amount of data, which need adequate management to ensure the quality of information maximizing knowledge-gleaning and protecting the data from loss or misuse (Schneider and Orchard, 2011).

In amplicon-based metagenetics studies, conserved regions of a phylogenetic marker are amplified by PCR, sequenced, and assigned to an operational taxonomic unit (OTU). In detail, in metagenetics and metagenomics studies, the generated data must be subjected to: quality control of the sequences, elimination of the chimeric sequences, grouping of the sequences on the basis of similarity and clustering, and taxonomic assignment.

Appropriate analytic pipelines are able to screen, trim and filter the raw sequences. Among these, the Quantitative Insights into Microbial Ecology (QIIME) pipeline, which combines original published tools and algorithms directly into the pipeline, is a widely used analytical tool (Nilakanta et al., 2014; Cocolin et al., 2013; De Angelis et al., 2015; Medina et al., 2016; Randazzo et al., 2017; Rodriguez-Gomez et al., 2017). QIIME is an open-source software pipeline able to manage the sequencing data supporting a wide range of microbial community analyses and visualizations that allow users to interact with the data (Caporaso et al., 2010). To guarantee an appropriate and high level of accuracy, in terms of OTUs detection, sequences that pass the quality filters are subjected to denoising and chimera checking. The detection and removal of chimeras is of critical importance since they may be misinterpreted determining an inaccurate estimation of diversity and generating spurious inferences of differences between populations. For

**Table 5**  
Applications, weakness and challenges of omics approaches on table olives.

Omics	Target	Application	Weakness	Challenges
Metagenetics	Analysis of a single type of 16S rRNA encoding gene or ITS region.	<ul style="list-style-type: none"> <li>✓ Identification of spoilage or foodborne pathogens;</li> <li>✓ Study of microbial diversity;</li> <li>✓ Identification of non-cultivable microorganisms of table olives;</li> <li>✓ Application to various fermented food matrix to identify spatial and temporal variations during fermentation process.</li> </ul>	<ul style="list-style-type: none"> <li>✓ Inability to distinguish between metabolically active cells and inactive;</li> <li>✓ Lye treatment of table olives can compromise the DNA and the sequencing detection.</li> </ul>	<ul style="list-style-type: none"> <li>✓ Examine in depth table olives microbiota through the identification and characterization of VBNC (viable but non culturable) microorganisms and to allow their isolation and cultivation.</li> </ul>
Transcriptomics and Metatranscriptomics	Analysis of mRNA or total RNA of microbial cells and ecosystem.	<ul style="list-style-type: none"> <li>✓ Identification of RNA transcripts of microbial cells under specific conditions;</li> <li>✓ Identification of whole gene expression and functions of microbial ecosystem;</li> <li>✓ Measurement and evaluation of microbial gene expression.</li> <li>✓ Identification of key genes involved in metabolisms of biofilm formation, VOCs production, proteins or specific metabolites.</li> </ul>	<ul style="list-style-type: none"> <li>✓ Difficulty on manipulation and extraction of mRNA;</li> <li>✓ Environmental factors can compromise the gene expression of the microbiota;</li> <li>✓ High estimated costs.</li> </ul>	<ul style="list-style-type: none"> <li>✓ Comprehension of microbial gene dynamics involved in fermentative processes;</li> <li>✓ Separation of bacterial RNA from the matrix;</li> <li>✓ Separation and preservation of microbial mRNA from the food matrix;</li> <li>✓ Training of qualified personnel for the processing of bioinformatics data.</li> </ul>
Proteomics and Metaproteomics	Analysis of the whole set of proteins (proteome) encoded by genome, including their structure and function.	<ul style="list-style-type: none"> <li>✓ Study of metabolic, physiological state and environment effects on gene expression and proteins of the microorganisms;</li> <li>✓ Comprehension of total proteins, expressed at a certain time by microorganisms;</li> <li>✓ Improvement, validation and quality control of bioprocess;</li> <li>✓ Characterization and detection of biofilm-forming microorganisms and bacteria, responsible of undesired effects;</li> <li>✓ Investigation of a multitude of bacterial process through the proteome-guided optimization of strains for biotechnological use.</li> </ul>	<ul style="list-style-type: none"> <li>✓ Ineffective extraction method could compromise the amount and structure of isolated proteins;</li> <li>✓ Interference of food-matrix proteins;</li> <li>✓ Impossibility to identify less abundant proteins with gel-based method (2-DE, SDS-PAGE).</li> </ul>	<ul style="list-style-type: none"> <li>✓ Improvements in extraction and separation techniques, identification and data searches of proteins;</li> <li>✓ Comprehension of specific mechanisms of proteomic adaptation involved in microbial performances (carbohydrates utilization, energy metabolism, osmotic stress resistance).</li> </ul>
Metabolomics	Analysis of endogenous and exogenous small molecules (VOCs and/or non-VOCs).	<ul style="list-style-type: none"> <li>✓ Study of metabolome, able to reflect the microbial cell's biochemical state;</li> <li>✓ Comprehension of small molecules generated from metabolic pathways;</li> <li>✓ Detection of specific group of metabolites, identified and quantified in a sample under certain conditions;</li> <li>✓ Study of the metabolite profile of unknown compounds responsible for changes in microbial systems.</li> </ul>	<ul style="list-style-type: none"> <li>✓ Difficulty in identifying metabolic compounds in complex food matrices;</li> <li>✓ Low level of purification and selective extraction of metabolites;</li> <li>✓ The use of unsuitable solvent can compromise the extraction of metabolic compounds.</li> </ul>	<ul style="list-style-type: none"> <li>✓ Utilization of specific techniques able to reveal different biological molecules of metabolome;</li> <li>✓ Efficiency on biomarkers identification for the quality and authenticity of food;</li> <li>✓ Efficiency on biomarkers identification with positive effect on human health;</li> <li>✓ Possibility to discriminate, inform and predict metabolic processes of microorganisms, involved in table olives fermentation.</li> </ul>

