The microbiota of the grapevine holobiont: A key component of plant health

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Review

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Pauline Bettenfeld [a,b,1], Jasmine Cadena i Canals [a,1], Lucile Jacquens [a], Olivier Fernandez [b], Florence Fontaine [b], Evert van Schaik [a], Pierre-Emmanuel Courty [a,2,*], Sophie Trouvelot [a,2]

[a] Agroécologie, AgroSup Dijon, CNRS, Université de Bourgogne, INRAE, Université de Bourgogne Franche-Comté, Dijon, France
[b] Université de Reims Champagne-Ardenne, Unité Résistance Induite et Bioprotection des Plantes EA 4707 USC INRAE 1488, SFR Condorcet FR CNRS 3417, Reims, France

HIGHLIGHTS

- Grapevine interacts different microbiota living around and within its tissues
- Addition of microbial genes to plant genome gives supplementary functions to the holobiont
- The composition of grapevine microbiota varies according to endogenous and exogenous factors
- Microbiota variations can lead to perturbations of grapevine metabolism
- The link between symptom emergence of dieback and microbial imbalance is currently studied

GRAPHICAL ABSTRACT
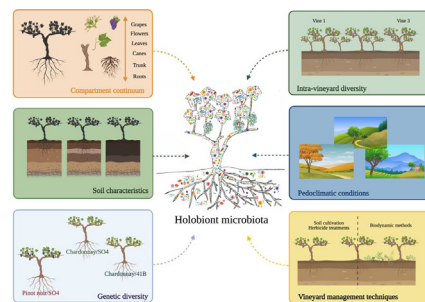
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ABSTRACT

Background: Grapevine is a woody, perennial plant of high economic importance worldwide. Like other plants, it lives in close association with large numbers of microorganisms. Bacteria, fungi and viruses are structured in communities, and each individual can be beneficial, neutral or harmful to the plant. In this sense, microorganisms can interact with each other and regulate plant functions (including immunity) and even provide new ones. Thus, the grapevine associated with its microbial communities constitutes a supra-organism, also called a holobiont, whose functioning is linked to established plant-microorganism interactions.

Aim of review: The overall health of the plant may be conditioned by the diversity and structure of microbial communities. Consequently, an optimal microbial composition will consist of a microbial balance allowing the plant to be healthy. Conversely, an imbalance of microbial populations could lead to (or be generated by) a decline of the plant. The microbiome is an active component of the host also responsive to biotic and abiotic changes; in that respect, a better understanding of the most important drivers of the composition of plant microbiomes is needed.

Key scientific concepts of review: This article presents the current state of the art about the grapevine microbiota and its composition according to the plant compartments and the influencing factors. We also

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I. Introduction

Grapevine is a perennial plant of global economic importance: the International Organization of Vine and Wine estimated that 7.4 million hectares were planted with vineyards worldwide in 2018 (including 3.7 in Europe and 2.2 in Asia, the two most important surfaces) and produced 77.8 million tons of grapes. The diversity of technical routes (*e.g.,* pruning, fertilization) and associated soils and climates allow the production of a wide variety of wines (263 million hectoliters in 2019). The organoleptic characteristics of wines depend on different factors such as the localization of the vineyard, the winemaking process or the microbial flora associated with grapes and the winery. These concepts are at the origin of the notion of "terroir", which encompass the biotic and abiotic parameters of a given region to explain the production of a wine with unique characteristics [1–3].

The hologenome theory of evolution emerged in 2008. It is based on four axioms: (1) all animals and plants establish symbiotic relationships with microorganisms, (2) symbiotic microorganisms are transmitted across generations, (3) the host-symbiont association affects the fitness of the holobiont within its environment, (4) variations in the hologenome come from changes in the host or the microbiota genomes; under environmental stress, the symbiotic microbial community can change rapidly [4,5]. Therefore, the plant microbiota gathers all eukaryotic (fungal, protozoan, chromistan) and prokaryotic (bacterial, archaeal) microorganisms as well as viruses living in association with them.

Most of the currently published studies on grapevine microbiota mainly target fungal and/or bacterial communities. The microbiota is found in a latent or active state in each organ, from the roots to the aerial parts, in the form of endophytes (*i.e.,* colonizing internal tissues) or epiphytes (*i.e.,* on the surface of tissues, in contact with the environment in the rhizosphere, lignosphere, caulosphere, phyllosphere, anthosphere or carposphere) [6,7]. The endophytic and epiphytic bacterial and fungal communities associated with the different grapevine organs are influenced by the taxonomic composition of the soil surrounding roots, which is the main reservoir of microorganisms (endophytic bacteria [8–14] and fungi [15–19]). Arbuscular mycorrhizal fungi (AMF) constitute a separate category among soil microbes. They form a mutually beneficial symbiosis with grapevine roots called mycorrhiza [20]. AMF, together with certain endophytic bacteria, promote grapevine growth and resistance to biotic or abiotic stresses [21,22].

Plant-fungus and plant-bacterium interactions are triggered by the ability of microorganisms to fix themselves on plant tissues and live within them. This led to the ideas of the *microbiome* as the "set of genes brought by microbes forming the microbiota within a holobiont" [23] and the *microbiota* as a "second plant genome", a supplementary source of genes and functions, or a full component of plant defense [6,24,25].

Considering the holobiont as a functional whole opens up new fields of investigation, particularly in terms of biotechnological applications [23,26]. While metagenomic methods are used to identify the present microbial genes and associated functions, transcriptomic, proteomic and metabolomic methods are used to study the spatio-temporal and functional dynamics of the grapevine holobiont [24]. Each of these -omics methods is applied individually in plant research, including research on the grapevine, but their combination is still rare.

II. Origin, structure and composition of the plant microbiota

II.1. Origin of the plant microbial community

II.1.1. Getting into the plant

Finding microbial species both present outside and inside the different plant compartments suggests that microbes find entry points in the plant and then reach endospheric tissues. The root system gathers different gateways: intercellular junctions in the epidermis where root hairs or lateral roots emerge or wounds on the rhizoplane are widely used by soil microorganisms. Once the plant innate immunity is overcome [27], they colonize the root cortex or the vascular system to spread within the host. It appears that the following colonization *via* grapevine roots [28], 28 % of rhizosphere microorganisms can colonize the root endosphere, and 4 % can reach the aerial parts [11,29].

Roots exude a various range of compounds differing in quality and quantity among plant species and developmental cycles. This rhizodeposition leads to an active selection of soil microbes, resulting in different bacterial and fungal communities living nearby in the surrounding soil or within plant roots [30,31]. Different gateways have also been described in aerial parts, such as leaf stomata, trichomes, surface wounds or hydathodes [32,33]. Piercing and sucking insects (*e.g.,* leafhoppers, wasps) can also inject microorganisms directly into the plant vascular system [34,35].

II.1.2. Mechanisms and origins of microbiota dispersal

The microbiota is dispersed from grapevine to grapevine [36,37] or the surrounding flora and fauna [38] and the environment through different mechanisms: anemochory, zoochory, hydrochory and anthropochory. As agrosystems, vineyards are strongly modified by humans (anthropization), who can also be a source of microorganisms [39].

