



Review

# Microbiota Ecosystem Services in Vineyards and Wine: A Review

Isabel García-Izquierdo <sup>1</sup>, Victor J. Colino-Rabanal <sup>2,\*</sup>, Mercedes Tamame <sup>1</sup> and Fernando Rodríguez-López <sup>3</sup>

<sup>1</sup> Instituto de Biología Funcional y Genómica (IBFG), CSIC-Universidad de Salamanca, 37007 Salamanca, Spain; igi@usal.es (I.G.-I.); tamame@usal.es (M.T.)

<sup>2</sup> Departamento de Biología Animal, Ecología, Parasitología, Edafología y Química Agrícola, Facultad de Ciencias Agrarias y Ambientales, Universidad de Salamanca, 37007 Salamanca, Spain

<sup>3</sup> Departamento de Economía Aplicada, Facultad de Ciencias Agrarias y Ambientales, Universidad de Salamanca, 37007 Salamanca, Spain; frodriguez@usal.es

\* Correspondence: vcolino@usal.es; Tel.: +34-676-643-770

**Abstract:** The domestication of vines started in Asia 11,000 years ago, although it was not until the 19th century that oenology was established as a scientific discipline thanks to the research of Louis Pasteur on the role of microorganisms in wine fermentation. At the present time, the progression in next-generation sequencing (NGS) technologies is helping to facilitate the identification of microbial dynamics during winemaking. These advancements have aided winemakers in gaining a more comprehensive understanding of the role of microbiota in the fermentation process, which, in turn, is ultimately responsible for the delivery of provisioning (wine features and its production), regulating (such as carbon storage by vineyards, regulation of soil quality, and biocontrol of pests and diseases) or cultural (such as aesthetic values of vineyard landscapes, scholarly enjoyment of wine, and a sense of belonging in wine-growing regions) ecosystem services. To our knowledge, this is the first review of the state of knowledge on the role of microbiota in the delivery of ecosystem services in the wine sector, as well as the possibility of valuing them in monetary terms by operating logic chains, such as those suggested by the SEEA-EA framework. This paper concludes with a review of management practices that may enhance the value of microbiota ecosystem services and the role of smart farming in this task.

**Keywords:** ecosystem services; microbiota; vineyard; wine



**Citation:** García-Izquierdo, I.; Colino-Rabanal, V.J.; Tamame, M.; Rodríguez-López, F. Microbiota Ecosystem Services in Vineyards and Wine: A Review. *Agronomy* **2024**, *14*, 131. <https://doi.org/10.3390/agronomy14010131>

Academic Editor: Youssef Roupheal

Received: 6 September 2023

Revised: 29 December 2023

Accepted: 2 January 2024

Published: 4 January 2024



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## 1. Introduction

The human transformation of nature on a global scale, especially in recent decades, has led to a marked decline in indicators related to ecosystem health and biodiversity [1] and, with it, a decline in the benefits that all humans derive from ecosystem services. Ecosystem services can be defined as the conditions and processes through which natural ecosystems and their component species sustain and enable human life [2,3]. The main classifications group them into three broad categories: provisioning, regulating, and cultural [4,5]. The ecosystem services concept is the main tool used for calculating the value of natural capital [6].

Minimising the negative consequences of human transformations on the environment requires that each production sector adopts practices to reduce (or even neutralise) its net impact on ecosystems and biodiversity, while keeping (or even increasing) the flow of benefits that we obtain from nature. One of the production sectors with the greatest impact is agriculture, which is required to meet the food demands of the growing world population [7,8]. In fact, one of the main challenges for agriculture in the 21st century is the generation of multifunctional landscapes in which food is produced (provisioning service) at the same time as it promotes the supply of many other regulating and cultural services [9,10].

The wine sector is no stranger to this goal. Currently, vineyards occupy 7.3 million hectares worldwide, producing up to 260 million hectolitres to satisfy an estimated world

consumption of 236 million hectolitres [11]. Efforts are being made in different wine regions in the form of pilot projects to integrate ecosystem services, biodiversity, and multifunctionality as relevant elements in vineyard management decision making [12–17]. Nevertheless, despite being a provider of relevant ecosystem services, the role of microbiota is commonly ignored in most approaches [18].

Agriculture that is not only environmentally friendly but also a producer of nature has the potential to provide nature-based solutions. Within such a paradigm, this review aims to compile and critically analyse the state of knowledge on the role of microbiota in the provision of ecosystem services in the wine sector, especially in vineyards but also in wineries. This review is structured into several sections, including a historical overview of the main scientific advances on microbiota and wine, the concept of terroir and the biogeography of the microbiota, the ecosystem services provided by the microbiota both in vineyards and in wineries, the impact that agricultural management systems have on this microbiota and therefore on ecosystem services, and methodologies for the quantification of this contribution in economic terms. The potential and limitations of this approach are also discussed, as well as the main lines of future research and possible applications.

## 2. Microbiota and Wine: The Evolution of Our Scientific Knowledge

Approximately 11,000 years ago, vines were domesticated in Western Asia to yield table and wine grapes [19], with evidence of oenological practices around 7000 years ago (5400–5000 BC) in the South Caucasus region [20]. These first wines were probably the serendipitous combination of chemistry and biology, specifically the microbiota present in grapes [21]. Domesticated varieties from Western Asia spread into other parts of the world through early agricultural communities. In Egypt, archaeological remains have provided evidence of grapevine cultivation on the Nile River since the Predynastic Period (4000–3100 BC) [22]. Jars with tartaric acid and tartrate residues are also proof from 4000 years ago of wine fermentation and storage processes in China (Jiahu region) [23,24]. In Europe, vine cultivation spread along trade routes, with vineyards planted on the Iberian Peninsula as early as the third millennium BC, even before the Phoenicians arrived [25]. In Ancient Greece (800 BC), wine was considered a basic element of everyday life, prompting the planting of vines in Greek colonies. However, the most advanced domestication of wine took place in the Roman Empire. The Romans already made the first grafts in the 1st century BC [26], when they began to use not only traditional amphorae but also wooden vats (51 BC) to preserve wine. However, considering microbiota, it has not yet been possible to find samples of microorganisms from before 1000 BC, with *Saccharomyces cerevisiae* being the first fermenting yeast to be identified [27,28].

