Ecosystem Functions of Microbial Consortia in Sustainable Agriculture

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Abstract: Knowledge of the agricultural soil microbiota, of the microbial consortia that comprise it, and the promotion of agricultural practices that maintain and encourage them, is a promising way to improve soil quality for sustainable agriculture and to provide food security. Although numerous studies have demonstrated the positive effects of beneficial soil microorganisms on crop yields and quality, the use of microbial consortia in agriculture remains low. Microbial consortia have more properties than an individual microbial inoculum, due to the synergy of the microorganisms that populate them. This review describes the main characteristics, ecosystem functions, crop benefits, and biotechnological applications of microbial consortia composed of arbuscular mycorrhizal fungi (AMF), plant growth-promoting rhizobacteria (PGPR), and *Actinobacteria*, to promote the restoration of agricultural soils and, consequently, the quality and health of agricultural crops. The aim is to provide knowledge that will contribute to the development of sustainable and sufficiently productive agriculture, which will adapt in a good way to the pace of the growing human population and to climate change.

Keywords: microbial consortia; arbuscular mycorrhizas; plant growth-promoting rhizobacteria; *Actinobacteria*; ecosystem functions; agriculture; sustainability; resilience; multifunctionality; soil microorganism; soil biodiversity

1. Introduction

Currently, conventional agriculture and its practices are presented as a major threat to soil vitality [1], causing the alteration of microbial functional diversity and thus worldwide soil degradation, threatening the food chain and safety [2–4]. The intensification of agriculture through excessive and sometimes inappropriate use of chemical pesticides has led to land degradation and environmental pollution in several agroecosystems, which have contaminated water bodies and degraded soils, subsequently leading to the loss of biodiversity by killing beneficial plants, animals, insects, aquatic ecosystem, and other wildlife, and in some cases even poisoning the farm workers [5–7]. Another example is intensive agriculture under plastic covers, which profoundly affects soil quality because it greatly alters the water cycle as well as organic carbon (C) and other nutrient contents. On the one hand, natural rainfall is restricted under plastic tunnels, increasing the salinity of the soil in the upper layers. Likewise, soil acidification caused by the excessive application of minerals and nutrients, frequently used under plastic covers, increases the negative effect on soil quality over time, resulting in lower crop yields [8,9]. In addition, the intensive tillage changes the carbon–nitrogen (C/N) ratio due to loss of soil organic matter through erosion and leaching, causing soil degradation [10]. Nevertheless,

there is still great potential in soils, which requires adopting strategies that protect them from harmful agricultural practices [6,11].

Although there are multiple strategies for addressing sustainable agriculture and feeding people by reducing environmental impacts, it has been widely reported that promoting agricultural practices that increase biodiversity and the composition of soil microorganisms, such as organic or agro-ecological agriculture, represents an important alternative for obtaining good quality food and improvements in environmental, economic, and social aspects [12–14].

Increased microbial biodiversity stabilizes the functioning of agro-ecosystems and increases the resilience to climate change [15]. Since ancient times, microorganisms have been present in association with plants and animals, giving them multiple benefits in a dynamic equilibrium, which has been attributed to multiple communication systems. Among them are chemical messages at the rhizosphere level [16–18]. These communication systems are fundamental in the agricultural ecosystem, since they regulate all biogeochemical processes in the soil, maintaining its fertility and health. These processes include the decomposition, nutrient cycling, and maintenance of organic matter, control of pathogens, degradation of contaminants, and reduction of greenhouse gases (GHG), which directly affect both crop productivity and the environmental quality [19–21].

In order to benefit from the enormous potential of the soil microbiome, it is necessary to know the distribution and composition of microbial communities in different territories and on different time scales, such as seasonal variations [22]. This information also allows predicting the changes that can be generated in a global climate change scenario. In addition, not knowing the effects of the loss of diversity in specific places and times, it can generate a great impact on ecosystem sustainability and therefore on human well-being [23–25]. The greater the diversity of microorganisms in the soil, the greater the functionality of that soil [26,27], which in turn means food with a higher nutraceutical quality proportional to the soil nutrition and health.

Recently, increasing attention has been given to crops rich in nutrients, minerals, antioxidants, or other metabolites, as they represent a higher food quality and reduce the risk of chronic diseases [28–30]. In this context, new crop practices have emerged that allow obtaining high yields of biomass with a high concentration of beneficial metabolites. The development of biofertilizers made up with beneficial microbial species has emerged [31], as well as the development of microbial consortia of different soil microorganisms [32].

Thus, it is necessary to understand the processes that determine the composition and abundance of soil microorganism communities in order to obtain their multiple benefits in agricultural systems and indirectly in human health. This review aims at describing the main characteristics, ecosystem functions, crop benefits, and biotechnological applications of microbial consortia composed of arbuscular mycorrhizal fungi, plant growth-promoting rhizobacteria, and *Actinobacteria*, to promote sustainable agriculture and thus the quality and health of agricultural crops.