The soil is now often seen as a bacterial reservoir. It has been observed that the microbial communities of leaves, grapes and flowers share many more taxa with the soil than among them [29,40]. 28 % of the endophytes found in the biocompartments they studied (bulk soil, rhizosphere, roots, cordons, canes and sap) were of soil/rhizosphere origin [28]. Some microorganisms in the aerial parts can come from the soil through tillage, which generates dust that may deposit on leaves, berries, and trunks [41]. Indeed, as a perennial part, the trunk is also a microbial reservoir for annual parts (shoots, leaves, grapes; [42]).

II.2. Different microbiota within the plant

The studies that covered the microbiota in the soil – roots – aerial parts continuum found pronounced microbiota differences between belowground and aboveground compartments (**see Table 1** and Fig. 1). Indeed, it seems that the bacterial specific richness and diversity vary following a decreasing gradient from the soil to the aerial parts [41,43,44]. In addition, fungal specific richness and diversity appear to decrease from the bulk soil to the endorhizosphere, with a sharp decrease from the surrounding soil to the endorhizosphere; this suggests a significant limitation of root colonization by fungi [45].

These differences seem more evident when studying epiphytes; while endophytes, which move around the whole plant through the sap, appeared to be more mixed [28]. Moreover, functional

Table 1
Bacterial and fungal microbiota associated with grapevine compartments.

	BACTERIA			FUNGI			TOTAL DIVERSITY
	Majority phyla	Majority genus	References	Majority phyla	Majority genus	References	
Phyllosphere	*Acidobacteria* **Actinobacteria** *Bacteroidetes* **Firmicutes** *Gemmatimonadetes* **Proteobacteria**	*Arthrobacter* **Bacillus** *Blastococcus* *Curtobacterium* **Enterococcus** *Flavobacterium* *Methylobacterium* *Pantoea* **Pseudomonas** *Sphingomonas* **Streptococcus**	[9,19,31,44–46]	**Ascomycota** *Basidiomycota* *Zygomycota*	**Alternaria** **Aureobasidium** *Cladosporium* *Guehomyces* **Epicoccum** *Mucor* *Pandora* *Rhizopus* *Sporormiella*	[19,32–34,45–51]	
Reproductive organs	*Acidobacteria* *Actinobacteria* *Bacteroidetes* *Firmicutes* **Proteobacteria**	**Bacillus** *Blastococcus* *Enterobacter* *Erwinia* *Gaiella* **Massilia** *Methylobacterium* *Micrococcus* **Pseudomonas** **Sphingomonas**	[11,31,43,44,46,47,52]	**Ascomycota** *Basidiomycota*	*Alternaria* **Aureobasidium** **Botrytis** **Cladosporium** *Cryptococcus* *Davidiella* *Guehomyces* **Penicillium** *Sporobolomyces* *Rhodotorula*	[46,47,53–55]	
Woody parts	*Acidobacteria* *Actinobacteria* *Bacteroidetes* *Chloroflexi* **Proteobacteria** *Verrucomicrobia*	*Achromobacter* **Bacillus** *Bradyrhizobium* *Cellulomonas* *Curtobacterium* **Pseudomonas** **Sphingomonas** *Xanthomonas*	[43,44,56,57]	**Ascomycota** *Basidiomycota*	*Cladosporium* *Alternaria* *Chaetomium* *Aureobasidium*	[34,56]	
Soil, roots, rhizosphere	**Actinobacteria** **Acidobacteria** *Bacteroidetes* *Chloroflexi* *Firmicutes* *Planctomycetes* **Proteobacteria** *Verrucomicrobia*	**Bacillus** *Blastococcus* **Clostridium** *Flavobacterium* *Gaiella* *Methylobacterium* *Micrococcus* *Nitrososphaera* **Pseudomonas** **Rhizobium** *Steroidobacter* **Sphingomonas**	[27,30,31,40,42,44,57–61]	**Ascomycota** *Basidiomycota* *Chytridiomycota* *Glomeromycota* *Mortierellomycota* *Mucoromycota* *Zygomycota*	*Alternaria* *Archeospora* *Aspergillus* *Dactylonectria* *Fusarium* *Glomus* *Mortierella* *Mucor* *Paraglomus* *Penicillium* *Peziza* *Phaeoacremonium* *Sclerocystis* *Trichoderma*	[30,41,51,59,60,62–66]	
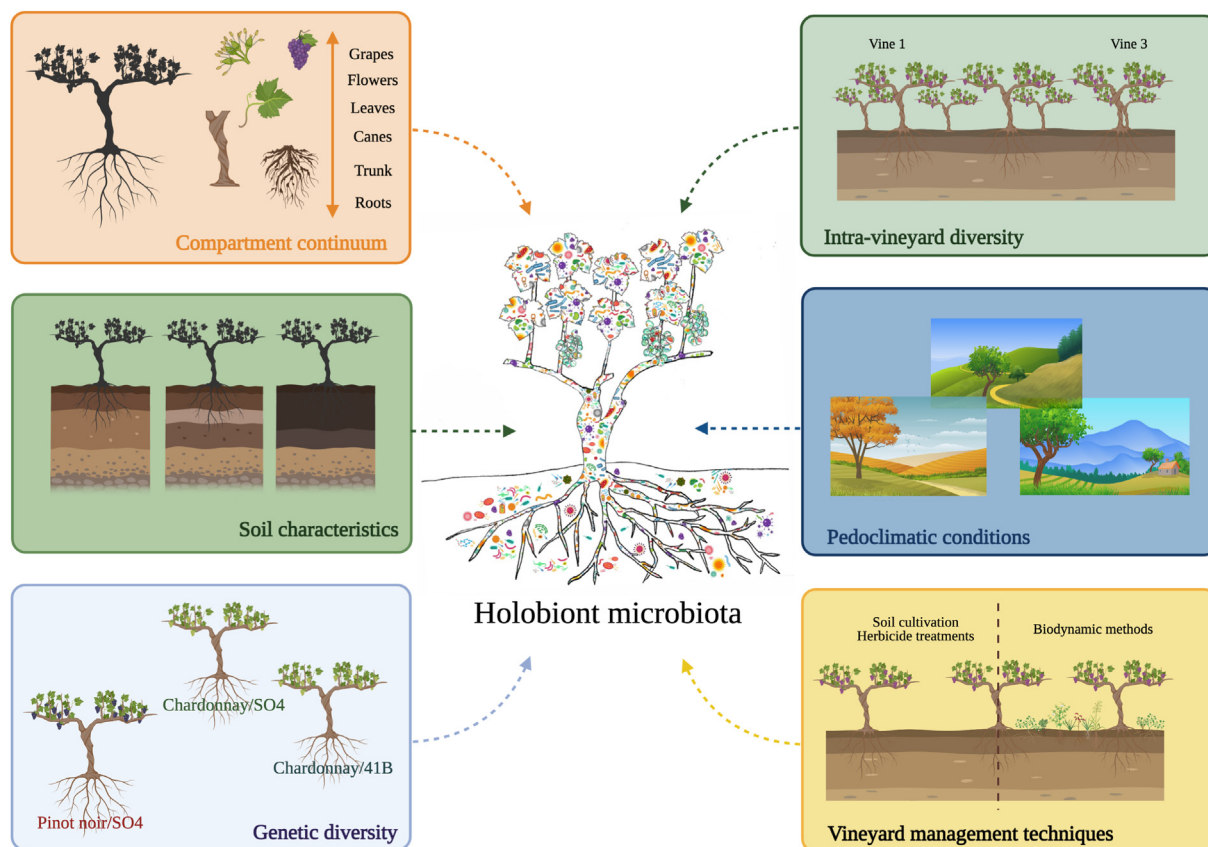
Fig. 1. Factors known to affect the composition and the structure of grapevine microbiota.

differences between the microbiota from aerial or underground tissues were found [29]. The environmental conditions of the compartments strongly differ in terms of temperature, moisture, light incidence or even human contact. In consequence, it is no surprise that the diversity and structure of microbial communities of grapevine should be compartment dependent and that the diversity found in aerial parts is lower as opposed to the underground compartments [29,38,46–48].