Although oenology has evolved historically along with the production and elaboration of wine itself, it was not established as a scientific discipline until the 19th century with the research carried out by Pasteur on the role of microorganisms in wine fermentation. Pasteur obtained the first patent on alcoholic fermentation in 1857 and described the role of yeast strains in the production of different wines [29,30]. He also studied viticultural diseases and obtained a patent on the preservation of wine through pasteurisation [31]. Thanks to his contribution, in 1890, Hermann Müller carried out the first inoculation of grape must with a pure yeast culture, thus bringing forth the concept of controlled fermentation, which has survived to the present day with certain improvements in the control and reliability of the process [32]. Oenology has continued to evolve since then, studying the interactions of microbiota in both alcoholic fermentation and malolactic fermentation for wine production [33,34]. Another research effort has focused on the process of the domestication of oenological yeast strains, i.e., the artificial selection of strains with improved desirable characteristics that are adapted to environments with different stress factors, such as changes in temperature, acidity, and oxidative stress [35,36]. Now we know that *S. cerevisiae* stands out among the large number of yeast species involved in the different stages of fermentation due to its high fermentative capacity, ethanol tolerance, and strong resistance to the toxicity of different metabolites, thus being

able to prevail in the final stages of fermentation [37–40]. Considering these properties, optimal hybrid starters formed by *S. cerevisiae* and *Saccharomyces* spp. or *S. cerevisiae* and non-*Saccharomyces* have been created for controlled fermentation, guaranteeing the predictability and reproducibility of wines over time [41,42]. At present, the use of starter cultures is widespread in wineries, modulating the aromatic profile of the wine because of their enzymes, such as esterase,  $\beta$ -glucosidase, proteolytic, and pectinolytic enzymes. In addition, starters may increase the glycerol content and thus decrease the alcohol content of wines [43,44]. At the same time, however, the use of starters represents a risk for the loss of genetic diversity in indigenous yeast populations [45].

In recent years, next-generation sequencing of DNA (NGS) techniques has enabled researchers to study the genomes of entire microbial communities, including those of unculturable organisms. Particularly, the use of techniques based on high-throughput sequencing (HTS) and omics, such as metabarcoding, meta-transcriptomics, meta-proteomics, and metabolomics, has opened up a new scenario in wine research. These technologies provide a powerful approach to a more complete understanding of the complexity of microbial communities in different environmental niches, helping greater monitoring and diagnosis, among other aspects [46–48]. Thus, HTS-based studies have allowed for the identification of microbial dynamics during winemaking, helping winemakers better understand and control the fermentation process and improve the final product's quality [49–53]. In 1996, *S. cerevisiae* was the first eukaryotic organism for which a complete genome sequence was obtained [54]. It is now known that, as a result of the domestication process, more than 90% of the fermenting yeasts of *S. cerevisiae* in wineries around the world come from the same cluster as a consequence of their domestication [55]. The advances are even greater in the role played by microbiota in vineyards. NGS has enabled the identification and characterisation of diverse microbial populations in the vineyard ecosystem, facilitating the description of the virome [56], mycobiome [57], and bacteriome [58] of vineyards in different parts of the world. These developments have provided insights into the potential of the microbial communities that play essential roles in vineyards' health and productivity [59] in processes such as nutrient cycling, disease suppression, or plant–microbe interactions [60,61]. Moreover, NGS has aided in deciphering the microbial components that contribute to the distinct characteristics of wines from different regions, the terroir [62–64]. New NGS advances allow for an ever-deeper understanding of the microbiome of vineyards. For example, the use of amplicon sequence variants (ASVs) instead of operational taxonomic units (OTUs) since 2013 has allowed for a finer distinction between sequences, enabling a more precise taxonomic identification, which is very useful for taxonomic groups that have close taxa with different functionalities in vineyards [65–68]. However, synthetic genomics—the construction of viruses, bacteria, and eukaryotic cells whose genome has been completely synthesised in the laboratory [69]—allows for the design of a generation of industrial microorganisms that will introduce notable improvements in aspects such as the organoleptic properties of wine or the reduction in ethanol concentration in light-bodied wines [70–72]. In this regard, strains that favour certain aromas have already been produced through the engineering of metabolic pathways and the fusion of synthetic enzymes [70,73,74].