2. Discussion

2.1. Arbuscular Mycorrhizal Fungi (AMF)

At the ecological level, mycorrhizal network theory allows the analysis of interactions between plant fungal soil partners as complex multi-species of underground networks [33]. Among the microorganisms present in the soil, AMF are fundamental to soil ecology and agriculture [34]. They form a symbiotic composite association with 93% of terrestrial plant families, including multiple agricultural crops. They are the oldest known and most prevalent associations in nature [35,36].

AMF belong to the subphylum Glomeromycotina, containing the Archaeosporales, Diversisporales, Glomerales, and Paraglomerales [37], and their symbiosis with plants consists of receiving carbohydrates and lipids from the plant and having specific structures, such as arbuscules and vesicles, that allow the exchange of nutrients with plants at the level of the root bark [38,39]. These have several functions and benefits for plants, which are mainly related to increased nutrient uptake, promoting phosphorus (P),

iron (Fe), and zinc (Zn) uptake by crops through direct plant–root pathways [40,41], positively affecting crop growth, yield, and reproductive success; thus, reducing fertilizer needs in agricultural systems [42,43].

The establishment of mycorrhizae alters the biological and physicochemical properties of the rhizosphere, leading to the formation of the so-called mycorrhizosphere, where they improve the soil structure, water retention [44], and have an important effect on the induction of systemic resistance to biotic stresses [45].

Conventional agriculture, with its intensive practices, generates a decrease in the diversity of arbuscular mycorrhizae, which means that fewer species of slow colonization potential and rapid sporulation prevail. This leads to a considerable decline in ecosystem functions of arbuscular mycorrhizae [46,47]. All the benefits that arbuscular mycorrhizae provide to crops can be used in sustainable agriculture to reduce the environmental impact and obtain food of higher nutritional quality that benefits humans [48,49]. Within these alternatives, organic agriculture is the most widely reported [50–54].

AMF can be an excellent alternative as biofertilizer in agriculture, as shown by multiple laboratory and field studies [31,55]. In highly degraded soils, the application of an external inoculum could be beneficial to overcome situations of biotic or abiotic stress in soils, for which it is necessary to consider the characteristics of the agricultural system to select the AMF species [56,57]. In the same context, it is suggested to apply a mixture of species, since a consortium will always be more effective in soil recovery than a single mycorrhizal species [58]. On the other hand, it has also been proposed to promote communities of native species, which are equally effective; however, in this case we can avoid a possible ecological risk of an external inoculum, for example, by inoculating an aggressive strain that could displace the beneficial autochthonous species [59]. The different benefits of microbial consortia in agricultural crops are presented in Table 1.

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Table 1. Beneficial effects of arbuscular mycorrhizal fungi in agroforestry management.

AMF Species	Crops	Beneficial Effects	Condition	Reference
Funneliformis mosseae *Rhizophagus irregularis*	Chickpea (*Cicer arietinum* L.)	Increases plant biomass, production and grain quality	Field	[55]
Glomus intraradices	Tomato (*Solanum Lycopersicum* L.)	Improve the yield	Field	[60]
Glomus intraradices	Tomato (*Solanum Lycopersicum* L.)	Root knot nematode suppression	Greenhouse	[61]
Rhizophagusintraradices, *Glomus aggregatum, Glomus viscosum, Glomus etunicatum,* and *Glomus claroideum*	Corn (*Zea mays* L.)	Improves crop growth, yield and grain quality	Field	[62]
Glomus mosseae, Glomus intraradices	Alfalfa (*Medicago sativa* L.)	Increase in glomalin-related soil protein (GRSP) and stability of soil aggregate	Greenhouse	[63]
AMF natives	Corn (*Zea mays* L.)	Increased absorption of K, Ca and Mg	Field	[64]
AMF native consortia: *Glomus mosseae, Glomus fasciculatum, Glomus etunicatum, Glomus intraradices, Scutellospora* sp.	Green pepper (*Capsicum annuum* L.), parsley (*Petroselinum crispum* (Mill.) Fuss), carrot (*Daucus carota* L.), and tomato (*Solanum lycopersicum* L.)	Increased plant and root biomass and yield quality	Greenhouse and field	[65]
Glomus fasciculatum, Glomus clarum, Glomus etunicatum, Glomus versiforme	Long pepper (*Piper longum* L.)	Improve growth	Greenhouse and field	[66]
Glomus intraradices	Potato (*Solanum tuberosum* L.)	Improve biomass yield	Field	[67]
Glomus intraradices, Glomus mosseae, Glomusetunicatum	Strawberry (*Fragaria ananassa* Duch.)	Improve productivity	Field	[68]
Glomus mosseae, Glomus hoi	Sunflower (*Helianthus annuus* L.)	Improve biomass yield	Greenhouse	[69]