II.2.1. Belowground compartments: Fine roots and rhizosphere

The sharpest microbial differences are found between the outside and the inside of the roots, confirming the selection by the plant of only certain strains that will be able to cross the rhizoderm and live inside the plant (for bacteria: [29,49]; for fungi: [28,45]). However, the significant discrepancies among the different studies for certain bacterial taxa (*e.g.*, *Chloroflexi* and *Gemmatimonadetes*) show that other factors than root selection act on relative bacteria abundances ([28,29,50] ; see Fig. 1 for other hypotheses considered). Rhizospheric soil is enriched in *Ascomycota*, compared to endosphere roots that are richer in *Basidiomycota* [45]. This difference is found at the trophic level: saprotrophs are relatively more abundant in the soil than in the rhizosphere or endorhizosphere, but pathotrophs and symbiotrophs are not.

However, we have noted that the primers used to amplify fungal sequences target different types of strains (especially mycorrhizal or non-mycorrhizal ones). Consequently, most of the studies devoted to the total fungal diversity of vineyard soils exclude mycorrhizal fungi to only focus on non-mycorrhizal ones, and *vice versa* [51–56]. This choice can result in a taxa bias in some studies.

II.2.2. Aboveground compartments: Woody parts, phyllosphere, anthosphere, carposphere and spermosphere

If we concentrate on the aerial organs, we can differentiate two types of compartments: the annual structures (shoots, leaves, flowers and berries) are differentiated over a vegetative cycle, whereas the perennial structures (woody parts: trunk, spurs and canes) persist year after year, and are reserve structures (especially for sugars and nitrogen) and a microbiota reservoir as explained before. Woody compartments are not completely homogenous, in particular, because of the coexistence of living and dead tissues. We can assume that the microbiota associated with the perennial woody parts is subject to less variation than the microbiota of other aerial parts because of its permanence. It is more diverse because more it is stable over time.

The bacterial microbiota of epiphytic bark is described as being more complex than it is on leaves and grapes [42]. The majority of grapevines planted in European vineyards are grafted, *i.e.*, formed from a scion (a grapevine variety selected for its wine-making qualities) associated with a rootstock (selected according to its interactions with the soil and its resistance to stresses). In grafted plants, bacterial species seem to be fairly regularly distributed according to the woody area and despite diversity, gradients mentioned later, whereas fungal species appear to be more specific to the part of the sampled wood [38].

Among the aboveground vegetative compartments, the phyllosphere is the most studied vegetative compartment, probably owing to its accessibility. The upper and lower surfaces of leaves are subjected to different thermal and water constraints, leading to variations in the abundance and diversity of bacteria (more microorganisms in the upper surface than in the lower one, despite being exposed to greater UV radiations and temperature and moisture variations [57]).

Finally, among the anthosphere, carposphere and spermosphere, there is no doubt that the berry microbiota has been the most studied. Generally, the latter is rarely considered for its link with plant health but more for its effect in wine-making ([58–60] for example). Nevertheless, flower and seeds microbiota have also been the focus of other works. Namely, Compant *et al.* explored endophytes of reproductive organs and found that even the pips were colonized by bacteria (although less than other compartments) [11]. This could also suggest a possible transmission of microbiota between the plant and its descendants (*i.e.* zygotes) [61].

II.3. Differences and similarities among compartments lead to core microbiota

Despite the microbial selection leading to taxonomic differences between compartments [62], the existence of a continuum of species from the underground parts to the aerial parts is at the origin of the concept of core microbiota. The core microbiota can be understood as a set of species found within a single individual in all the studied compartments, but also as a set of species found in a given compartment on different individuals, whatever their genotype, age, location, and the climate or edaphic properties [29,63]. The 10 dominant bacterial phyla in the soil, leaves and grapes are *Actinomycetes, Proteobacteria, Firmicutes, Bacteroidetes, Gemmatimonadetes, Acidobacteria, Nitrospirae, Chloroflexi, Verrucomicrobia* and *Planctomycetes* (*e.g.* [13,41,43,64]). This core microbiome can also be demonstrated on a fungal scale, for example with the predominance of *Ascomycota* genus *Cadophora, Cladosporium, Penicillium* and *Alternaria* in the wood of different rootstocks at different developmental stages [65]. Interestingly, the existence of a core microbiome of grapevine (*Vitis vinifera*) independent of the region, the climate and the sampling method was demonstrated [29]. These authors analyzed grapes from New York and Bordeaux as well as grape juice from California and identified several OTUs present in more than 80 % of the samples. In another study, a core mycobiota whose majority composition is independent of the sampled site or season and the grapevine organ considered was also highlighted in a study in Hungary ([66], see Fig. 2).

III. Factors influencing the microbiota in healthy grapevines

The fact that microorganisms are in permanent interaction with each other and with the plant, but also that they can pass from a latent to an active state (whether pathogenic, beneficial or neutral), raises the question of the factors influencing the microbial status of grapevine at a given time. These factors can be termed endogenous (*e.g.*, plant genotype, plant age) or exogenous (*e.g.*, climatic, geographic parameters, cultivation practices) [6,67] (see Fig. 1).

III.1. Genetic diversity of the grapevine

Plant genetic diversity is one of the intrinsic factors influencing the microbiota, more specifically in grapevine both at the scion and rootstock level [68,69]. This can be seen in different studies carried out on the rhizosphere with the same variety grafted onto different rootstocks [28,48,62,69–71] and with different cultivars grafted onto the same rootstock [15].