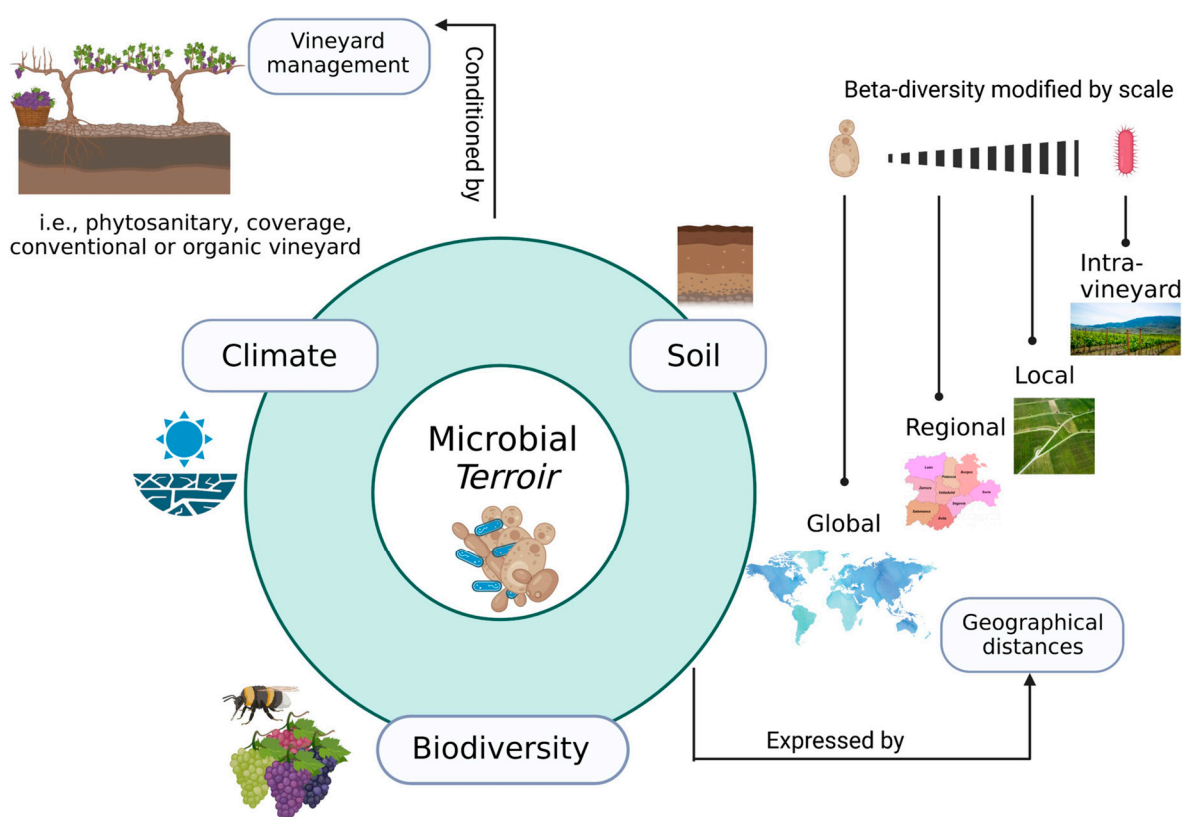
Overall, the information obtained through these methods has the potential to transform vineyard management practices and contribute to more sustainable and efficient wine production [75–77].

### 3. Terroir and Microbiota of Wine

When tasting a wine, some of the first perceived differentiating aspects (such as aroma, acidity, and colour) are related to the area in which the physicochemical, biological, and cultural interactions of the vineyard take place: the terroir [69,78,79]. This term is frequently used nowadays, not without controversy and despite its poor widespread understanding [76,80]. In the traditional definition of the International Wine Organisation (OIV), the terroir initially referred to an “area in which collective knowledge of the interactions

between the identifiable physical and biological environment and applied vitivincultural practices is developed”, including specific soil, topography, climate, landscape characteristics, and biodiversity features (OIV/VITI Regulation 333/2010). Given advances in the understanding of the role of microbiota in wine and vineyard distinctiveness, recent studies within the literature already consider it an integral part of this terroir [81–83].

In biogeographical terms, since microorganisms operate in a particular ecological niche with specific environmental conditions, spatial differences can be found in the microbial communities present in each region [49,84,85]. It has been demonstrated that the distribution of the microbiota is influenced by geographical, environmental, and management factors, generating a region-specific microbial terroir that contributes distinctive qualities to the wines [61,86–90] (Figure 1). Research on this microbial terroir has shown that some OTUs of the microbiome can act as a geographical signature of a vineyard or wine region [91].



**Figure 1.** Factors such as climate, soil, and surrounding biodiversity condition the microbiome of the specific microbial terroir in each vineyard (**centre of the figure**). These factors are shaped by crop management practices (**upper left corner**). The interaction between these elements defines a biogeography of microbiota in vineyards with differences expressed at different geographical distances and in which fungi are more site-specific and bacteria tend to have more cosmopolitan distributions (**right side**).

Differences in the spatial patterns of microbial communities in vineyards are expressed at different scales. Considerable differences have been observed between vineyards in different parts of the world [92] and between wine-growing regions [93–96]; however, landscape factors and local variations in the ecological niche are known to produce significant differences at the local scale [97–100]. Intra-vineyard variability is also a significant factor as differences in microbial composition can be even greater than between plots [101,102]. Hence, it is possible to identify a hierarchy within spatial distances, following a broad trend

whereby the diversity of microbiota rises with the distance [63], while a common core of genera, or even species, has been described globally [92] (Figure 1).

Isolation by geographic distance is somewhat shaped by environmental heterogeneity, which defines microbiota spatial patterns in vineyards. Climate and soil differences between areas contribute to microbial community dissimilarities between vineyards [103,104]. At the wine-growing landscape scale, the factors behind these spatial patterns are also related to vineyard practices [97,105–107], grape variety [85,92,98], and microclimate conditions [98,99,108,109]. The surrounding ecosystems also seem to be involved in the composition of microbial communities in vineyards. Thus, nearby forests shape the fungal communities in the vineyard, not only because of the natural yeasts they host but also because of the social insects (e.g., wasps) that act as vectors for transporting microorganisms from the forest to the grapes [110–113].

The microbiomes of vineyards have also shown significant differences between the soil and the vines themselves. The soil acts as the main reservoir of microbiota and shows a certain level of concurrence with the different parts of the vine (roots, leaves, flowers, and grapes) [58,91]. While bacterial diversity decreases from the soil to the aerial parts [82,114], the main change in fungal-specific diversity occurs between the soil and the rhizosphere [115].

The variety of vines also conditions the microbial communities present in vineyards. For example, bacterial species, such as *Enterococcus*, *Massilia*, *Kocuria*, *Pseudomonadales*, and *Pantoea*, are more likely to appear in varieties, such as Merlot, Syrah, Cabernet Sauvignon, and Zinfandel, while species such as *Bacillus*, *Turicibacter*, and *Romboutsia* have a greater prevalence in Pinot Noir. As for fungal species, *Cladosporium*, *Phoma*, and *Sporormiella* appear in Zinfander, Lon, and Gem [108,116,117].

The spatial patterns of fungi and bacteria generally differ, which is partly explained by variations in responses to environmental effects or vineyard management practices [118–123]. On a global scale, although spatial distance explains beta diversity in both, climate is more related to alpha diversity in fungi than in bacteria [63], with some bacteria also responding to climate variables [104]. In addition, the dispersal of fungi by wind is probably more limited than that of bacteria due to the larger spore size compared to bacterial cells [112,124,125]. As a result, the diversity of fungal communities increases with distance, a pattern that is much less marked in bacterial genera. Thus, while fungi are more site-specific, bacteria tend to have more broad-based distributions but with notable local and intra-vineyard differences at the same time [87,93,126]. Overall, the fungi, which are more representative of each territory, define the microbial geographical signature of the different winegrowing regions and vineyards to a greater extent [94,127].

