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Review

Soil Microbial Communities and Wine Terroir: Research Gaps and Data Needs

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Abstract: Microbes found in soil can have a significant impact on the taste and quality of wine, also referred to as wine terroir. To date, wine terroir has been thought to be associated with physical and chemical characteristics of the soil. However, there is a fragmented understanding of the contribution of vineyard soil microbes to wine terroir. Additionally, vineyards can play an important role in carbon sequestration, since the promotion of healthy soil and microbial communities directly impact greenhouse gas emissions to the atmosphere. We review 24 studies that explore the role of soil microbial communities in vineyards and their influence on grapevine health, grape composition, and wine quality. Studies spanning 2015 to 2018 laid a foundation by exploring soil microbial biogeography in vineyards, vineyard management effects, and the reservoir function of soil microbes for grape-associated microbiota. On the other hand, studies spanning 2019 to 2023 appear to have a more specific and targeted approach, delving into the relationships between soil microbes and grape metabolites, the microbial distribution at different soil depths, and microbial influences on wine flavor and composition. Next, we identify research gaps and make recommendations for future work. Specifically, most of the studies utilize targeted sequencing (16S, 26S, ITS) which only reveals community composition. Utilizing high-throughput omics approaches such as shotgun sequencing (to infer function) and transcriptomics (for actual function) is vital to determine the specific mechanisms by which soil microbes influence grape chemistry. Going forward, understanding long-term effects of vineyard management practices and climate change on soil microbiology, grapevine trunk diseases, and the role of bacteriophages in vineyard soil and wine making would be a fruitful investigation. Overall, the studies presented shed light on the importance of soil microbiomes and their interactions with grapevines in shaping wine production. However, there are still many aspects of this complex ecosystem that require further exploration and understanding to support sustainable viticulture and enhance wine quality.

Keywords: wine; vineyard; terroir; soil; microbial composition; function

Introduction:

The concept of terroir in wine refers to the unique combination of environmental factors, including soil, climate, topography, and human practices, that influence the characteristics of grapes and, ultimately, the flavor and quality of wine (Guzzon et al 2023, Leeuwen et al 2004). While terroir is traditionally associated with macro-level factors such as climate, topography, physical and chemical soil characteristics, recent research has highlighted the role of microbiota, specifically grapevine-associated microbial communities, in potentially shaping the terroir effect (Di et al 2019, Belda et al 2017).

Grapevines host a diverse array of microorganisms, including bacteria, yeasts, and fungi, both on the surface of the grapes, within the grapevine itself and the bulk soil (Gilbert et al 2014, Bokulich

et al 2014). These microbial communities can vary significantly between vineyards, regions, and even individual vines (Griggs et al 2021). They play a crucial role in vineyard ecology, interacting with the plant and influencing its growth (Wagner et al 2014), health, and the development of grapes. For example, grape-associated yeast community is a vital component of the vine-wine system contributing to terroir (Chalvanti et al 2021). Additionally, the diversity and proportion of yeast species change with the grape's maturation stage. As grapes begin to ripen, they are predominantly inhabited by basidiomycetous yeasts (Barata et al 2012). As maturation continues, these initial colonizers are replaced by ascomycetous species that exhibit oxidative or weak fermentative properties, including *Hanseniaspora*, *Metschnikowia*, *Pichia*, and *Candida* (Barata et al 2012). Notably, *Saccharomyces cerevisiae*, the primary yeast responsible for wine fermentation, is infrequently observed. In contrast, overmatured, damaged, or botrytised grapes favor the growth of yeasts with robust fermentative characteristics and others like *Pichia*, *Zygoascus hellenicus*, *Zygosaccharomyces*, and *Torulaspora* (Nisiotou et al 2007; Nisiotou and Nychas, 2007; Barata et al 2012).

The microbiota associated with grapevines can influence terroir in several ways based on which they can be classified into three categories:

Soil microbiota: Soil is an essential component of terroir, and the microbial communities within the soil can impact vine health and grape characteristics. Microbes in the soil interact with the vine's root system, affecting nutrient availability, water uptake, and overall vine physiology. Links to the production of metabolites that influence grapevine metabolism and flavor compounds in the grapes is suggested in some literature but not conclusive (Martins et al 2013, Zhou et al 2020, Zarraonaindia et al 2015). Additionally, knowledge concerning variability within and between vineyards and regions and their contribution to wine terroir is still fragmented.