Rootstock genotypes and their produced rhizodeposition are major drivers of microbial selection and structure in the rhizosphere [72]. Therefore, it came as no surprise that the host genetic control of the microorganisms was more evident in a mature 25-year-old vineyard than in a younger, 7-year-old one [52]. Additionally, genetics plays a crucial role in the innate immune system - a natural barrier microorganisms encounter when establishing a relationship with host plants (*e.g.*, [73,74]. Therefore, the fact that certain rootstocks are resistant or confer resistance to certain pathogens is understandable (*e.g.*, [75–77]). As regards the aerial
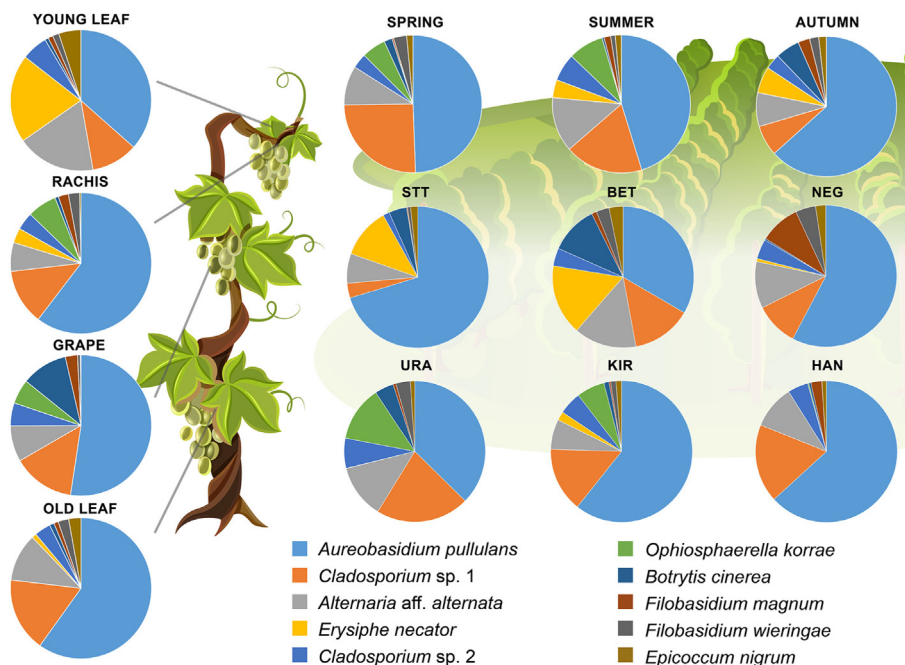
Fig. 2. Above-ground parts of white grapevine *Vitis vinifera* cv. Furmint share core members of the fungal microbiome. Four different compartments (young leaf, old leaf, grape and rachis) have been sampled in 6 different vineyards (STT, BET, NEG, URA, KIR, HAN) in Hungary, at three different developmental stages (spring, summer, autumn) within the same growing year. The fungal endophytic microbiome is dominated by *Aureobasidium pullulans, Cladosporium* spp. and *Alternaria alternata* at every site, season and plant organ, according to Knapp *et al.,* 2021 [66].

parts, the influence of genetics seems to be more complex. Indeed, Singh *et al.* explored the microbial diversity of the phyllosphere and the carposphere of 279 grapevine varieties cultivated in two experimental vineyards around Montpellier (France). They divided the cultivars into three genetic pools and found that genotype had an impact on microbial composition at a particular geographic location [78]. Nevertheless, when they compared five commercially important varieties sampled in three different climatic regions, they concluded that the terroir effect was more important than the genotype effect [46]. Moreover, they observed that the variety-dependent differences in microbiota were greater on the berries than on the leaves. Interestingly, the taxa that best contribute to differentiate cultivars are fermentation microorganisms, which could participate in the typicity of grape variety [40,58]. Finally, differences in the composition of the microbial communities of leaf samples from nine grapevine varieties cultivated in the same plot have been evidenced [79]. Such results further proved that variety could be an important factor affecting the microbial community.

III.2. Intra-vineyard diversity

Today, most vineyards are planted with identical individuals: clonal selection is very common in viticulture and vegetative propagation is the usual practice. Therefore, if we do not consider epigenetics, it is quite easy to evaluate certain factors such as plant age and the phenological stage within a population of genetically identical individuals.

III.2.1. The age

Some studies are focused on vineyard age and compare individual grapevines cultivated in the same plot as regards bacterial endophytes [70], wood fungal pathogens [80], stem fungi [81], rhizosphere soil bacteria [82], or AMF [56]. A positive correlation between grapevine age and the specific diversity of fungal endophytes has been demonstrated [81]. However, the "plant age" fac-

tor may not always be most determining in microbiota variation (*e.g.*, the rhizosphere microbiota [54]).

III.2.2. The phenological stage

Numerous studies have characterized the microbiota in different compartments of grapevine throughout the season, and according to its phenological stages. The "season" or "developmental" variables do not seem to influence the associated microbiota over the year (*e.g.,* comparison of bacterial microbiota in bulk and rhizosphere soil at the flowering and early fruit development stages [83], AMF diversity in the roots [56], endophytic fungal microbiota in aerial tissues [66]). Other studies reveal that the microbiota is unstable over a full growing season (different abundances of wood [65] or soil fungal communities [71,84], high structuring of the leaf microbiota during the vegetative cycle [19,37,85], variations of the culturable bacterial endophyte community [8]).

III.2.3. The plot location

It has also been shown that the microbiota associated with the very same plants can also vary [8,52] or not [86] over successive years, highlighting the impact of seasonality or of variable agronomic practices from one year to another. Finally, interestingly enough, intra-plot variability can be greater than inter-plot differences [87]. Even if the main determinants of the variations observed over successive years are sometimes discussed, these results may acknowledge the importance of specific interactions between microorganisms, host plant and rhizospheric functioning, which can change through sampling seasons.

III.3. Use of phytosanitary inputs

The microbiota composition is sensitive to chemical treatments, as shown by studies comparing vineyards under conventional, sustainable or biodynamic agriculture. The sensitivity of the soil microbiota is dependent on the method [88–90]: the vineyards cultivated under organic farming show greater specific fungal

and bacterial richness and diversity [71,87,91]. It is likely that the products applied for fertilization, weeding and phytopathogen control directly and indirectly influence microbial communities [53,92]. On the other hand, differences in soil microbial communities have been mainly explained by the absence or presence of cover plants, regardless of how they were removed (soil cultivation or herbicide treatment) [93].

Besides the soil microbiota, epiphytic [85] and endophytic [94,95] bacterial or fungal communities can also be affected by pest management [41,60,87]. When nitrogen and sulfur are artificially added to soils over a long period, the microbial diversity associated with the roots is modified, which means that anthropogenic activities (*e.g.* fertilization) can modify the rhizosphere microbiota [30,96,97]. However, the changes in microbial communities in response to chemical treatments and technical itineraries appear to be transient over time [98]. Overall, the results are controversial. Furthermore, it is extremely difficult to draw general conclusions about this point, as two plots under the same practice (conventional, organic, or biodynamic) can receive completely different treatments.

III.4. Soil characteristics, climate and geography

Phytosanitary products have an impact on the composition of the soil microbiota, which is the main reservoir of the aerial microbiota. In that case, we can hypothesize that the soil composition has a major impact on the microbiota composition of the whole grapevine [29,92,99]. Grapevine is a worldwide crop established in diverse pedoclimatic conditions (soil characteristics like grain size, moisture, salinity, nutritional qualities; locations at different altitudes, air temperatures, under different irradiance levels). Vine-growing regions have their own "terroirs", which affect the taste of wine by giving it unique organoleptic properties. The definition of terroir also involves the characterization of the associated microorganisms, because the yeasts naturally present on grapes in the vineyard, in the winery environment or inoculated before the fermentation process significantly impact the final characterists of wines. The grape microbiota varies depending on microclimate variations as well as available nutritional resources [40,42,58,60]. Correlations between rainfall, temperature and the phyllosphere microbiota have been established [98].

The sensitiveness of the microbiota to geographic factors differs among compartments: we can assume that the impact of the terroir is greater on the microbiota of perennial organs than on the microbiotas of leaves or berries [42]. The identification of distinct soil microbial communities in relation to the vineyard location supports the idea that soil microbial communities are decisive in the link between edaphic properties and terroir [92,100,101]. The structure of soil microbial communities can be strongly determined by water stress [102] or altitude [54,86]. This can be explained by variations in air temperature, but also soil characteristics (moisture, clay content and mineral elements). Thus, the physicochemical gradient has a strong impact on the soil microbiota [103]. Likewise, the soil pH, organic carbon content or even phosphorus content have a significant impact on fungal and bacterial communities [104]. A few studies are less assertive as to the importance of the soil chemical characteristics [88] or geographic location on microbial communities, with other factors appearing to be more important (*e.g.*, a stronger compartment effect [45]). Ranking the factors that influence the composition of the microbiota seems to be difficult.

