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MICROBIAL DIVERSITY ON GRAPE SURFACE AND ITS RESEARCH STATUS

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Abstract. The microbial diversity of grape surfaces, also known as "microbial terroir", plays a critical role in winemaking and has applications in crop health and plant protection. Next-generation Sequencing (NGS) has revolutionized our understanding of grape surface microbiota by providing insights into the complex and dynamic microbial communities present on grape berries. NGS studies have confirmed the existence of distinct regional differences in grape surface microbial diversity, highlighting the concept of microbial terroir. This diversity is influenced by various natural and human factors, such as soil type, climate, vineyard management practices, and grapevine genetics, which contribute to the unique microbial terroir of each location. The application of NGS in studying microbial terroir has not only advanced our knowledge of grape and wine science, but also has implications in crop health and plant protection. The identification and characterization of microbial communities using NGS can help to develop sustainable and eco-friendly strategies for managing grapevine diseases and pests. The ongoing research in this area is expected to further expand our understanding of microbial terroir and its applications, contributing to the advancement of grape and wine science, and promoting environmentally responsible grape production practices. Based on bibliometric analysis, the current research focuses on the selection autochthonous *S. cerevisiae*, non-*Saccharomyces* and LAB. Plant growth-promoting bacteria considered as a new agroecological manageme. Interest in the role of natural microbial diversity in winemaking remains high.

Keywords: *Microbial terroir, microbial diversitiy, grape, non-saccharomysis yeast, biological control agents, bibliometric analysis.*

Rezumat. Diversitatea microbiană de pe suprafața strugurilor, cunoscută și ca "terroir microbial", joacă un rol crucial în procesul de producție a vinului și are aplicații în sănătatea și protecția plantelor. Secvențierea noii generații (Next-generation Sequencing - NGS) a revoluționat percepția asupra microbiotei suprafeței strugurelui, oferind informații despre comunitățile complexe și dinamice de microorganisme prezente. Studiile NGS au confirmat existența diferențelor regionale distincte în diversitatea microbiană a suprafeței boabelor de strugure, evidențiind conceptul de terroir microbial. Această diversitate este influențată de diferiți factori naturali și umani, precum tipul de sol, climatul, practicile de gestionare a viței de vie și genetica strugurilor, care contribuie la terroirul microbial unic al fiecărei locații.

Aplicația NGS în studiul terroirului microbial nu numai că a avansat cunoștințele în domeniul științei strugurilor și vinului, dar are și implicații în sănătatea plantelor și protecția plantelor. Identificarea și caracterizarea comunităților microbiene utilizând NGS pot contribui la dezvoltarea de strategii durabile și prietenoase cu mediul pentru gestionarea bolilor și dăunătorilor la vița de vie. Cercetarea continuă în acest domeniu este așteptată să extindă în continuare înțelegerea noastră asupra terroirului microbial și a aplicațiilor acestuia, contribuind la avansarea științei despre struguri, vinuri și promovarea practicilor responsabile de producție a strugurilor în concordanță cu mediul înconjurător. Pe baza analizei bibliometrice, cercetarea curentă se concentrează pe selecția de *S. cerevisiae* autohtone, non-*Saccharomyces* și LAB. Bacteriile care promovează creșterea plantelor sunt considerate o nouă metodă de gestionare agroecologică. Interesul pentru rolul diversității microbiene naturale în producția de vin rămâne ridicat.

Cuvinte cheie: *Terroir microbial, diversitate microbială, strugure, drojdii non-saccharomyces, agenți de control biologic, analiză bibliometrică.*

1. Introduction

Wine production is characterized by distinct regional characteristics known as "terroir." With the advancements in biological technology, particularly high-throughput sequencing technology, also known as Next Generation Sequencing (NGS), there is increasing evidence supporting the role of microbial communities or microbial diversity in shaping the concept of "microbial terroir" in the wine industry. NGS has helped numerous countries and regions identify the microbial terroir of their wines and wine grapes [1-3].

The winemaking process is a complex interplay of microbial activities, with grape berries being a crucial source of microorganisms. Apart from enology applications, the study of microbial diversity also holds significant importance in plant protection. As concerns about environmental pollution and food safety rise, many traditional vineyards are transitioning to organic practices. In this context, research has shown that grape surfaces harbor numerous microorganisms that can be harnessed for local antagonism, providing an environmentally friendly alternative to pesticides and mitigating food safety concerns arising from pesticide residues [4-5].