Epiphytic microbiota: The microorganisms present on the grape, leaf and bark surfaces are the epiphytic microbiota. To date, literature suggest that the composition of epiphytic microbiota can be influenced by vineyard management practices, such as the use of pesticides or fungicides (Martins et al 2013, Bokulich et al 2016, Guzzon et al 2023). The extent to which epiphytic microbiota can affect the fermentation process and contribute to the sensory attributes of the resulting wine is largely unknown. Recent research has begun to indicate that yeasts and bacteria on grape skins can influence the initiation and progression of fermentation, leading to different flavor profiles (Sancho-Galan et al 2021).

Endophytic microbiota: Endophytes are microorganisms that live within the tissues of grapevines. These microbes can have various effects on the vine, including enhancing nutrient uptake, modulating the plant's immune system, and producing bioactive compounds. The presence and diversity of endophytic microbiota can vary between grape varieties and vineyard sites, contributing to the unique terroir expression as suggested by Compant et al (2011), Pacifico et al (2019) and Hamaoka et al (2022), to name a few.

Among the studies to date on the influence of microbial communities on wine terroir, the contribution of the soil microbiome remains inconclusive and least scientifically explored. To address this gap, we review the current state of knowledge of soil microbiota contribution to terroir expression. We present research gaps and highlight future areas of research that warrant attention. For the purpose of this paper, we focus on literature that specifically looks at microbial communities in the soil.

Understanding the influence of soil microbial communities on wine production is crucial. In addition, it is important to explore how microbial biogeography and activity might respond to climate changes. By studying the complex interactions between soil microorganisms, and the environment, we can gain valuable insights into the role of soil microbiota in shaping terroir. This knowledge allows us to comprehend how soil microbial communities contribute to the unique characteristics and flavors found in wines, ultimately helping us manage and manipulate these communities to enhance desired terroir traits or preserve the distinctiveness of specific terroirs. Therefore, in addition to reviewing the literature on soil microbiota in vineyards, we also discuss vine management practices including disease and topics of interest such as phages and their likely relationship with soil microbiota and wine terroir.

Current State of Knowledge on the Microbiota Contribution to Terroir Expression:

We ran a pubmed literature search with the keywords ‘soil’, ‘microbial communities’, and ‘wine terroir’, resulting in 24 studies between 2015 and 2023 (Table 1) and five review papers (Belda et al 2017, Liu et al 2019, Alexandre et al 2020, Cobos et al 2022, Wei et al 2022). There are other studies that focus on grapevine microbiomes in plant parts and not the bulk soil. These were not considered for the purpose of this study.

Table 1. List of studies on soil microbial communities in vineyards.

Year	Source	Methodology
2015	Burns et al 2015	16S rRNA
	Morrison-Whittle & Goddard 2015	26S rDNA
	Zarraonaindia et al 2015	16S rRNA & shotgun metagenomics
2016	Burns et al 2016	16S rRNA
2017	Castenada & Barbosa 2017	shotgun metagenomics
	Mezzasalma et al 2017	16S rRNA & ITS
2018	Hendgen et al 2018	16S rRNA & ITS
	Chou et al 2018	16S rRNA
	Wei et al 2018	16S rRNA & ITS
	Morrison-Whittle & Goddard 2018	26S rDNA
2019	Gupta et al 2019	16S rRNA & ITS
	Liang et al 2019	16S rRNA
2020	Ramirez et al 2020	16S rDNA
	Liu et al 2020	16S rRNA & ITS
	Aguilar et al 2020	16S rRNA, ITS1, ITS2
2021	Teixeira et al 2021	DNA-based assays to detect Single Nucleotide Polymorphisms (SNPs) on three genes of the anthocyanin pathway (UFGT, F3H and LDOX)
	Rivas et al 2021	16S rRNA
	Torres et al 2021	16S rRNA & ITS1
2022	Yan et al 2022	ITS1
	Geiger et al 2022	ITS2, ITS4
	Gobbi et al 2022	16S rRNA & ITS
	Regecova et al 2022	ITS
2023	Larsen et al 2023	16S rRNA & ITS1

	Nanetti et al 2023	16S rRNA
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The concept of ‘terroir’ is intriguing. Despite the surge in literature in the last decade, further research is needed to elucidate the mechanisms by which soil microbes influence grape chemistry and how this can be leveraged to enhance wine quality. Additionally, exploring microbial network dynamics in vineyard soils and understanding how these interactions affect plant health and wine quality could be a fruitful area of investigation.