The microbial diversities of plants of different ages or varieties combined with conventional or organic farming have been compared with diverse outcomes. The most important differences can be mainly explained by pest management (before the impact of the cultivar) [94,95], or by the concerned tissue (before the

impact of the cultivar) [46]. Soil management can affect the rhizosphere microbiota more strongly than plant age does [54]. The main driver of the microbial community composition can also be the organ, with edaphic factors explaining the community structure within organs [29].

The degree of influence of the various factors (*e.g.*, vineyard age, type of soil management, rootstock) also appears to be variable depending on the microbes concerned: the impact of soil management and vineyard age on the rhizosphere microbiota has been found greater on bacteria than on fungi [89]. Unfortunately, most of the comparative studies have tested several factors simultaneously, which complicates the task of confidently attributing cause-effect relationships.

IV. Plant fitness depends on microbiota

Among the microorganisms found in grapevine tissues, some are beneficial, others are pathogenic, and others are neutral, relative to their interactions within the host. Also, depending on their status (*i.e.* beneficial *vs* detrimental) in the plant and the fact that they colonize or not certain tissues/compartments, the repercussions generated on the plant could be diverse. Considering the holobiont concept described above, we can suppose that plant health is intimately linked to the interactions between the plant and its microbiota, as it is in the animal kingdom [105]. In other words, the holobiont balance is likely to affect plant fitness [23,30].

IV.1. Beneficial and detrimental microorganisms

IV.1.1. Services provided by beneficial microbiota

The identification of beneficial properties has led to the emergence of bioprotection strategies based on strains with biofertilization (the ability to make mineral nutrients bioavailable to the grapevine), biostimulation (the ability to synthesize a growth-promoting compound) or biocontrol properties (the ability to eliminate pathogens by predation, suppression of virulence factors or niche competition [106]). Among the microbial groups mentioned above, arbuscular mycorrhizal fungi (AMF) and plant-growth-promoting bacteria (PGPB) play such a positive role [107,108].

IV.1.1.1. Bio-fertilization. Some PGPB can solubilize forms of phosphorus that cannot be assimilated by the grapevine by transforming organic phosphorus into soluble ionic phosphate [109]. This bacteria type has been found in several compartments of grapevine: species of *Pseudomonas, Enterobacter, Arthrobacter* and *Bacillus* in the rhizosphere [110,111], *Bacillus* and *Pantoea* in branches [112], *Pantoea* in the endocaulosphere [70]. AMF associated with roots, greatly increase the exploitation of the soil and supply additional water and nutrients [22]. This colonization results in a better fitness of the plant, whose aerial and root biomass values increase [21,113,114]. The increased water uptake capacities and the formation of soil micro-aggregates near the roots that promote water retention enhance the water stress tolerance of mycorrhizal grapevines. Mycorrhizal grapevines also better tolerate iron deficiency, the presence of heavy metals, or soil salinity [22,108].

IV.1.1.2. Biostimulation. Other PGPB can synthesize phytohormones that promote plant growth and help plants face stresses. For example, *Bacillus licheniformis* and *Pseudomonas fluorescens* produce abscisic acid and limit water stress on the roots of *in vitro*-grown plantlets [115,116].

IV.1.1.3. Biocontrol. The rhizosphere bacteria and endosphere bacteria of shoots and branches, like *Achromobacter xylosoxidans,*

Bacillus subtilis or *Pseudomonas fluorescens*, can produce sidero-phores that limit iron availability and deprive other (pathogenic) microorganisms of it [70,110,112]. Some bacteria also degrade certain virulence factors produced by phytopathogens (*e.g.*, oxalic acid produced by *Botrytis cinerea* on leaves [117]). The last type of interaction between a biocontrol agent and a pathogen is parasitism. For instance, *oomycetes* can parasitize the mycelial structures of pathogenic fungi (*e.g., Pythium oligandrum* against *Phaeomoniella chlamydospora* [118]).

Mycorrhiza-induced resistance (MIR) promotes a better tolerance of mycorrhized plants to abiotic and biotic stresses, namely biotrophic and necrotrophic pathogens and nematodes [119]. For example, the AMF *Rhizophagus intraradices* can reduce the number of root galls formed by the nematode *Xiphinema index* (responsible for the transmission of the grapevine fanleaf virus [120,121]) and could reduce the detrimental effects of the fungus *Armillaria mellea* (responsible for *Armillaria* root rot disease [122]).

The number of services that microorganisms can render to grapevines is large. The presence of these microorganisms (PGPB or AMF) within microbial communities seems essential to the health of the holobiont. We can suppose that an imbalance of the specific richness or abundance of these species compared to others could be the cause or at least an aggravating factor of the development of certain declines of grapevine.

IV.1.2. Grapevine declines caused by the presence of pathogenic microorganisms

Like any perennial crop, grapevine is subject to many biotic stresses during its life cycle. Among them and in the context of sustainable viticulture, microbial agents (viruses, bacteria and fungi) are undoubtedly the most problematic since they require constant phytosanitary control [123]. If the literature is particularly rich concerning grapevine fungal diseases (the most consuming of pesticides), the fact remains that viral and bacterial diseases also have a strong impact on the crop production and sustainability of the vineyard.

IV.1.2.1. Fungal actors.
Many declines are directly linked to the presence of a fungal pathogen [124–126]. For some fungal species, pest control strategies exist, are effective and the resulting declines could remain limited. This is the case with *Plasmopara viticola*, *Erysiphe necator* or *Botrytis cinerea* (*e.g.* [127–130]). On the other hand, such strategies are very limited and often not effective enough for other species. This is particularly the case for pathogens involved in grapevine trunk diseases (GTD). Indeed, esca, eutypa dieback and *Botryosphaeria* dieback are major declines affecting young and old vineyards, while others like black-foot or Petri disease (one of the five syndromes composing esca complex) are commonly found only in young vineyards [131,132].

Symptoms common to most GTDs are rotting of the wood (visible through cankers that affect part of or all the trunk section) as well as discoloration and drying out of the shoots and leaves, which can sometimes occur suddenly and late in relation to the primary infection [131,133]. Eutypa dieback is currently found in France, Australia and California [132]. Several *Diatrypaceae* species are responsible for this decline, but the most important one seems to be *Eutypa lata* [133–135].

In *Botryosphaeria,* dieback is caused by a complex of around 30 taxa belonging to different *Botryosphaeriaceae* species (*Botryosphaeria, Diplodia, Dothiorella, Lasiodiplodia, Neofusicoccum, Neoscytalidium, Phaeobotryosphaeria, Spencermartinsia*), which cause trunk wood cankers or shoot dieback [133,134,136]. The fungal list involved in the esca decline complex is slightly shorter, but the number of candidates remains substantial (*i.e., Phaemoniella chlamydospora,* different *Phaeoacremonium* and *Fomitiporia* species, *Eutypa lata* and *Stereum hirsutum* [131,133]).