Microbiome differences can appear not only in space but also in time. Although inter-annual variations in the microbiota of a vineyard have barely been studied, some research has found that vintage can significantly affect the biodiversity of vineyard-associated microorganisms [85,128–130]. In contrast, other studies have shown that differences between vintages are not significant [102]. Moreover, during the vine growing period, alpha diversity experiences a decline, while beta diversity undergoes an increase. This trend implies that microbiomes are progressively reshaped by interactions between hosts and microbes [104].

What happens in the vineyard is transferred to the winery. All ecological interactions that take place between the microbiota, the plant, and the environment play an important role in the outcome of wine fermentation. In fact, it has been shown that up to 60% of microbial diversity must come from taxa derived from the soil, leaves, and grapes of the vine [96,108,117,131], while the communities present in that which is freshly harvested must be more similar to those found in berries; as fermentation progresses, they become more and more similar to the communities present in the vine bark [94,132,133]. Thus, it is possible to identify microbial biomarkers associated with each terroir among the different stages of fermentation and for different wine grape varieties [96]. Moreover,



winery surfaces harbour seasonally fluctuating populations of bacteria and fungi with relevance to wine fermentation [134].

#### 4. Ecosystem Services Provided by Microbiota in Vineyards and Wines

Microbiota provide ecosystem services both for vineyards and for the quality of the final product, wine. This review uses the classification proposed by the United Nations System of Environmental-Economic Accounting, which identifies three main groups: provisioning, regulating, and cultural ecosystem services [5].

##### 4.1. Provisioning Ecosystem Services

Within the category of provisioning ecosystem services, microbiota are closely linked to wine production through fermentation. They also provide remarkable genetic diversity that can benefit the wine industry and wine cultures.

##### 4.1.1. Biomass (Crop) Provisioning Services

Without microbiota, humans would simply not have wine. It plays a fundamental role in fermentation, transforming grape must into wine. Thanks to studies based on HTS, the existence of a large microbial pool that includes fungi and bacteria in spontaneous wine fermentation has been proven [47,51,53,135]. The different strains of oenological yeast have been “domesticated” over the years, adapting by evolutionary mechanisms to environments with many stress factors in the fermentation process [35,36,136]. Thus, regarding alcoholic fermentation, indigenous species of the genera *Hanseniaspora*, *Candida*, *Pichia*, and *Metschnikowia* are involved in the first steps of the process, producing secondary metabolites (such as acids, alcohols, and esters) and enzymes (such as esterases, lipases, and proteases) that can affect the final quality of the wine [137]. These species can grow at low ethanol concentrations, but when this exceeds 5–7% and the abundance of fermented sugars begins to decrease, they start to decline and die [138]. Other yeasts, such as species of *Brettanomyces*, *Kluyveromyces*, *Schizosaccharomyces*, *Torulasporea*, and *Zygosaccharomyces*, may also be present during fermentation and subsequently in wine, some of which are capable of adversely affecting sensory quality [35]. Due to its high fermentation capacity, ethanol tolerance, and strong resistance to the toxicity of different metabolites, *S. cerevisiae* prevails in the final stages of fermentation [38,41], being nearly unique in those fermentations with commercial starters, or else, accompanied by other species, such as *Torulasporea delbrueckii*, *Zygosaccharomyces fermentati*, *Kluyveromyces thermotolerans*, *Hanseniaspora guilliermondii*, and *Dekkera anomala* in spontaneous fermentation [49,96,137]. For malolactic fermentation, *Oenococcus oeni* is the dominant species [139–141]. Apart from the gradual growth of different yeast species during fermentation, the existence of the underlying successional development of different strains within each species has also been described [138].

Microbiota play a remarkable role in the organoleptic characteristics of wine. For example, beneficial yeast species of *Debaryomyces* may produce enzymes, such as  $\beta$ -glucosidases, which increase the concentration of desirable organoleptic compounds in wines [142]. *Lachancea thermotolerans*, *Pichia kluyveri*, *Rhodotorula mucilaginosa*, and *Metschnikowia* spp. may improve the flavour and aroma of wine [33,41,76,143]. Species of bacteria, such as those included in the genus *Lactobacillus*, contribute to the synthesis of methyl and isobutyl esters and the formation of red and black fruity wine fragrances. *Fructobacillus* is closely related to the synthesis of aromatic alcohols and the generation of fruity flavours [144].

In spontaneous fermentation, the soil microorganisms that are present in grape berry and those present only in berries (coming from insects, birds, etc.) produce wines with greater complexity than those fermented with pure starters, providing a bouquet of flavours perceived as more attractive to consumers [131,132,145,146]. These spontaneously fermented wines are practically impossible to reproduce in later vintages or in some regions, mainly due to terroir differences [21,42]. However, these wines are unpredictable due to fermentation arrests and can deteriorate due to the appearance of certain undesirable yeast species, such as *Brettanomyces* spp. [147].

#### 4.1.2. Genetic Material Services

The oenological microbiota constitutes a reservoir of great genetic diversity, with a wide variety of *Saccharomyces* and non-*Saccharomyces* yeast species and strains, which stems from mechanisms such as heterozygosity, nucleotide and structural variations, horizontal gene transfer, and intraspecific hybridisation [39,148]. This genetic diversity is likely to provide resilience to climate change in wine production [47,50,135] and can be exploited to obtain higher quality wines [149–151] or to generate non-GMO hybrids to be used as commercial starters that do not suppress the native microbial flora [152]. The species most sought after are those that ferment well and produce less ethanol, more glycerol, and more attractive aroma compounds. Some of these yeasts are non-*Saccharomyces*, such as *Hanseniaspora vineae* and *Metschnikowia fructicola* [152], or other species of *Saccharomyces* belonging to the sensu stricto complex [153,154], such as *S. kudriavzevii*, which can produce more aroma compounds and even higher amounts of other alcohols, such as phenylethanol. *Saccharomyces uvarum* also produces more aromatic compounds, such as alcohols and esters. *Saccharomyces bayanus* is cryotolerant, allowing for fermentation at lower temperatures [32,155–159]. In addition, the sequential fermentation of *S. cerevisiae* with non-*Saccharomyces* yeasts, such as *Meyerozyma guilliermondii* and *Hanseniaspora uvarum*, enhances floral and fruity aromas in wines [150].