Earlier studies from 2015 to 2018 (Burns et al 2015, Morrison-Whittle & Goddard 2015, Zarraonaindia et al 2015, Burns et al 2016, Castenada & Barbosa 2017, Mezzasalma et al 2017, Hendgen et al 2018, Chou et al 2018, Wei et al 2018 and Morrison-Whittle & Goddard 2018) laid a foundation by exploring soil microbial biogeography in vineyards, vineyard management effects, and the reservoir function of soil microbes for grape-associated microbiota. For instance, Zarronaindia et al (2015) mentions that belowground bacterial communities differed significantly from those aboveground, and yet the communities associated with leaves, flowers, and grapes shared a greater proportion of taxa with soil communities than with each other, suggesting that soil may serve as a bacterial reservoir. Mezzasalma et al 2017 shared that grape microbiome could be influenced by farming practices and climate conditions. This was deduced by observing microbes present at harvest, and prior to fermentation. However, later studies (2019 onwards) appear to have a more specific and targeted approach, delving into the relationships between soil microbes and grape metabolites, the microbial distribution at different soil depths, and microbial influences on wine flavor and composition.

Concerning bacterial populations, twelve studies found *Proteobacteria* to be the most dominant phylum present (Aguilar et al 2020, Burns et al 2015, Casteñada & Barbosa 2017, Gobbi et al 2022, Gupta et al 2019, Hendgen et al 2018, Liang et al 2019, Liu et al 2020, Rivas et al 2021, Torres et al 2021, Wei et al 2018, and Zarraonaindia et al 2015), majority of which also found *Actinobacteria* to be present in high abundance. Ten studies noted *Acidobacteria* to be present in high abundance (Aguilar et al 2020, Burns et al 2015, Casteñada & Barbosa 2017, Gobbi et al 2022, Gupta et al 2019, Hendgen et al 2018, Liang et al 2019, Liu et al 2020, Rivas et al 2021, and Zarraonaindia et al 2015), while eight studies identified the presence of *Bacteroidetes* in high abundance (Aguilar et al 2020, Burns et al 2015, Casteñada & Barbosa 2017, Gobbi et al 2022, Hendgen et al 2018, Liu et al 2020, Wei et al 2018, and Zarraonaindia et al 2015). *Gemmatimonadetes* was noted in six studies, though not as dominant as the aforementioned phyla (Casteñada & Barbosa 2017, Gobbi et al 2022, Gupta et al 2019, Hendgen et al 2018, Liu et al 2020, and Torres et al 2021), seven studies identified *Firmicutes* as one of the present phyla (Casteñada & Barbosa 2017, Gobbi et al 2022, Hendgen et al 2018, Liang et al 2019, Liu et al 2020, Rivas et al 2021, Wei et al 2018, and Zarraonaindia et al 2015), and ten studies identified *Planctomycetes* in a mix of high, medium, and low abundance (Aguilar et al 2020, Burns et al 2015, Casteñada & Barbosa 2017, Gobbi et al 2022, Gupta et al 2019, Hendgen et al 2018, Rivas et al 2021, Torres et al 2021, Wei et al 2018, Zarraonaindia et al 2015).

Commonly observed fungal phyla were *Ascomycota*, *Basidiomycota*, *Chytridiomycota*, *Mucoromycota* and *Clomeromycota*. Nine studies found *Ascomycota* in high abundance and in some cases the most abundant. (Aguilar et al 2020, Casteñada & Barbosa 2017, Gupta et al 2019, Hedgens et al 2018, Liang et al 2019, Liu et al 2020, Morrison-Whittle & Goddard 2018, Torres et al 2021, Wei et al 2018, and Yan et al 2022). *Basidiomycota* was observed in 9 studies although in high, medium, and low abundance (Aguilar et al 2020, Casteñada & Barbosa 2017, Gupta et al 2019, Hedgens et al 2018, Liang et al 2019, Liu et al 2020, Morrison-Whittle & Goddard 2018, Torres et al 2021, Wei et al 2018, and Yan et al 2022). *Chytridiomycota* and *Mucoromycota* were observed but not as dominant as the other phyla Basidiomycota and Ascomycota (Liu et al 2020, Wei et al 2018, and Yan et al 2022, Aguilar et al 2020, Hedgens et al 2018). *Glomeromycota*, was observed but in low abundance (Aguilar et al 2020, Gupta et al 2019, Liu et al 2020).