2.2. Plant Growth-Promoting Rhizobacteria (PGPR)

The PGPR are a diverse group of bacteria that colonize the plant rhizosphere, showing a positive impact on the environment. The most widely reported bacterial species are of the genera *Bacillus*, *Pseudomonas*, *Lactobacillus*, *Acetobacter*, *Azospirillum*, *Paenibacillus*, *Serratia*, *Burkholderia*, *Herbaspirillum*, and *Rhodococcus* [70]. The interactions between the plant and PGPR are synergistic, leading to relevant benefits for both the plant crops and the plant microbiome. On the one hand, the plant promotes PGPR establishment through the production of storage substances, such as carbohydrates, organic acids, and minerals, as well as the production of root exudates, which are used by the PGPR for nutrition [71, 72] or as a tool to establish symbiotic interactions, such as the mycorrhizal or dinitrogen-fixing nodulation [16]. The establishment can be endophytic, leading to the colonization of the inner plant structures, including seeds, or to the colonization of the plant intercellular spaces; the establishment can involve also the free-living bacterial cells in the rhizosphere [73,74]. Once established, PGPR show a benefit for plant growth (in terms of yields per hectare of land), crop quality traits, and plant health through direct or indirect mechanisms regulated for biotic and abiotic stress [70,74]. Direct mechanisms promote plant growth by releasing substances stimulating aerial biomass production, root development, and stem elongation. This is achieved through the release or solubilization of phosphates and other nutrients such as potassium (K), zinc (Zn), and silicon (Si); the uptake of biologically fixed di-nitrogen (N2); the chelation of iron (Fe) and other micronutrients, such as Zn, Boron (B), Calcium (Ca), Magnesium (Mg), and Copper (Cu) [70,75,76]; and the increase in available lithospheric oxygen [77]. In addition, PGPR usually synthesize phytohormones, such as gibberellins (gibberellic acid, GA3), auxins (indoleacetic acid, AIA), cytokinins, ethylene, and abscisic acid (ABA) [70,76], which model plant growth and plant cell division. These substances can induce the production of the enzyme 1-aminocyclopropane 1-carboxylate deaminase (ACC), which reduces the level of ethylene in the roots of the crops, thus improving the root length and density [78]

Indirect mechanisms of plant health induction involve modification of the rhizosphere environment and its ecology, inducing systemic resistance and stimulating the innate resilience of the plant (basal genetic resistance) [79]. Among them, PGPR release substances such as siderophores, antibiotics, pigments, organic acids (malic, acetic, citric, oxalic, lactic, formic, gluconic, and 2-keto-gluconic), water-soluble vitamins (niacin, thiamine, and biotin molecules or antioxidants), and volatile organic compounds (monoterpene alcohols) [80]. These substances activate the protection mechanisms of plants against herbivores, insects, and pathogenic microorganisms, and promote the synthesis of physical and chemical barriers against abiotic stress. In turn, they allow PGPR to be more competitive in niche colonization since they can interfere with the quorum detection signal and inhibit the formation of biofilms by pathogenic bacteria [81].

PGPR also promote the synthesis of hydrolytic enzymes (such as glucanases and chitinases) that produce morphological changes in the fungal mycelium, such as the fracture and lysis of the spikes [82], preventing the development of pathogenic fungi. *Pseudomonas frederiksbergensi*, *Bacillus* spp., and *Planomicrobium* spp. have been shown to be effective in improving tolerance to cold and saline stress, which has been linked, e.g., to the activity of antioxidant molecules [73,83–87]; the production of volatile terpenoids by *Pseudomonas* spp. and *Bacillus* spp. have increased the protective barriers against soil-borne pathogens in *Mentha piperita* and *Vitis vinifera* plants [80,88].

The application of PGPR over time led to relevant benefits in agroforestry management (Table 2). In this context, species of *Azospirillum*, *Pseudomonas*, and *Paenibacillus* have been used for their beneficial effects on the growth and yield of different cereal crops, such as wheat and rice [72,89]. Specifically, *Pseudomonas* spp. and *Paenibacillus* spp. have shown a high capacity to make Fe3+ available to plants [89]. *Bacillus* spp. and *Pseudomonas* spp. strains have proven to be excellent biofertilizer inoculants, having direct and indirect effects on insect pests associated with agricultural crops and also for the biological control of nematodes [90–92]; the bacterium *Pseudomonas frederiksbergensis* OS261 has been used as a biostimulant under water- and salt-stress conditions [86].

Table 2. Beneficial effects of plant growth-promoting rhizobacteria in agroforestry management.