#### 4.2. Regulating Ecosystem Services

The interactions between biological communities (including microbiota) and the physical and chemical properties of the soil environment are fundamental to the processes, functions, and ecosystem services provided by nature in vineyards, such as carbon storage [78], regulation of soil quality [160], formation of soil structure [161], or the biocontrol of pests and diseases [78,162,163].

##### 4.2.1. Carbon Storage

As vineyards are a potential source of carbon storage [164], with differences among vine ages [165] and grape varieties [166], soil microorganisms are of great importance in regulating organic carbon dynamics [167], as taxa such as *Patescibacteria*, *Synergistetes*, *Chloroflexi*, *Actinobacteria*, *Deinococcus-Thermus*, and *Atribacteria* can degrade organic carbon to produce organic acids [168].

##### 4.2.2. Soil Quality Regulation Services

Microbial communities play a pivotal role in shaping soil nutrient dynamics, and any shift in their activities and functions has the potential to jeopardise soil biogeochemical cycles, ultimately impacting the availability of nutrients to plants [78,169–171]. Thus, there are specific microbial consortia that lead to nitrogen fixation and nutrient mineralisation, metabolising, for example, recalcitrant forms of N, K, and P to release these essential elements for vine nutrition [172–174].

##### 4.2.3. Soil and Sediment Retention Services

Given the characteristics of the crop, its management, and its location in topographically complex areas, vineyards present a particularly favourable context for soil loss compared to other agricultural land [175,176]. The microbiome can contribute to reducing this problem. In this regard, the arbuscular mycorrhizal fungi (AMF) of the subphylum *Glomeromycotina* promote the formation of soil aggregates and thus the prevention of soil erosion [177–181]. AMF develops a dense mycelial network in the soil [182,183], which, together with the secretion of sticky substances comprised of proteins [184], can have a binding action on soil particles and improve their structure, leading to increased structural stability and soil quality [185–187]. Thus, a reduction in AFM is expected to increase the risk of erosion [188].

#### 4.2.4. Biological Control Services

Understanding the microbial ecology of vineyards has implications for disease management and the development of more sustainable and eco-friendly approaches to protecting grapevines. Bacteria present in the rhizosphere and endosphere of vine shoots and branches, such as *Achromobacter xylosoxidans*, *Bacillus subtilis*, and *Pseudomonas fluorescens*, can produce siderophores that limit the availability of iron, thus reducing the presence of pathogenic microorganisms. Some bacteria also degrade virulence factors (e.g., oxalic acid) produced by plant pathogens, thus reducing the severity of damage [189]. By making good use of the functionalities provided by the microbiome, chemical products are starting to be replaced by selected bacterial strains, endophytic fungi, and yeasts that show defensive responses to grapevine pathogens [190], such as powdery mildew (*Uncinula necator*), downy mildew (*Plasmopara viticola*), or *Botrytis cinerea*, which can negatively affect the quality of the final product [191,192]. This biocontrol is provided by species such as *Lysobacter capsici* (AZ78), *Trichoderma* spp. [193–197], and *Aureobasidium pullulans* [198–200]. The use of these microorganisms instead of chemical fungicides helps in the production of certified organic wines [201,202]. Biological control of microorganisms is an active field of research in which significant progress is being made. For instance, strains of *Arthrobacter* spp., *Rhodococcus* spp., and *Bacillus mycoides* with an excellent ability to reduce the growth of mycotoxins from the fungi *Aspergillus carbonarius*, *A. niger*, and *A. flavus* have recently been isolated from organic vineyard soils [203]. In addition, some yeasts derived from grape must are also effective against pathogens such as *B. cinerea* [204], making them potential candidates for industrial application as biological control agents.

#### 4.2.5. Nursery Population and Habitat Maintenance Services

Microbiota can provide better soil conditions for vine development. For example, the fungus *Aerobasidium pullulans* is known to metabolise inorganic sulphur used as a fertiliser and pesticide and to absorb copper employed as a fungicide, which in high concentrations is toxic to the plant [198,199].

### 4.3. Cultural Ecosystem Services

Beyond the provisioning services, an ancestral culture has been created around wine, expressed in a rich tangible and intangible heritage that is ultimately based on the fermentation process carried out by the microbiota. These cultural services are expressed in the form of enotourism, the aesthetic values of vineyard landscapes, the scientific development of oenology, the scholarly enjoyment of wine, the identity and sense of belonging in wine-growing regions, symbolism, and even certain spiritual values [15,78,205].

#### 4.3.1. Recreation-Related Services

Enotourism includes all tourist activities related to the world of wine: wine tasting, visits to vineyards and wineries in different wine-growing regions, festivals, and other organised wine-related events [206]. The differences between wine production terroirs are what give “typicity” and “identity” to the wine produced in different territories and, ultimately, a “sense of place” to the communities linked to its production.

#### 4.3.2. Visual Amenity Services

The beauty of the landscape increases the market value of wine-related products [15,79,205]. Given that humans aesthetically prefer healthy plants and that the fungal and bacterial diversity of leaves is closely related to the health status of grapevines [133], the microbiota is also related to the visual appreciation of vineyard landscapes.

#### 4.3.3. Education, Scientific, and Research Services

The diversity provided by the different terroirs encourages scientific research in the field of oenological microbiology, aimed at unravelling the interactions between the microbiota, the vine, and the final product [78,207].