Among the reviews that came up, Belda et al (2017) highlights the underestimated role of the soil microbiome in wine production. The study reveals that the soil-associated microbiota significantly influences soil chemistry, grapevine health, and the final sensory properties of wines,

calling for a deeper understanding of these crucial interactions for precision enology practices. Liu et al (2019) emphasizes the role of microbial biogeography, shaped by geographical, climatic, and viticultural factors, as a new perspective to enhance regional characteristics and optimize wine production by managing the present microbes. Relevant to the current study, a review (Alexandre et al 2020) highlights that the role of region-specific microbial communities (microbial terroir) in defining wine characteristics is still debated, requiring further research for a clearer understanding. Cobos et al (2022) discusses how the grapevine microbiome offers potential sources for new and promising biocontrol agents that could serve as effective tools in controlling grapevine trunk diseases. Lastly, Wei et al (2022) discusses the benefits of mimicking natural ecological cultivation to enhance microbial diversity, and sustainability in large-scale natural wine practices.

Together, these studies contribute to a comprehensive understanding of the complex interactions between soil microbiomes, grapevines, and the production of high-quality wine. However, there are still many aspects of this complex ecosystem that require further exploration and understanding to support sustainable viticulture and enhance wine quality. For the purpose of this review, we discuss vineyard management, diseases, phages and next-generation sequencing as topics that are important drivers of our knowledge of the changing landscape of soil microbes in vineyards.

Long-Term Effects of Vineyard Management:

Vineyard management is a critical aspect of the overall health and productivity of vineyards. Its decisions have both short-term and long-term effects on the ecosystem. The long-term effects are significant, with soil health being a key concern (Giffard et al 2022). Vineyard managers use techniques like cover cropping, composting, and organic fertilizers to maintain soil health, which not only ensures grapevines' long-term viability but also contributes to the sustainability of the vineyard ecosystem. Therefore, understanding the long-term impacts of these practices can be instrumental in developing sustainable and environmentally friendly viticultural methods.

Several studies have touched upon the topic of long-term field experiments involving different management practices (Table 1). However, to fully grasp the implications of various agricultural approaches on soil biodiversity and vineyard microbiomes, further research is warranted. Investigating the effects of climate change on microbial community dynamics, their functional roles, and their implications for wine production can help prepare the wine industry for potential challenges (Rivas et al 2021). Notably, one of the few papers that discusses soil diversity impacts through climatic condition changes was Rivas et al (2021). The study indicates a consistent set of microorganisms in both soil and wine, from various phyla, that remain steady over multiple vintage years from Argentina.

In addition to investigating long-term effects, comparative studies spanning different viticultural regions worldwide can offer valuable insights (Tofalo 2021). Specifically, soil tilling in viticulture is likely to have significant implications on nutrient and soil organic carbon content with correlations to the microbial community composition and associated function (Smith et al 2016). Yet, the impact of this practice on soil microbial abundance, richness and its link to wine terroir remains unexplored. Notably, studies report highly variable results on the number of unique operational taxonomic units (OTUs) in tilled vs. no-till fields (Andrade et al 2002, Buckley & Schmidt 2003, Jangid et al 2011). Such cross-regional analyses have the potential to reveal both common patterns and unique characteristics associated with specific wine-producing areas.

Moreover, there is significant promise in leveraging advancements in precision viticulture (Ferro & Catania 2023) for targeted microbial management in vineyards. The integration of cutting-edge technologies into viticulture can optimize soil microbial communities, bolster grapevine health, and elevate overall wine quality. Delving into the potential of precision viticulture to influence the dynamics of vineyard microbiomes can lead to innovative practices that maximize wine production efficiency while maintaining environmental sustainability. Multispectral, hyperspectral and thermal sensing are among the most widely used sensors for vineyard monitoring over the last two decades. Vineyard canopy images are also used extensively as alternatives to more destructive techniques to measure soluble solids content, and anthocyanin content, both measures of grape quality

(Loggenberg et al 2018). Such images would be vital in predicting an impending poor harvest following severe environmental stress such as drought or heavy precipitation events.

Grapevine Trunk Diseases:

Grapevine trunk diseases remain a significant threat to the wine industry (Kenfaoui et al 2022). The most common microorganisms that grapevines tend to be most susceptible to are *Plasmopara viticola* (downy mildew), *Elsinoe ampelina* (anthracnose), *Guignardia bidwellii* (black rot), *Erysiphe neator* (powdery mildew). However, confusion remains concerning the cause, and progression of the disease, many of which result in serious infections, loss of yield or quality. Interestingly, recent research (Li et al 2023) has demonstrated associations between belowground microbiota *Fusarium spp.* and exacerbating progression of grapevine trunk disease. In-depth studies are needed to decipher the interactions between the host grapevine and the diverse fungal communities, some of which may act as opportunistic pathogens under specific conditions. Such insights can aid in devising targeted strategies for disease management and prevention. Another particularly intriguing area of research is the role of both asymptomatic and symptomatic grapevines in harboring pathogenic fungi. Understanding the differences in microbial communities between these two states can shed light on the mechanisms underlying the progression of trunk diseases (Fall et al 2023).