IV.1.2.2. Viral actors.
Grapevine is probably the crop that harbors the greatest number of viruses, which live as a parasite/pathogen inside its cells. The recent expansion of high-throughput sequencing technologies has given acceleration to the discovery of unknown grapevine infecting viruses. To date, more than 70 viruses and five viroids have been identified on *Vitis vinifera* [137]. Although the pathogenicity of all these viruses has not been established, a number of them are responsible for severe grapevine diseases [138]. Such viruses affect several compartments of the grapevine: mainly the leaves (*e.g.*, grapevine fanleaf virus, Arabis mosaic virus, grapevine leafroll associated viruses, grapevine fleck virus), but also the wood (*e.g.*, rupestris stem pitting, corky bark, Kober stem grooving). The causal agents belong to the *Nepovirus, Ampelovirus, Vitivirus, Foveavirus, Marafivirus* or *Maculavirus* genera. Viruses are most of the time transported by biotic vectors (nematodes, cochineals), but transmission can also occur through pruning or grafting [139,140]. Infection is systemic (the virus is present in all the grapevine compartments).

IV.1.2.3. Bacterial actors.
All grapevine tissues can be affected by three major bacterial declines caused by pathogenic bacteria growing and circulating in the vascular system [141]. Bacterial necrosis, whose symptoms are often confused with those of frost or hail (drying out of the leaves and inflorescences and presence of lesions, bursts and cankers on the bunches and the shoots), is caused by *Xylophilus ampelinus*. The European grapevine (*V. vinifera*) is the only known host [142] and this bacterium can grow on grapevine in a latent state without expressing symptoms.

Pierce's disease is characterized by the degradation of xylem vessels and the disturbance of the trunk water flux due to the presence of *Xylella fastidiosa*. Consequently, the leaves dry out, become necrotic and drop [143]. The shoots are also affected, with later bud break and diminished chlorotic growth. However, since the optimum growth conditions for *X. fastidiosa* are warmer environments (*i.e.*, close to 28 °C), that explain why this pathogen is not prevalent in areas where winter temperature drops under 0 °C [144]. Finally, crown gall is caused by *Agrobacterium vitis*, a bacterium that lives quite frequently in the vascular system of the grapevine without causing apparent damage [145]. Nevertheless, tumors of variable sizes can develop following wounds.

IV.2. Appearance of symptoms: An imbalance of the microbial diversity?

The appearance of symptoms, characteristic of a given pathology, is conditioned by the presence of a plant pathogen or of a complex of pathogenic agents whose virulence will be expressed. Decline symptoms are commonly visible only in certain tissues, even if the plant is completely colonized [146]. In addition, pathogens can be present in a latent, harmless form in the plant tissues for years before the decline becomes visible [147,148]. These findings raise the question of the nature of the triggering event.

IV.2.1. Microbial balance is sensitive to abiotic and biotic stresses
IV.2.1.1. Impacts of abiotic stresses.
The impact of certain abiotic stresses (*e.g.,* heat, water) on triggering or worsening symptoms has been studied and confirmed [148–150] even if it seems that these stresses are not related to the early phase of infection [151]. The fact that cultural practices or abiotic stresses also influence the composition and structure of the microbiota enlightens the hypothesis of a microbial shift associated with certain grapevine declines. Note, however, that the microbial shift could either be the direct cause of the decline or the consequence of the impact of another stress (with an indirect cause and effect relationship). This hypothesis was confirmed by studies mainly carried out on annual plants [152–154] as well as on some perennial plants too

(shifts in the microbiota linked to horse chestnut bleeding canker disease in [155], to olive knot disease in [156], to huanglongbing in citrus in [157] or to acute oak decline in [158]).

IV.2.2.2. Impacts of biotic stresses
IV.2.2.2.1. Human interventions. The expression of some decays has been linked to human intervention, *e.g.*, in the case of crown gall. Both the soil and contaminated plant material used in nurseries (in spite of hot water treatments) are sources of *Agrobacterium vitis*. Once the bacterium is inside the vascular system, any kind of stress that requires cell multiplication can cause the appearance of crown galls: grafting procedures, wounding due to the passage of farming devices, pruning or removing suckers are plausible human activities causing the development of this illness [145,159,160]. Therefore, we can easily relate human intervention to the development of this decline as such.

IV.2.2.2.2. Microbial pathogens. Despite technological advances in metagenomics and the significant reduction in costs associated with these techniques, there are only few studies to date that focus on the comparison of the microbiota in symptomatic (*i.e.,* declined) and asymptomatic grapevines, especially for bacterial dieback. In the case of crown gall disease, *A. vitis* has been found significantly present only on the graft point of ill plants compared to healthy ones [159]. Interestingly, specific richness was higher in the graft union of infected plants than in the graft union of healthy grapevines. Moreover, the dominating microbiota varied throughout the year in healthy samples, while in symptomatic ones, the same three species (*Pseudomonas* sp., *Enterobacteriaceae* sp. and *Agrobacterium vitis*) prevailed year-round. In Pierce disease, the absence or presence of the disease impacts the endophytic communities present in the canes. A positive correlation between has been found between this decay and four taxa with very low relative abundances: *Bacillus, Pediococcus, Caulobacter* and *Dialister* [161].

The existing work on fungal declines has mostly been carried out in relation to wood declines, especially esca. In their study, Bruez *et al.* analyzed the fungal microbiota of wood tissues of grapevines with no foliar symptoms of esca or eutypa dieback [80]. Despite the absence of visible symptoms, they found many GTD pathogens among the community and concluded that a balance via competition was maintained between pathogenic fungi, mycoparasites and saprobes and prevented the development of symptoms. These results are supported by another study in which it is shown that the differences in fungal composition between symptomatic and asymptomatic plants are less important than differences between organs within a same plant [99]. The factors that trigger the imbalance allowing pathogens to express themselves still remain to be identified.

Earlier, Bruez *et al.* compared the wood fungal communities of plants with and without visible leaf symptoms of esca. No significant differences in the composition of the communities were demonstrated. In addition, the necrotic areas of the wood were not richer in pathogenic fungi than the others [162]. Similar results were highlighted by [47] and [146] (see Fig. 3). It seems that the onset of symptoms cannot be correlated with the mere presence of the fungus responsible for the decline inside the wood or with its greater or lesser abundance [38] (this is also the case for other fungal diseases such as *hoja de malvón* [126]). A recent study even supposes that *Fomitiporia mediterranea* virulence (one of the pathogenic fungi responsible for esca) and in particular its capacity to degrade wood is due to an interaction with certain bacteria present in the wood [163]. Nevertheless, significant differences in endophytic bacterial composition have been found between the wood of symptomatic grapevines and the wood of asymptomatic grapevines, whether they were necrotic or not: important differences for *Bacillales* - more abundant in asymptomatic plant -, *Xanthomonadales, Rhizobiales, Enterobacteriales* and unidentified

taxa - more abundant in symptomatic grapevines - [162]. Moreover, rhizosphere bacteria are more numerous at the base of asymptomatic plants than at the base of plants whose leaves show symptoms of esca [140].

The community composition does not vary [164]. Differences in microbial communities between symptomatic and asymptomatic plants, when they exist, seem to be localized at the level of the grapevine rhizosphere, not in the wood or the leaves (see Fig. 3; [146,165,166]. The abundance of the genera *Phaeoacremonium* and *Phaeomoniella* has been found higher in soils associated with symptomatic grapevines compared to asymptomatic ones [55]. Therefore, the source of pathogenic inoculum would be located in the soil and could be neutralized by the presence of other bacteria, hence a balance in the soils associated with asymptomatic plants (like *Curvularia* or *Coprinopsis*, more abundant in asymptomatic samples).