Based on research conducted over the past two decades, this work highlights the importance of studying microbial diversity on grape surfaces, the advancements in research technology, and the microbial terroirs of various countries. Furthermore, a bibliometric analysis of 453 papers from Web of Science was conducted to analyze the current status and prospects of research on microbial diversity on grape surfaces.

2. Microbes on the grape surface

The surface of grape berries constitutes a complex microbial habitat, inhabited by epiphytic microorganisms such as bacteria, yeast, and filamentous fungi [6-8]. These microorganisms play a crucial role in crop health and can also interfere with the winemaking process, potentially exerting a significant impact on wine quality [9].

2.1. The role of microbes on grape surface

Numerous microorganisms are involved in the winemaking process, with *Saccharomyces cerevisiae* being the main organism responsible for converting grape juice into wine. However, native yeasts have been found to play a crucial role in shaping the chemical

and organoleptic properties of wine. Non-*Saccharomyces* yeasts, in particular, are known to produce more complex aromas through their metabolic activities, this conclusion already confirmed by lots of researches, which are listed in Table 1. The ecology of natural yeast flora is therefore an important factor that can significantly impact wine quality [10].

Table 1

The main influence of non-saccharomyces on sensory characteristics

Non-saccharomyces	Metabolite	Sensory characteristics	Reference
<i>Hanseniaspora/Kloeckera</i>	2-Phenylethyl acetate, Mannas	Floral rose petals hints, mannoproteins	[11-12]
<i>Hanseniaspora vineae</i>	Benzyl acetate	Floral jasmine aroma	[13]
<i>Lachancea thermotolerans</i>	2-Phenylethyl acetate, Ethyl lactate, Lactic acid	Floral, rose petals hints, strawberry, toffee, Citric acidity	[14]
<i>Metschnikowia pulcherrima</i>	2-Phenylethanol, Monoterpens	Rose-like odour, Floral	[15]
<i>Pichia kuyveri</i>	Mercaptohexanol, Mercaptohexyl acetate	Grapefruit, passion fruit,	[16]
<i>Schizosaccharomyces pombe</i>	Mannoproteins	Softening astringency	[17]
<i>Torulaspora delbrueckii</i>	3-Phenylethyl acetate, Ethyl hexanoate, 3-Ethoxy-1-propanol	Flower, honey, apple, black currant, solvent	[18]
<i>Wickerhamomyces anomalus</i>	2-phenylethyl acetate, Isoamyl acetate, Ethyl acetate	Flower, honey, banana, fruity	[19]

The ascomycete *Botrytis cinerea*, *Aspergillus carbonarius*, and *Penicillium expansum* are considered the most destructive fungi in viticulture [20]. The traditional approach to combat them is the use of fungicides. However, repeated use of fungicides can lead to resistance in *Ascomycetes*, negatively impact the natural microbial community, and result in chemical residues on grape berries and vineyards [21]. Furthermore, due to increasing concerns over food security and environmental protection, the European Union has imposed strict restrictions on the use of fungicides [22].

As an effective alternative to fungicides, biological control agents (BCA) act on pathogenic agents through three pathways: (i) competition for space and nutrients, (ii) production of bioactive molecules, and (iii) induction of defense-related responses in grapevines [23]. Yeasts of the genera *Metschnikowia*, *Pichia*, or *Candida*, which are commonly used as BCAs in viticulture, are part of the natural microbiome of grape berries [20]. Table 2 lists the known grape pathogenic microorganisms and their BCA. Therefore, understanding

the structural and functional diversity of microbial communities on grape berry skins is crucial for the development of native antagonists.