Bacteriophages for Bacterial Community Regulation and Pathogenic Inactivation in Soil:

In winemaking, the soil's microbial diversity, including bacteriophages, can indirectly influence grape chemistry by affecting nutrient availability, water stress, and overall grapevine health (Mao et al 2019). Bacteriophages are viruses that infect and replicate within bacterial cells, and they are abundant in various environments, including vineyards and wineries. Bacterial communities in the soil play crucial roles in nutrient cycling, plant health, and grapevine interactions. Bacteriophages can selectively target specific bacterial species, altering the microbial composition and dynamics in the soil, including pathogen inactivation (Mao et al 2019). Braga et al (2020) demonstrated that changes in phage pressure could likely impact soil bacterial community composition and diversity with important implications for soil functions. Indeed, changes in soil microbiomes may lead to variations in grape metabolite composition, impacting the grapes' flavor and aroma compounds. The field of bacteriophages in wine is still relatively new (Chaib et al 2022), and more research is needed to fully understand their role in their interactions with bacterial communities, and their impact on wine characteristics.

Next-Generation Sequencing: Gaps and Research Needs

To identify and quantify the microorganisms present in the soil (Table 1), several studies have opted to use next-generation sequencing. Among the studies we reviewed, 16 focused on amplicon sequencing of the 16S rRNA gene, which is widely used in molecular biology and microbiology for the identification and classification of microorganisms, particularly bacteria and archaea. 12 papers focused on sequencing the ITS regions and their subregions, and 2 papers used 26S rDNA. ITS and 26S rDNA are used widely to characterize eukaryotic organisms. Relevant to wine making, yeast communities were of interest to these papers. Only 2 studies utilized shotgun sequencing, that analyze entire genomes and complex microbial communities without the need for prior knowledge of specific DNA regions.

Although targeted sequencing (16S rRNA, ITS and 26S rDNA) can reveal insights into the microbial community composition, shotgun sequencing offers a broader picture of the entire genome, making it suitable for functional information as well. However, the information obtained from shotgun sequencing (also sometimes referred to as whole genome sequencing) can only lead to inferences about function. On the other hand, transcriptomics provides insights into the active metabolic pathways and biological processes occurring in the soil, giving a more dynamic view of microbial activity than just analyzing the microbial composition. To our knowledge, there are no

studies that have utilized transcriptomics to investigate the actual function of soil microbial communities in vineyard settings.

Metagenomics and transcriptomics of soil microbial communities in vineyards offers a powerful tool for gaining functional insights into soil microbiomes, supporting sustainable vineyard management, and contributing to the production of high-quality wines with a distinct terroir. Firstly, it helps in predicting the roles of microorganisms in nutrient cycling, organic matter decomposition, and other essential processes for vineyard health (Zarik et al 2016). Secondly, transcriptomics helps in monitoring how soil microbial communities respond to changes in environmental factors, such as climate, soil management practices, and agricultural inputs (Stewart et al 2011). Thirdly, this type of analysis can help identify specific microbial species or groups that play essential roles in promoting soil health, enhancing nutrient availability, and protecting grapevines from diseases. Such beneficial microbes can be targeted for potential use as biofertilizers or biocontrol agents. Lastly, such methods helps in understanding how soil microbes contribute to the regional identity of wines (terroir), which is essential for promoting authenticity and quality (Nwachukwu & Babalola 2022).

Conclusion

The influence of soil microbial communities on grapevine-associated microbiota is an area of active research and ongoing exploration. While there is growing evidence supporting the significance of soil microbial influence on grapevines and their associated microbiota, aspects of this interaction remain subject to debate and further investigation. For example, Zarraonaindia et al (2015) focused on the spatial and temporal dynamics of bacterial communities associated with grapevine organs (leaves, flowers, grapes, and roots) and soils. The study explored factors like vine cultivar, edaphic parameters, vine developmental stage, and vineyard that influence the microbial communities, but it did not directly address the influence of soil on grape microbiota. On the other hand, Chou et al (2018) investigated the impact of under-vine soil management practices (herbicide application, soil cultivation, and natural vegetation) on the microbiomes of soil and grapes in a Riesling vineyard. The study showed that soil management practices influenced the soil microbiome but did not have corresponding changes in the grape-associated microbiome, suggesting that other vineyard management practices or environmental factors may be more influential in shaping the grape microbiota. To further understand the specific mechanisms by which soil microbial communities influence grapevine associated microbiota, next-generation sequencing methodologies (-omics) is needed to characterize the function and genes involved.

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