These results bring into question the differential sensitivity of some fungal or bacterial taxa to biotic or abiotic variations. This is key because answering it could explain the appearance of microbial imbalances in decline situations.

*IV.2.2. What happens in the rhizosphere microbiota of declined grapevines?*
Given how plants recruit microorganisms, especially rhizosphere ones, we can hypothesize that the appearance of symptoms in declining plants is a consequence of a disruption of this recruitment. It is essential for the plant to maintain a permanent balance between recruiting beneficial microorganisms and restricting pathogens. This is not easy because the entry routes are the same [31]. On the one hand, some studies, essentially conducted with annual plants, have shown important active recruitment of beneficial microorganisms in response to the decline, through the secretion of metabolites that stimulate specific microbes in the community [167]. On the other hand, the location of microbes could change (epiphytes become endophytes [13]), raising the question of the determining factors of this change, and its potential modification in case of disease.

As explained previously, anthropogenic activities (*e.g.* fertilization through nitrogen or sulfur deposition) can also modify rhizospheric microbiota, demonstrating the importance of the chemical composition of soils in the establishment of microbial communities. Thus, when studying plant decline, the hypothesis that the microbial imbalance observed in the rhizosphere is due to disruptions of rhizodeposition is plausible. We already know that the composition of root exudates varies according to plant age [168–170] and genotype [72,171,172]. Abiotic stresses like drought or heat can modify rhizodeposition too [173,174].

On the other hand, changes in rhizodeposition have been linked to biotic interactions. For example, the presence of fungal endophytes in *Poaceae* has been correlated to changes in rhizodeposition [175]. The presence of nematodes or other pathogens has an impact on the quality and the quantity of exudates [176,177]. Mycorrhization has a significant impact on the nature of root exudates [178,179]. Thus, the influence of microorganisms (whether pathogenic or not) external to the plant on exuded metabolites seems to be proven, essentially in annual plants.

IV.2.3. Altered functions of the root microbiota may be related to the onset of symptoms
In the case of woody plants, the symptoms of decline can often be linked to problems with the storage and the management of reserves – *e.g.,* a lower photosynthesis rate or vascular system degradation [23,180]. The quality and quantity of root exudates are directly linked to the physiological state of the plant (including the quality and quantity of its reserves; Fig. 4). The appearance of
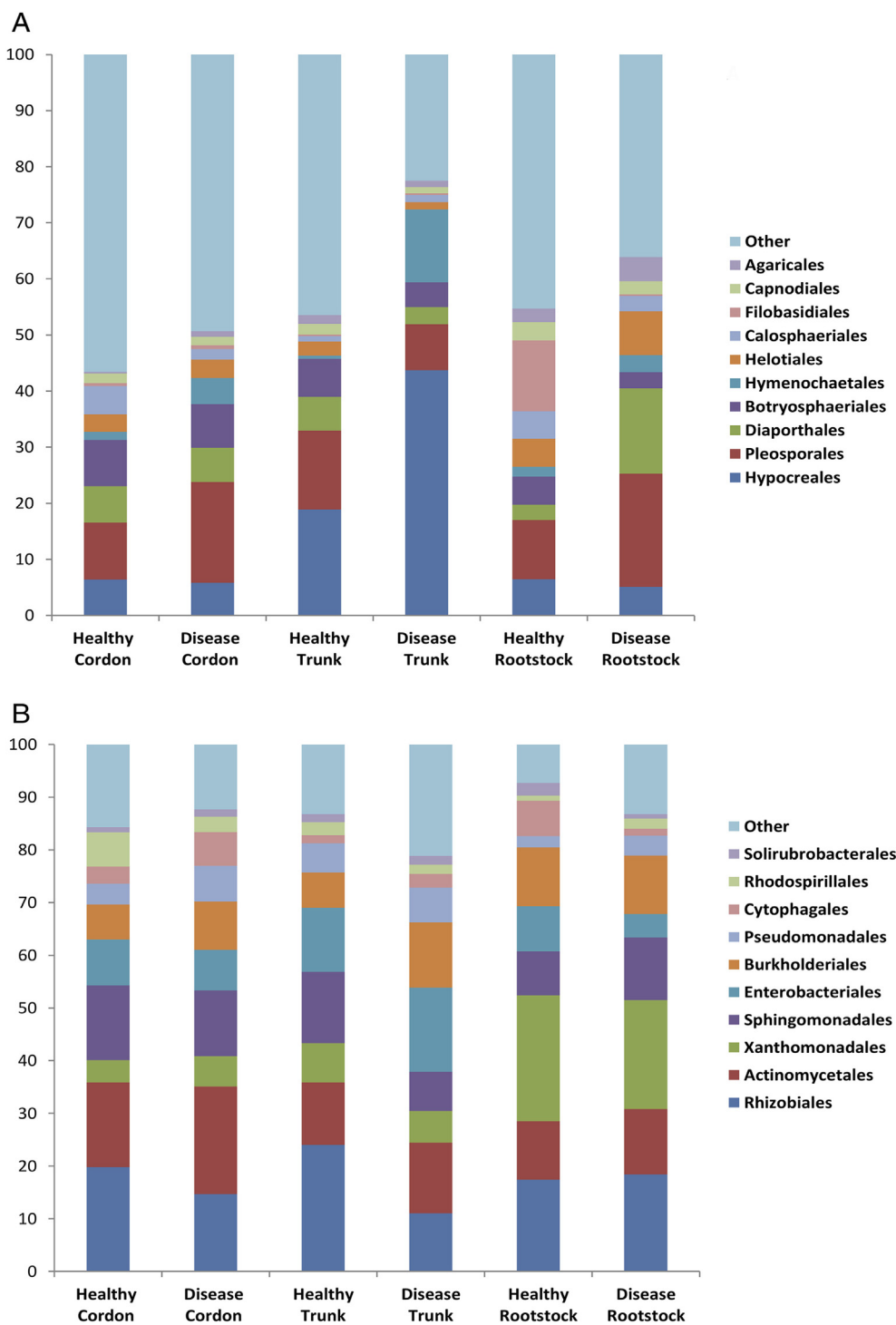
Fig. 3. Meta-barcoding analysis of fungal (A) and bacterial (B) microbiota colonizing non-necrotic woody tissues from healthy and esca-diseased young grapevines. DNAs were extracted from different organs: rootstock, trunk and cordon. Only the 10 most abundant orders are displayed. In this experimental context, fungal and bacterial microbiota varied according to organs but not diseased plant status (**according to Bruez et al., 2020** [146]).

decline symptoms can be explained by two interrelated hypotheses:

– The presence of a pathogen in the aerial parts disturbs certain metabolic processes, like storage [181]. In consequence, rhizodeposition can be modified, and so can the composition of the rhizosphere microbiota [182–184]. This leads to an alteration of the functions performed by this microbiota ([157]; see Fig. 4), and can contribute to weakening the plant.

– An imbalance in the rhizosphere microbiota leads to a modification of the elements taken up by the plant. As a result, storage is altered and the plant is weakened and more susceptible to the pathogens present in its tissues in a latent manner.