Table 2

The pathogenic microbe and biological control agents

Pathogenic microbe	Grape disease	Biological control agent	Reference
<i>Botrytis cinerea</i>	Gray mold	<i>Bacillus sp.</i> , <i>C. membranifasciens</i> , <i>M. guilliermondii</i> , <i>Ralstonia sp.</i> , <i>Issatchenkia terricola</i> , <i>Aureobasidium pullulans</i> , <i>Metschnikowia pulcherrima</i> , <i>Pichia guilliermondii</i>	[24]
<i>Penicillium expansum</i>	Blue mold	<i>Rahnella aquatillis</i> , <i>Cryptococcus laurentii</i> , <i>M. pulcherrima</i>	[24]
<i>Aspergillus niger</i>	Aspergillus ochratoxin	rot, <i>Issatchenkia orientalis</i> , <i>M. pulcherrima</i> , <i>Issatchenkia terricola</i> , <i>C. incommunis</i> .	[25]
<i>Aspergillus carbonarius</i>	Black mold	<i>Aureobasidium pullulans</i> , <i>Metschnikowia pulcherrima</i> , <i>Kluyveromyces thermotolerans</i> , <i>Issatchenkua orientalis</i> , <i>Candida sake</i>	[26]

2.2 The factors impact on grape microbial diversity

Grape microbial diversity can be influenced by various factors, including human-related factors and natural factors. Among human-related factors, vineyard management, particularly fungicide usage, has been frequently reported. In recent years, there has been a growing interest in organic and biodynamic vineyard management in viticulture, and this trend is also reflected in studies on grape microbial diversity. A research carried out between conventional and biodynamic vineyards revealed that farming practices shape the fungal community influencing wine traits linking the wine with the viti-vinicultural area of origin [27]. Besides, the microorganism of grape from organic vineyard had advantages in fermentation speed and wine sensory quality [28].

The active ingredients and application modalities of fungicides, such as contact, superficial or systemic, can influence the structure of yeast communities on grape berry surfaces [29]. In a long-term study on fungicide use in vineyards, it was observed that yeasts other than *Metschnikowia pulcherrima* had higher tolerance to sulfur compared to penconazole, suggesting that sulfur-based fungicides had little effect on yeast community structure. As sulfur-based fungicides are permitted in organic vineyards, low doses of sulfur-based fungicides could be used as a strategy for organic vineyard management. Barba [21] reported that sulfur-based fungicides had no negative effects on yeast, while copper-based

fungicides significantly inhibited the growth of *Saccharomyces cerevisiae*. However, studies by Massieux et al. [30] Hengst et al. [31], and Merrington et al. [32] suggested that copper-based fungicides could impact microbial structure.

Furthermore, a study by Neza Cadez [33] found that fungicides containing active ingredients such as iprodione, pyrimethanil, and fludioxonil plus cyprodinil had effects only on specific microbial species, and that their impact on the microbiome was minimal after a safety interval, even if the microbiome changed during application. In the same study, researcher figured out that a fungicide containing pyrimethanil suppressed the growth of all basidiomycetous yeast species, while the sporadically occurring fermentative yeasts were unaffected.

Rocio Escribano-Viana [34] found that the use of bio-fungicides has no significant effect on the structure of microbial communities. Similarly, a study utilizing NGS sequencing methods also reported no discernible differences in the microbial community composition on grape surfaces among organic, conventional, and biodynamic vineyards, with the cultivation mode only influencing certain microbial abundances [35].

As a result, the management of vineyards and viticultural practices that regulate the presence or absence of microorganisms are considered crucial for sustainable grape production in the region. Climatic factors, such as temperature, ultraviolet light, and rainfall, can impact the number and diversity of microorganisms, but understanding the specific effects of these factors on the microbial community is challenging due to the complexity of the interactions [36-37]. For instance, previous studies have reported conflicting findings, with some suggesting that higher rainfall leads to higher microorganism populations, while others propose the opposite [38].

Most of the research in this field has primarily focused on bacteria of oenological interest, such as acetic acid bacteria (AAB) and lactic acid bacteria (LAB), which are commonly found on grape berries [39-40]. However, these studies were limited by the methodologies available at the time. The advent of high-throughput sequencing methods has significantly advanced the understanding of other bacteria in the grapevine microbiota.

It is evident that the influence of climate on microorganisms is multifaceted and not yet fully elucidated. Multiple studies have shown that the microbial community is influenced by various factors, including variety, vintage, and geography [41-43]. Unlike human factors, natural factors' impact on the microbial community has received less attention, with researchers typically conducting statistical analyses on the microbial community grouped by different natural factors that are concluded to be statistically significant.