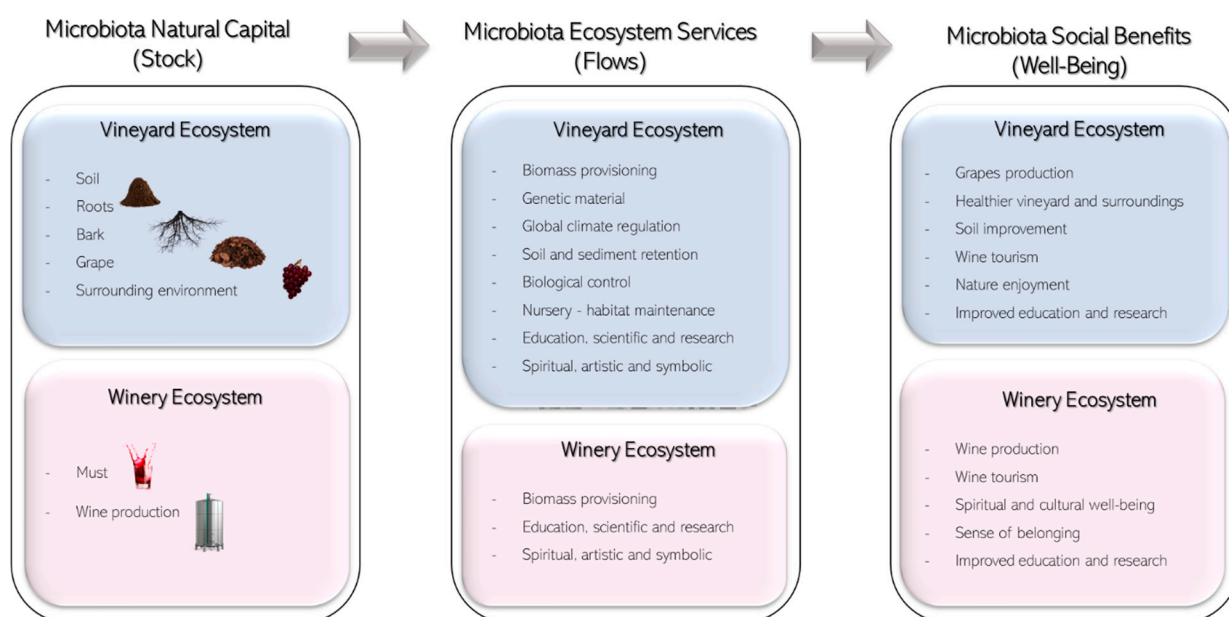


#### 4.3.4. Spiritual, Artistic, and Symbolic Services

Wine has been linked to various myths, rites, and religious cults for thousands of years [208–211]. The Greek god Dionysus, reinterpreted as Bacchus in Roman mythology, was the revealer of wine culture. Among Egyptian deities, Hathor, the goddess of wine, was carved into the amphorae used to store it, while Osiris gave the people instructions on how to harvest the vine and store the wine. The Sumerians incorporated the goddess Geshtinanna, a name that means “mother vine”, as found in various inscriptions.

### 5. Economic Valuation of Microbiota Ecosystem Services in Vineyards and Wine

Ecosystem services provided by microbiota for vineyards and wine are valuable because they increase society’s well-being. The conceptual connections between microbiota natural capital and the enhancement of well-being can be thought of as a sequence that links the ecosystems, the intermediate ecosystem services, the final ecosystem services, and the value created for the beneficiaries, such as the one in Figure 2.

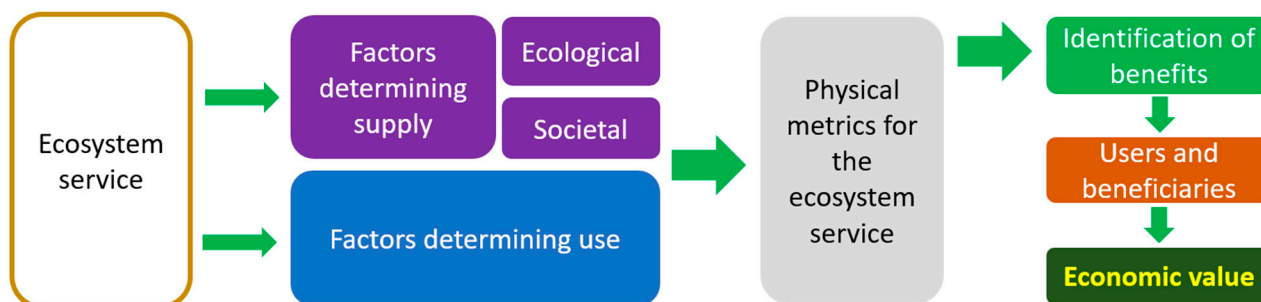


**Figure 2.** Social benefits of vineyard and winery microbiota as natural capital.

Turning these value connections into monetary terms may be useful for decision-making (see below). This can be done by operating standard economic valuation techniques, which are frequently applied for the economic valuation of environmental assets and the ecosystem services they provide. These techniques and their results are not without debate; however, their general acceptance is higher if the value connections are clear, the beneficiaries are identified, and the benefits for them can be assessed to some extent.

In March 2021, the United Nations Statistical Commission posed the UN System of Environmental–Economic Accounting–Ecosystem Accounting (UN SEEA-EA) as the new standard for countries to report the state of their natural capital. This framework is set to define the common ground for the economic valuation of ecosystem services in the coming years; thus, it is worth drawing from it when dealing with specific elements in this field.

The UN SEEA-EA advocates the use of real or inferred exchange prices as the main source of information for the economic valuation of ecosystem services rather than estimated shadow prices. Hence, valuation techniques based on market prices or costs are preferred over beliefs and judgments, whether they come from experts or users. The identification of logic chains for value assessment, such as the one shown in Figure 3, also suggests that this new framework is a proper way to disclose and arrange the valuation steps from the ecosystem service to its economic value.



**Figure 3.** Simplified logic chain from an ecosystem service to its economic value.

There are several reasons why estimating the economic value of ecosystem services from microbiota may be useful. First, the use of monetary terms allows for the aggregation of different physical flows. Second, it provides a framework in which the services from diverse ecosystems can be weighed and compared. Third, it may be useful to make informed preservation decisions. Fourth, it may help to identify new promising lines for research.