To verify these hypotheses in the case of diebacks impacting grapevine, clues can be provided by the small number of studies exploring the relationships between the rhizosphere microbiota and declines due to nutritional dysfunctioning. D'Amico *et al.*
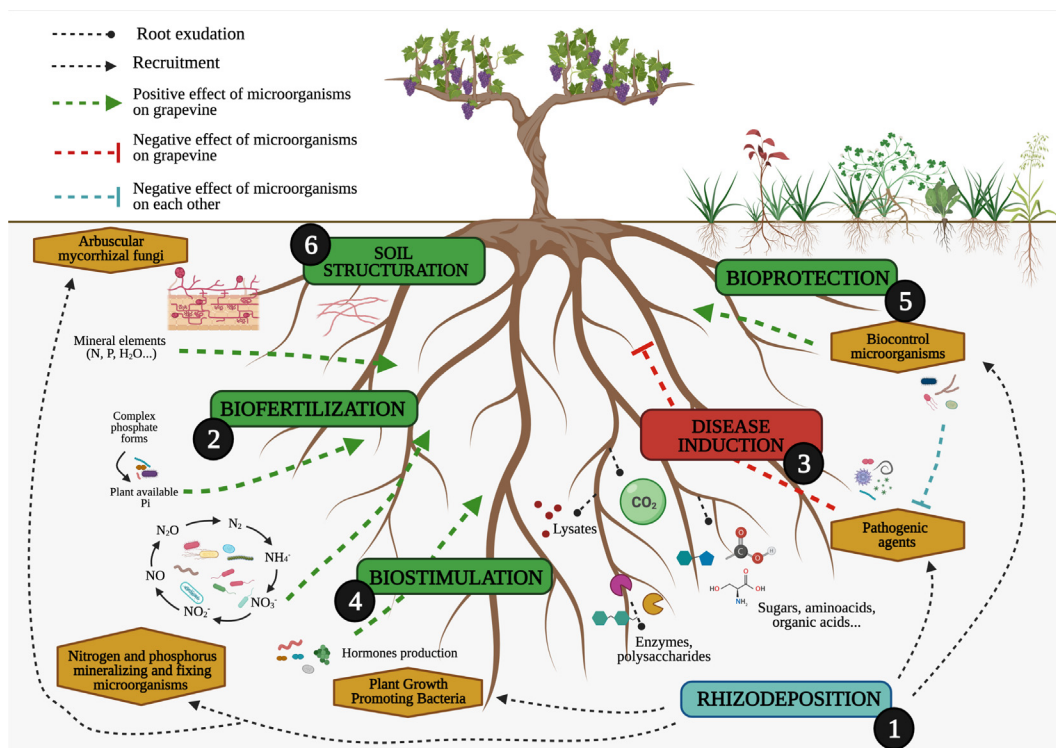
Fig. 4. Grapevine-microorganism and microorganism-microorganism relationships in the soil. Such types of interactions are multiple and complex: 1 Root exudates recruit and feed microorganisms. 2 Some microorganisms are nitrogen or phosphorus fixators and mineralize organic matter. Arbuscular mycorrhizal fungi (AMF) supply the host with nutrient resources that are inaccessible to the roots because of their location (**biofertilization**). 3 Some pathogenic agents can induce declines. 4 In addition to their ability to induce the production of phytohormones by plants, certain plant-growth-promoting bacteria (PGPB) can synthesize them directly. Certain phytohormones regulate plant growth and increase plant tolerance to biotic and abiotic stresses (**biostimulation**). 5 Some PGPB and AMF participate in the inhibition or suppression of pathogens *via* competition for ecological niches or for resources through antagonism, by inducing plant resistance, by interfering with the pathogen signaling systems or by suppressing pathogen virulence factors (**biocontrol/bioprotection**). 6 The mycelium and the mucilage of certain microorganisms enhance the cohesion between soil particles and create microaggregates; as a result, the soil structure is improved (inspired from [161]).

compared the rhizosphere microbiota of two different rootstocks – 1103P, known in Italy to give potassium deficits, and 5BB, which provides good K levels – to see if the differences in potassium uptake were attributable to the root microbiota [185]. The microbiota of 1103P had a reduced diversity compared to 5BB, particularly for microorganisms solubilizing potassium. In a study focused on the relation between microbiota and ferric chlorosis, the magnesium and chlorosis levels of the leaves were significantly correlated with the composition of the soil bacterial community: the bacterial microbiota of the grapevines displaying ferric chlorosis was significantly different from the microbiota of the healthy grapevines [101].

V. Conclusion and perspectives

Like all plants or other macroorganisms, the grapevine closely interacts with a large number of microorganisms that can modulate its physiology throughout its life cycle, keeping the grapevine holobiont healthy or not. The -omics sciences have marked a turning point in the history of biology, especially in the description of the taxonomic composition of the microbial communities of isolated compartments of healthy-looking and decaying grapevine.

To face the numerous diebacks that affect the grapevine, we need to better understand plant microorganism and microorganism-microorganism relationships, the functional contributions of microbes to the grapevine holobiont, and the changes within communities in a decaying context. Up to date, only few studies addressed the functional characteristics of the microbiota

through metabolomic and transcriptomic approaches in the grapevine holobiont.

Understanding the complexity of the grapevine holobiont is a crucial issue for the future of the wine industry. The study of microbiota in a holobiont context opens large windows onto reduced pesticide and chemical fertilizer inputs through biocontrol, biostimulation and bio-fertilization, which are key levers for the sustainable development of viticulture.

Ethical statement

This article does not contain any studies with human or animal subjects.

CRediT authorship contribution statement

PB and JCC initiated the writing of the manuscript. PEC and ST lead the project administration, got the funding, managed the writing, review & editing and supervised PB and JCC respectively. LJ and EvS contributed to the literature review. FF and OF co-supervised PB's PhD thesis with PEC. All the authors read and approved the final manuscript. All authors approved the submitted version.

Declaration of Competing Interest

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P. Bettenfeld is a PhD student, supervised by PEC, FF and OF. She studies metabolic and taxonomic modifications of the grapevine holobiont in response to fungal diebacks, in order to define biomarkers allowing the early detection of this dieback. She has already published a review in Trends in Plant Science with PEC, FF, OF and ST.

J. Cadena is a Master1 student. Her studies are about grapevine and diseases associated to grapevine. She was supervised by PEC and ST.

L. Jacquens is an assistant engineer working with ST. She is specialist in the study of genes encoding proteins involved in defense reactions.

O. Fernandez is lecturer at University of Reims (France). OF has studied Red-ox response of grapevine at the enzymatic and genetic level when associated with pathogenic fungi.

F. Fontaine is Professor at University of Reims (France). FF is specialized in the study of physiological modifications of grapevine in a dieback context.

E. van Schaik was post-doc in the team of PEC. EVS was involved in the study of bacterial and fungal communities, and in the study of hub species when comparing grapevine holobiont under decline conditions.

P.-E. Courty is Senior Scientist at INRAE Dijon (France). PEC is developing a research theme focused on the role of beneficial microorganisms associated with many plants, particularly arbuscular mycorrhizal fungi and growth-promoting bacteria. PEC works at different scales: from the biotrophic interface to the holobiont. PEC is specialist of transport systems and on diversity of bacterial and fungal communities. Finally, he is associate editor of several scientific journals on plant-microbe interactions (*e.g.*, New Phytologist).

S. Trouvelot is a lecturer at the University of Burgundy (France). ST is a specialist in the study of grapevine physiology and immunity and its "malfunction" during the expression of certain fungal diseases (mildew, powdery mildew, grey rot and wood diseases). PEC and ST are leading a project on the grapevine holobiont and its disfunctioning. In this project, they are associated with all co-authors of this manuscript.