In Dimitrois' study [44], location was found to have a more significant impact on yeast populations than grape variety and stage of ripening. Currently, most studies only report the composition of grape microbial diversity in specific production areas, which is commonly referred to as the concept of "microbial terroir" [45-46].

2.3 Microbial terroir

The International Organisation of Vine and Wine (OIV) defines "Terroir" as an area where the collective knowledge of interactions between human and natural factors shape the unique characteristics of the wine produced [47]. However, earlier research on terroir has often overlooked the role of microbes in this complex interplay of factors.

Microbes play a crucial role in crop nutrient availability, influencing biogeochemical cycles, rhizosphere-root interactions, and plant growth and health. Recent advancements in

high-throughput sequencing technology have provided deeper insights into the complex bacterial and fungal community structures associated with soil, rhizosphere, plant phyllosphere, and fruit surface. In the past decade, there has been extensive scientific research on the microbial composition of vineyards, revealing evidence of regional microbial communities that contribute to the characterization and typicality of regional wines [48].

The concept of 'microbial terroir', including 'yeast terroir', has been proposed to describe the link between microbial biogeography and regional wine characteristics [49]. This has significantly advanced our understanding of the factors that influence the microbial structure and diversity of vineyards within the context of terroir, which encompasses both natural and human factors. However, despite progress, there is still limited scientific evidence on the "potential microbial influence" on wine composition within the terroir concept, and many questions remain unresolved. These include the functional characteristics of microbial communities and their impact on plant physiology and grape composition, the role of vineyard microbiota origin and interannual stability, and their influence on wine sensory attributes [50-51]. Further research is needed to fully comprehend the complex interplay between microbes, terroir, and wine production.

3. The grape microbial diversity research

3.1 Identification method

Since the discovery of microorganisms in grape must by Louis Pasteur in the 19th century, conventional microbiological methods such as biochemical characterization, cultivation on agar media, and microscopic observation have been used to study microbial diversity associated with grapes. However, these traditional methods have limitations as they cannot provide species-level identification and may result in incorrect identification [52].

With the advent of polymerase chain reaction (PCR) technique, various PCR-based techniques such as PCR-Fingerprint, Droplet Digital PCR (ddPCR), PCR-denaturing gradient gel electrophoresis (PCR-DGGE), PCR-Restriction Fragment Length Polymorphism, and others have been employed for grape microbial diversity research. The bacterial small subunit ribosomal RNA gene (16S rRNA) and fungal ITS1-5.8S rRNA-ITS2 gene have been recognized as the gold standard for estimating phylogenetic diversity in microbial communities. Among the PCR-based techniques, RFLP and DGGE are commonly used methods [53, 54], their advantages and disadvantages are listed in Table 3.

PCR-RFLP is unable to provide population-level results, but direct PCR-RFLP analysis, which involves sampling random colonies on agar plates, can provide an idea of the proportion of different species. Although RFLP is often considered a culture-independent method, it is combined with culture methods in almost all researches related to grape microbial diversity [55].

On the other hand, DGGE is a culture-independent method that utilizes the different melting behaviors of DNA in different concentrations of denaturants to separate DNA fragments with the same size but different base composition, thereby allowing for the analysis of complex mixed microorganisms in grape samples. However, in practice, most studies on grape microbial diversity still combine culture methods with RFLP [56].

As a result, over the past three decades, molecular techniques targeting rRNA genes have been used in conjunction with culture-dependent methods to identify microorganisms after isolation and growth in pure cultures. Traditional culture-based methods have led to the isolation and identification of around 50 bacterial species and 70 genera of filamentous fungi.

PCR-DGGE is often considered suitable for less species-rich environments such as grape must, but it has low sensitivity and may not detect populations present at a relative abundance of less than 1% of the population, as reported by Andorrà et al. in 2010 [57].

Table 3

The advantage and disadvantage of main PCR based method

	Advantage	Disadvantage
PCR-DGGE	Culture-independent, directly applied to samples.	Low sensitive, only intense and well-separated bands can be sequenced
PCR-RFLP	Easily to applied to large number of samples	Difficult to use for complex communities

The advent of high-throughput, short-amplicon sequencing has revolutionized our ability to study microbial diversity within and across complex biomes. This cutting-edge technology, also known as next-generation sequencing (NGS), allows for the direct measurement and sequencing of PCR products from genes in specific regions, resulting in millions or even hundreds of millions of gene sequences. Some of the commonly used high-throughput sequencing platforms include 454 Life Sciences, ABI, Illumina, Pacific Biosciences' single-molecule sequencing technology, and Helicos Heliscope [58].