To reach these goals, the economic valuation of the ecosystem services provided by microbiota in vineyards and wines cannot cover the whole set of values from the entire microbiota at once for a very simple reason: without microbiota, we would not have wine; hence, we might obtain the wrong result that the value of microbiota equals the total value added by the wine industry, neglecting the rest of the contributions and, of course, missing the point [18]. Instead, we must necessarily focus on the value added by certain specific microorganisms, i.e., the marginal added value to vineyards and wine due to their presence or the marginal lost value due to their disappearance.

It is beyond the scope of this paper to provide economic valuations for the ecosystem services of microbiota, but a few examples of applications and methods will help explain the way in which they are calculated. In all cases, logic chains following the outline in Figure 3 can be identified for each ecosystem service to produce an economic value estimate once the benefits and beneficiaries have been bounded. The most visible case, of course, is provisioning services since microbiota play a central role in fermentation or in the production of enzymes that improve organoleptic characteristics. Provisioning services are usually valued by market data, and microbiota are no exception. The easy way to do this would be to start from the value of the final product (grapes or wine) and subtract all values not provided by microbiota, including winery installations, machinery, labour, and fertilisers. Since these latter values are usually hard to estimate, the most convenient way to estimate the economic value of microbiota provisioning services, when possible, might be from the comparison between the produced values with and without the presence of a certain type of microbiota or from the extra premium consumers are willing to pay for organic wines.

Regarding regulating ecosystem services, the main difficulty arises from the fact that, in many cases, their effects are not directly noticeable; hence, the use of market data is not so straightforward. The fraction of carbon storage that can be attributed to microbiota, for instance, can be calculated in tonnes and then valued from the standpoint of its replacement cost, i.e., the monetary cost of CO<sub>2</sub> allowances needed to equalise such a level of carbon storage. A different example is biological control services, which can be valued by calculating the avoided cost, i.e., the cost of the chemical products that can be replaced by bacterial strains, endophytic fungi, or yeasts that show defensive responses to grapevine pathogens. The main obstacle is that substitutability rates have not yet been clearly determined in the literature; thus, estimating actual cost avoidance becomes a complex task.

The economic valuation of cultural ecosystem services is also performed using sources of information related to market data, although its use is not straightforward. Recreation services can be valued by considering the cost of enjoying them, usually by applying travel

cost methods. Hence, for instance, the value of cultural services from specific microbiota may be assessed by calculating the differential amount of money that people are willing to pay to visit organic vineyards or wineries using indigenous yeasts.

## 6. Vineyard Management and Microbiota Ecosystem Services

Differences in vineyard management can modify microbial communities [212] and, by this means, have an impact on the type and quantity of ecosystem services provided. Some studies suggest that, together with geographical location and climate, vineyard management is related to the diversity of yeast taxa present in grapes [74,103,213,214]. In terms of bacterial composition, vineyard management seems to have a direct impact on the composition of its communities [162,215]. These differences may also reach and materialise in the must microbiome [216], although other authors have found no evidence of change [107,212].

Management practices, such as cover crop use, tillage, and soil amendments, can influence vineyard microbial communities [78]. Green cover in vineyards can increase microbial biodiversity [217], enhance soil health and nutrient cycling, and promote a more resilient and balanced vineyard ecosystem. The presence of green cover increases the input of organic matter into the soil through plant residues and root exudates. As these materials decompose, they provide a source of nutrients for the microbial community, improving soil fertility and supporting the growth and health of grapevines. At the same time, green cover contributes by preventing erosion, regenerating soil biodiversity [13,218], and improving visual amenity services [219]. Nonetheless, empirical evidence has indicated that the outcomes of inter-row management may fluctuate due to underlying edaphoclimatic conditions [220]. Considering agricultural inputs, organic amendments, such as manure and compost, are a direct source of carbon for soil microbiota and other organisms, leading to increased plant growth and the return of plant residues to the environment [221,222]. Comparatively, organic fertilisation systems lead to a notable increase in microbial biomass, induce shifts in the structure and composition of the soil microbial community, and enhance microbial activity, as opposed to the inorganic fertilisation approach [223,224]. In addition, the use of nitrogen fertilisers can lead to soil acidification, with considerable negative effects on the microbiota present in the soil [225–227]. Fungicides alter the microbial communities on the surface of grapes, with the effect of those used in organic agriculture (sulphur, copper) being stronger than those used in conventional agriculture [221,228–230]. Chemical herbicides, such as glyphosate, have also been shown to induce alterations in soil microorganisms [231].

Since management practices affect the microbiota, it is no surprise that the sort of cultivation system, whether conventional, organic, or biodynamic, also plays a role, as some research has shown [107,232–234]. Higher fungal diversity is found in organic and biodynamic viticulture, which seems to be related to organic fertilisers [198,199]. In organic vineyards, there is a higher presence of *Aureobasidium pullulans* (which can metabolise inorganic sulphur and absorb copper), while in conventionally managed vineyards, *Sporidiobolus pararoseus* (carotenoid producer) is predominant [235]. However, higher levels of pathogenic *Alternaria* spp. And yeasts *Rhodotorula* and *Sporidiobolus* have been detected in conventional versus organic vineyards, forming a general pattern of reduced fungal diversity with a predominance of a few fungal taxa in these conventional vineyards, probably because of the use of systemic fungicides [201]. Other types of management can also affect vineyard microbiota. For instance, altered vineyard microclimates under rain shelters reduce diseases caused by *Alternaria* and *Colletotrichum* spp. [130].

## 7. Towards Smart Farming: Microbiota as a Nature-Based Solution in Vineyards and Wineries

In the coming decades, the agricultural sector will face major challenges in providing food for a growing world population, but intensive cropping based on the use of mineral fertilisers, agrochemicals, and water will continue producing a negative impact

on biodiversity and ecosystem services [236]. Wine production is no exception to these environmental problems [237]. Indeed, in this type of crop, certain risks can prove to be even more severe. The placement of vineyards on steep slopes, coupled with irregular rainfall patterns (exacerbated by climate change), can lead to substantial soil erosion and degradation, significantly compromising soil structure and overall productivity [238–240].