these purposes, different softwares are available such as UCHIME (Cocolin et al., 2013), Black Box Chimera Check (B2C2) (De Angelis et al., 2015), ChimeraSlayer (Rodriguez-Gomez et al., 2017), and prinseq-lite program (de Castro et al., 2018; Medina et al., 2018). To grouping the sequences, based on similarity, and to clustering them, the sequence analysis tool USEARCH, is widely used for combining different algorithms into a single package (Cocolin et al., 2013; De Angelis et al., 2015; Medina et al., 2016). The Ribosomal Database Project (RDP), which is a Bayesian-type classifier, allows classifying up to genus-level sequences of bacterial and archaeal 16 S rRNA as well as intergenic ribosomal sequences (ITS) (De Angelis et al., 2015; Randazzo et al., 2017; de Castro et al., 2018; Medina et al., 2018). To in depth study the microbiota composition, the results are expressed as relative abundance of the different phyla, classes, orders, families, genera, and rarely species. The microbial community is evaluated in terms of richness and diversity through alpha and beta diversity indices (rarefaction, Good's coverage, Chao1 richness and Shannon diversity indexes) (Cocolin et al., 2013; De Angelis et al., 2015; Medina et al., 2016, 2018; Randazzo et al., 2017; Rodriguez-Gomez et al., 2017; de Castro et al., 2018).

Data analysis of metabolic compounds is intended to classify, discriminate and/or predict the metabolome of complex food matrices, such as table olives, during fermentation. Applying a discriminative analysis, is possible to evaluate the different metabolic profile among samples, without the support of statistical models or/and the implementation of metabolic pathways that may elucidate such differences (Cevallos-Cevallos et al., 2009). The use of internal standards, in VOCs analysis, has allowed the simultaneous, reproducible and accurate detection of the main metabolic compounds present in fermented green olives (Montaño et al., 1990; Sabatini and Marsilio, 2008). In addition, volatile compounds can be identified by comparing the component's mass spectrum and experimental Kováts retention index (I) with an authentic reference standard (Montaño et al., 1990; Sabatini and Marsilio, 2008; Sansone-Land, 2014). Moreover, statistical models, such as the one-way analysis of variance (ANOVA) and the multivariate data analysis (MVDA) can help to maximize the VOCs classification, highlighting the relations among these measurements (Cevallos-Cevallos et al., 2009). To underline the quantitative differences among samples, the Principal Components Analysis (PCA) is the most used statistical

tool. In addition, variation array, tertiary graphs, biplots, or codadenrogram can be applied to discriminate among samples (Garrido-Fernandez et al., 2017).

In proteomics analysis, protein sequence databases, such as SEQUEST, UniprotKB, and MASCOT, allow the identification of proteins. Automatic annotation servers, such as BlastKOALA, perform KO (KEGG Orthology) assignments to characterize individual gene functions and reconstruct KEGG pathways (Abriouel et al., 2017). Different software platforms, such as PEAKS Studio, can be used to discover proteomics, including protein identification and quantification, analysis of post-translational modifications (PTMs) and sequence variants (mutations), and peptide/protein *de novo* sequencing (Montoro et al., 2018). Integrate multi-omics approaches could increase the yield of information from genomics, transcriptomics, proteomics and metabolomics. For instance, MixOmics (R based software), presents a recent example of a modified concatenation-based approach. Software approaches for managing multi-omics data sets were also recently discussed for other environmental niches (O'Donnell et al., 2020) and they also could be applied for table olive ecosystem.

### 3. Conclusions and future perspectives

Table olives fermentation is an essential process by which the bitter phenolic compounds are removed by drupes, enhancing sensorial properties of the final product. Methods adopted for the investigation of table olives associated microbiota changed from the classical cultivation-based approach to the most recent omics sciences. For decades, table olives community have been investigated through culture-dependent techniques, revealing only the most adaptable microorganisms as responsible of fermentation. Subsequently, in the previous investigations, several achievements have been reached through the application of a polyphasic approach, combining traditional methods to culture-independent, especially in understanding the microbial species variation among olives cultivars and the widely applied process technologies (Spanish and Greek style).

In this review, we presented a large-scale genetic, proteomic and metabolomic analyses that have taken place in table olives field, helping to change the way to study table olives ecology. With the spread of high throughput methods, a high level of association and interaction of microbial population was revealed in table olives ecosystem. However, the potential application of omics techniques, clearly emerge and is still limited on the combination of microbiota and metabolomics, letting possible the discover of new biological markers with high specificity to fully understand the molecular mechanisms at stake in this complex food ecosystem. The application of a multi-omics approach to table olives ecosystem can be considered suitable to obtain a comprehensive view of the mechanisms that can affect sensorial traits and safety aspects of final product. In this way, it could be possible to improve the knowledge about what happens in a complex process, such as in table olives fermentation, and what the microbiota does in this matrix, shedding light to the importance of how “omics” approaches may lead to novel table olives biomarker molecules or molecular signatures with potential value in human health.

### Declaration of interests

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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