Compared to traditional sequencing methods, high-throughput sequencing is cost-effective and efficient, as it uses chip sequencing to simultaneously read and sequence millions of data points. These sequencing platforms generate massive amounts of data, with the HiSeq2000 sequencer from Solexa Technology, for example, capable of producing over 300G of data within just two weeks, equivalent to sequencing the human genome 100 times over [59].

Although high-throughput sequencing is a relatively new technology in grape microbial diversity research, emerging within the past decade, it has revealed a greater diversity than previously reported, even identifying several species that were previously unknown [60]. This method has made it possible to describe the microbial terroir, or the unique microbial community associated with the specific environmental conditions, on the surface of grapes [9]. Microbial terroir has been identified in various grape-growing regions around the world as Table 4 shows, shedding new light on the complex interactions between grapes and their surrounding microbial communities.

Table 4

The microbial terroir identified by NGS in the world

Country	Main genus identified	Reference
Spain	<i>Aureobasidium</i> , <i>Metschnikowia</i> , <i>lachancea</i> , <i>Candida</i> , <i>Pichia</i> , <i>Zygoascus</i> , <i>Hanseniaspora</i> , <i>Debaromyces</i> , <i>Cryptococcus</i> , <i>Rhodotorula</i> , <i>Sporobolomyces</i>	[61]
USA	<i>Alternaria</i> , <i>Aspergillus</i> , <i>Cladosporium</i> , <i>Coniothyrium</i> , <i>Epicoccum</i> , <i>Filobasidium</i> , <i>Lewia</i> , <i>Lophiostoma</i> , <i>Metschnikowia</i> , <i>Stemphylium</i> , <i>Ulocladium</i> , <i>Wickerhamomyce</i>	[62]

Continuation Table 4

Australia	<i>Alternaria, Aureobasidium, Botrytis, Candida, Cladosporium, Cystofilobasidium, Didymosphaeria, Epicoccum, Hanseniaspora, Kazachstania, Lophiostoma, Metschnikowia, Pichia, Rhynchogastrema, Saccharomyces, Saccharomycopsis, Seimatosporium, Torulaspora</i>	[63]
Italy	<i>Mycosphaerella, Sporobolomyces, Articulospora, Pyrenophora, Cadophora, Coprinellus, Phodosporidiobolus, Fusarium, Sphaeropsis, Coprinopsis, Sporisorium, Crepidotus, Saccharomyces</i>	[64]
Portugal	<i>Zygoascus, Metschnikowia, Vishniacozyma, Mycosphaerella, Filobasidium, Botrytis, Stenphylium, Cladosporium, Altemaria, Aureobasidium, Sporobolomyces, Rhodotorula, Hanseniaspora, Pichia</i>	[65]
Slovakia	<i>Aspergillaceae, Hanseniaspora, Kazachstania, Lachancea, Metschnikowia, Pichia, Pleosporineae, Saccharomyces, Saccotheciaceae, Starmerella</i>	[66]
China	<i>Massilia, Pantoea, Pseudomonas, Halomonas, Corynebacterium, Bacillus, Anaerococcus, Acinetobacterm Brevundimonas, Peptoniphilus, Paracoccus, Sphingomonas, Ginegoldia, Bifidobacterium, Staphylococcus</i>	[67]

4. The current research status

A bibliometric analysis was conducted to explore the current research status of microbial diversity in grape berries. The search was performed using the following keywords: "((grape* OR wine*) AND (microb* OR bacter* OR fung* OR microorg* OR yeast) AND (berry* OR skin* OR surface*) AND (diversity* OR community* OR abundance* OR richness* OR eco*))" on Web of Science, resulting in 1,875 records. From these records, 453 papers published within the past five years (2021-2023) were selected for further analysis.

The bibliometric analysis involved identifying high-frequency keywords (mentioned more than 30 times) using VOS viewer, and the co-occurrence of these keywords was examined. Figure 1 presents the relationship between the 27 high-frequency keywords obtained from the analysis, as shown in the co-occurrence network. This analysis provides insights into the key research areas and trends in the study of microbial diversity in grape berries, highlighting the interconnectedness of various concepts in this field.