In this context, “smart farming” can bring cutting-edge technology into play to enhance agricultural production in terms of quality, quantity, and sustainability [241]. Since the primary objectives of smart farming involve precise and location-specific interventions, microbiota are called upon to play a major role in these advances [242]. By nurturing a diverse and thriving microbial community, vineyard managers can promote environmentally friendly grape cultivation practices. However, although there are already many commercialised products based on the use of microbiota, such as biocontrol agents, biostimulants, and biofertilisers, intelligent management should go further and promote the sort of microbiota that provides relevant ecosystem services, while reducing the one that can provide negative functionalities as a nature-based solution in each vineyard. Therefore, there is a need to move quickly from promise to practice [243], generalising the ecosystem services approach to vineyard management practices, including microbiota.

There is still important work to be done in the identification of the taxa present in the microbial communities of vineyards, with some poorly described groups in which it is not yet possible to identify genera or species [63]. Furthermore, another major challenge is still to assign species to ecosystem functions. This is not straightforward, as redundancies are common and different microbial communities may provide the same function [244]. While NGS techniques allow for the identification of taxa, cultivable or not, present in an environmental sample, they are not intended to define the roles that taxa play within the microbial community in which they are part. Laboratory experiments with a given taxon are only partially useful because, in the vineyard, this taxon is part of a complex microbial community that can modify its functionality. In this sense, to study the role of ecological, structural, and functional characteristics in a controlled way in the laboratory without losing the complexity of the environmental samples, artificial synthetic communities are generated. These synthetic communities maintain the essential characteristics of the communities found naturally in the vineyard while reducing the number of components. Thus, it is possible to study the roles and functionality of the different taxa given the interactions within the microbial community. The generation of these synthetic communities requires the isolation of microorganisms, either individually or by the encapsulation of microspheres of a small number of microorganisms or by the sequential layering of microbes in a synthetic biofilm [245,246], as a preliminary step to the complete study of the metabolic interactions between different isolates [247–249]. The study of these synthetic communities generates invaluable information on the contribution of the community to the overall ecosystem function. However, there are still several limitations, including how to manage the knowledge acquired in synthetic communities when dealing with naturally established communities, intercellular communication between single and multiple species, and how cell consortia can be optimised or controlled in the long term [250,251]. Once the functionalities provided by specific taxa are identified, it is necessary to investigate how the population dynamics of these taxa and of different microbial strains respond to different agricultural practices. It is also necessary to further investigate the factors affecting the microbiome—a set that is formed by microorganisms, their genes, and their metabolites in each ecological niche—and the species composition of microbial communities, especially those related to vineyard management practices (such as green soils, tillage, surrounding vegetation, and soil amendments). This knowledge can enable the implementation of advantageous strategies, for instance, considering the constraints imposed by the limited dispersal of fungi and the significant influence of environmental conditions on bacteria [61]. The room for biotechnological applications and developments is also wide and very relevant, exploiting microbial properties, such as the ability to sustain and replicate themselves without requiring repeated inoculation [252]. More research efforts should focus on how

this microbiota is finally transferred to the properties of the wine and contributes to its quality and to the valorisation of the terroir, which involves improving our knowledge on the value of ecosystem services.

In terms of the valuation of ecosystem services, apart from the use values related to the provisioning, regulating, and cultural services, the maintenance of microbiota also has an option value by keeping open the possibility of a future benefit from microbial communities [253,254], be it in the form of provisioning, regulating, or cultural services. Furthermore, microbiota in vineyards also offer an insurance value in terms of an increase in ecosystem resilience, which serves as a safety net against global change, protecting humans and ecosystems from potential welfare losses [255–258]. This insurance value reduces the likelihood of future declines in the supply of ecosystem services resulting from changes in microbial communities [255,259].

Overall, the analysis of the ecosystem services provided by microorganisms in vineyards and wine production reveals the essential contribution of these invisible communities to the functioning and sustainability of viticultural systems. Microorganisms are key players in achieving optimal outcomes with their diverse influences, from soil health and vine vitality to fermentation and the sensorial profile of wine. Their complex and symbiotic interaction with the viticultural environment triggers a range of benefits, including the enhancement of final product quality and vineyard resilience against adverse factors. This analysis not only highlights the importance of a holistic approach to winemaking but also the potential for future research to understand the mechanisms behind the delivery of ecosystem services, thereby promoting more sustainable and resilient agricultural and winemaking practices [260].

**Author Contributions:** Conceptualization, V.J.C.-R., F.R.-L. and I.G.-I.; methodology, I.G.-I., V.J.C.-R., F.R.-L. and M.T.; validation, I.G.-I., V.J.C.-R., F.R.-L. and M.T.; formal analysis, I.G.-I., V.J.C.-R. and F.R.-L.; investigation, I.G.-I., V.J.C.-R. and F.R.-L.; resources, I.G.-I. and V.J.C.-R.; data curation, I.G.-I. and V.J.C.-R.; writing—original draft preparation, I.G.-I., V.J.C.-R. and F.R.-L.; writing—review and editing, F.R.-L., V.J.C.-R. and M.T.; visualization, I.G.-I., V.J.C.-R. and F.R.-L.; supervision, V.J.C.-R., F.R.-L. and M.T.; project administration, F.R.-L.; funding acquisition, F.R.-L. and V.J.C.-R. All authors have read and agreed to the published version of the manuscript.

**Funding:** The authors acknowledge financial support from Junta de Castilla y León research grant SA126P20, Análisis y valoración del capital natural asociado al sector vitivinícola de Castilla y León, for the period 2021–2023.

**Data Availability Statement:** No new data were created or analysed in this study. Data sharing is not applicable to this article.

**Conflicts of Interest:** The authors declare no conflicts of interest. The funders had no role in the design of the study; in the collection, analyses, or interpretation of the data; in the writing of the manuscript; or in the decision to publish the results.

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