The co-occurrence network is divided into 3 clusters, the details are shown in Table 5. Cluster 1 (in red color) consists of 12 keywords, this group of key words relates to various aspects of microbial communities and their role in wine fermentation.

S. cerevisiae is usually considered the most important microorganism, which converts sugar into alcohol. Many commercial strains of the *S. cerevisiae* species are used around the world in the wine industry, while the use of native yeast strains is highly recommended for their role in shaping specific, terroir-associated wine characteristics [68-69].

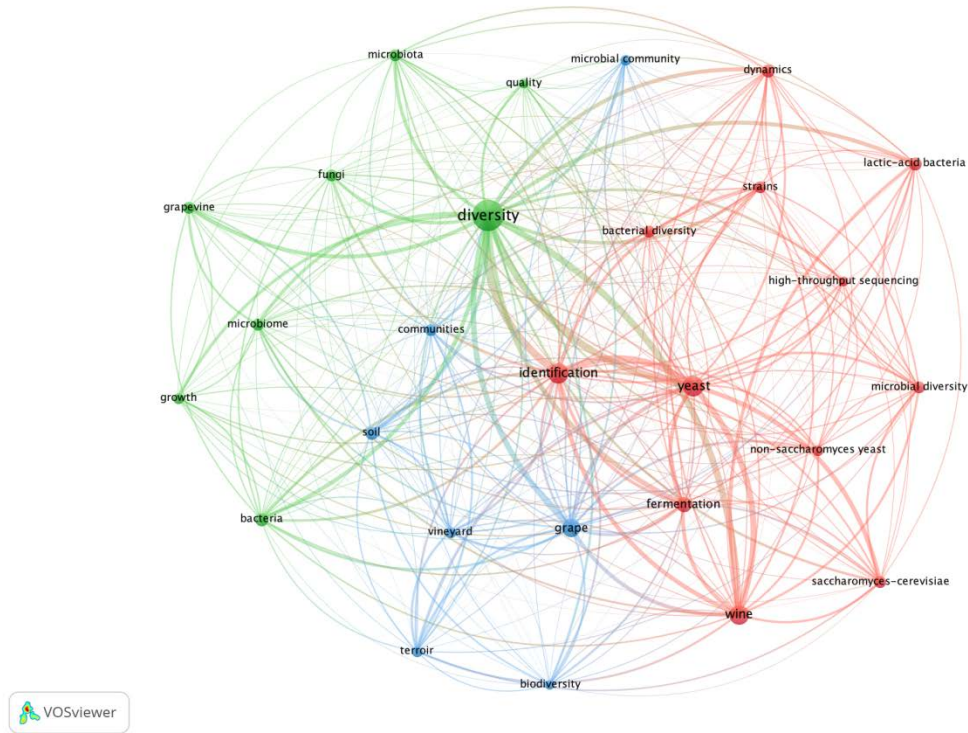


Figure 1. The bibliometric analysis.

Co-fermentation by non-*Saccharomyces* yeasts with *S. cerevisiae* has been widely used to improving sensory properties of wine [70-71]. Recently, researchers noticed that their effect on the biogenic amines (BAs) and Glutathione (GSH). BAs widely exist in the wine, which are often linked with off-odor, and they are harmful to health of human. The combination of two non-*Saccharomyces* yeast : *S. pombe* and *L. thermotolerans* can significantly reduce BAs levels in wine [72]. GSH is a non-protein thiol which has a strong antioxidant activity to reduce the SO₂ usage in the winemaking. It present in grape berries and produced by yeasts during fermentation [73]. These new discoveries about non-*Saccharomyces* yeast could provide new strategies for improving the quality of wine. Except *S. cerevisiae*, LAB also has a fundamental role in determining the quality chemical and aromatic properties of wine, especially red wine. Its by-products have important enzymatic activities that can release volatile aromatic compounds during malolactic fermentation [74], winemakers have attempted to replace commercially *O.oeni* with autochthonous LAB to obtain wines with more terroir and improve the wine quality[75-76]. In addition, searching for bacteria to use as BCA has become a research focus [77].

It can be observed the high-throughput sequencing is still the most frequency identification method for grape microbial diversity. There is another high frequency key word “dynamics”, the current dynamics of microbial diversity are not limited to grape ripening [78], but also include microbial diversity dynamic during winemaking [79].

Cluster 2 (in green color) consists of 8 keywords, most of which are similar to the Cluster 1, however, “grapevine” and “growth” are totally different. Under these key words, more on topic of plant protection and disease control. Grapevine offers different habitats for microorganisms, such as: roots, leaves, fruits, each of which is unique [80]. As it mentioned previously, researchers are funding the plant growth-promoting bacteria (PGPB) as new agroecological management [81]. It has been proven that PGPB are an excellent option to

prevent grey mould, and specific composition and functions of the rhizosphere microbial community contribute to the enhanced tolerance of some grapevines to salt stress [82].

Table 5

The clusters of key words

Cluster number	Key words number	Key words
Cluster1	12	Bacteria diversity, dynamics, fermentation, high-throughput sequencing, identification, lactic-acid bacteria, microbial diversity, non-saccharomyces yeast, saccharomyces-cerevisiae, strains, wine, yeast
Cluster2	8	Bacteria, diversity, fungi, grapevine, growth, microbiome, microbiota, quality
Cluster3	7	Biodiversity, communities, grape, microbial community, soil, terroir, vineyard

Cluster 3 (in blue color) consists of 7 words, in which, "terroir" is more attractive. The concept of terroir was discussed previously, however, the biodiversity of vineyard is an important composition of terroir [83]. Under this topics, researchers are interested in promoting cultivation and fermentation management strategies, advocate natural terroir attributes for grapes and wines [84-85].

5. Conclusions

The concept of "microbial terroir" refers to the unique microbial communities that are present on the surface of grape berries, and this concept has gained significant attention in recent years. The application of Next Generation Sequencing (NGS) in studying microbial terroir has provided valuable insights into the complex interactions between microbes and grapevines, with implications for both oenology and plant protection.

One of the key applications of microbial terroir is in exploring local wine styles. By studying the microbial communities on grape surfaces in different regions, researchers can gain a deeper understanding of how local environmental factors, such as soil type, climate, and vineyard management practices, influence the composition and activity of the microbial populations. This knowledge can provide a theoretical basis for developing unique wine styles that are characteristic of specific regions, known as "terroir wines". For example, certain microbial species may contribute to the production of specific aroma compounds or metabolites that are responsible for the unique sensory characteristics of wines from certain regions. This understanding of microbial terroir can help winemakers in their decision-making processes, such as grape selection, fermentation techniques, and aging practices, to enhance the quality and distinctiveness of their wines.

In addition to its significance in oenology, microbial terroir also has implications in the domain of plant protection. Understanding the diversity and dynamics of microbial communities on grape surfaces can provide valuable insights into the natural defense mechanisms of grapevines against pathogens. Some microbial species found on grape surfaces have been shown to possess biocontrol properties, inhibiting the growth of pathogenic microorganisms and reducing the need for chemical interventions. Therefore, studying microbial terroir can help in the development of safer and more environmentally friendly management strategies for grapevine diseases and pests. For instance, the

identification of specific beneficial microorganisms from local microbial terroir can lead to the development of biocontrol agents that can be used as alternatives to chemical pesticides, reducing the environmental impact and promoting sustainable grape production practices.

Despite the significant progress made in studying microbial terroir using NGS, our knowledge of grape-associated bacteria is still limited. There is a vast diversity of microbial species that inhabit the grape surface, and many of them may have important roles in grapevine health and wine production. Further research utilizing advanced NGS technologies and bioinformatics tools can help uncover the complex interactions and dynamics of microbial communities on grape berries, leading to a deeper understanding of microbial terroir and its applications in oenology and plant protection.

In summary, the analysis of the co-occurrence network reveals three clusters: Cluster 1 focuses on the role of microorganisms in wine fermentation, selection autochthonous *S. cerevisiae*, non-*Saccharomyces* and LAB are the trend. Cluster 2 explores plant protection and disease control in grapevines, including the use of plant growth-promoting bacteria. Cluster 3 emphasizes the importance of terroir and vineyard biodiversity in wine production. These findings provide insights into improving wine quality, sustainability, and understanding the complex interactions in grape microbial communities.

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