PGPR Species	Crops	Beneficial Effects	Reference
Azospirillum spp., *Pseudomonas* spp.	Rice (*Oryza sativa* L.)	Increase growth and yield	[72]
Bacillus spp., *Pseudomonas* spp. and *Azospirillum* spp.	Seedlings and cuttings	Increase the germination and the rooting of cuttings, biocontrol of bacterial wilt and the survival of plants after transplanting	[76]
Pantoea spp., *Serratia* spp., *Acinetobacter* spp., *Bacillus* spp., *Agrobacterium* spp., *Burkholderia* spp., *Pseudomonas* spp., *Ochrobactrum* spp.	Soybean (*Glycine max* L.)	Production of nodules with high capacity to fix nitrogen. Important inhibitory activity against pathogens	[82]
Pseudomonas frederiksbergensis	Red pepper (*Capsicum annuum* L.)	Biostimulant under water and salt stress conditions	[86]
Paenibacillus illinoisensis, *Bacillus* spp.	Peanut (*Arachis hypogaea* L.)	Increase growth and yield	[89]
Pseudomonas spp., *Paenibacillus* spp.	Calcareous soil	High capacity to make Fe^{3+} available to plants	[89]
Bacillus spp., *Pseudomonas* spp.	Wheat (*Triticum aestivum* L.)	Excellent biofertilizer inoculants, have direct and indirect effects on insect pests	[90,91]
Bacillus spp., *Pseudomonas* spp.	Soil	Control potential of *Meloidogyne javanica* and *Ditylenchus* spp. nematodes	[92]

In forest nurseries, strains of *Bacillus*, *Pseudomonas*, and *Azospirillum* have allowed an increase in germination and stimulation in the rooting of cuttings, biocontrol of bacterial wilt, and the survival of plants after transplanting, which has been associated with better root development and consequently to an increase in the uptake of nutrients [76].

Another application for legume crops is the production of root nodules, with a high capacity to fix atmospheric nitrogen (N2) in soybean (*Glycine max* L.). Species of the *Pantoea*, *Serratia*, *Acinetobacter*, *Bacillus*, *Agrobacterium* and *Burkholderia*, *Pseudomonas*, and *Ochrobactrum* have been used [82], some of them showing ancillary inhibitory activity against pathogens. However, species such as *B. cepacia* may also be involved in infection in humans and their use in agriculture is restricted [93]. Therefore, it is important to have a thorough understanding of the safety traits for human health of these microorganisms not having a long history of use before their field application. In the European Union, a recent legislative provision, the so-called Fertilizer Act [94], covers these borderline aspects and makes a clear distinction of what can be marketed as a biofertilizer or as a plant protection product. The placement on the market of the latter category falls under another regulation of the European Parliament and Council [95].

2.3. Actinobacteria

Actinobacteria (formerly known as *Actinomycetes*) are the largest group of prokaryotes and comprise six classes, six orders, and fourteen suborders within which there are both cultivable and non-cultivable species. Bacteria that are present in terrestrial environments can be easily recognized as they generate the characteristic earthy odor that produces an organic compound, known as geosmin ($C_{12}H_{22}O$).

Actinobacteria can colonize plant roots endophytically or adhere to epidermal or subcortical root cells. In this context, endophytic bacteria have been described to enter the host plant through root hairs, stomas, wounds, and sprouting hydathodes [96], while in free-living bacteria, structures such as flagella, fimbria, exopolysaccharides, and lipopolysaccharides may facilitate the bacterial attachment to the plant roots [96].

Actinobacteria are classified as Gram-positive, and can be either aerobic or anaerobic, and exhibit various morphological, physiological, and pigmentation traits characteristic of actinobacterial taxa [97–100]. The pigments are commonly known as melanoid polymers and are similar to humic substances present in soil [99,101]. These pigments are not necessary for the growth of bacteria but have a significant contribution to improved survival.

In addition to morphological identification, the identification of *Actinobacteria* has now been facilitated by the use of molecular tools. The genomic organization of *Actinobacteria* has reported more than 20 sequenced species, which is still a small number. In general, they differ from other bacteria by having a large genome ranging from 1 to 12 Mb in size that is characterized by a high content of G + C, even higher than 70%, and contain large plasmids [99]. Specifically, it is possible to use 16S rRNA sequence analysis and other preserved sequences to identify some actinobacterial genera [98,102,103]. The most referenced actinobacterial genera are *Microbispora*, *Microbacterium*, *Micrococcus*, *Micromonospora*, *Nocardia*, *Rhodococcus*, *Streptomyces*, *Streptosporangium*, *Streptoverticillium*, *Arthrobacter*, *Actinomyces*, *Corynebacterium*, and *Frankia*. These have been studied principally due to their great capacity to generate diverse bio-active molecules [101].

Actinobacteria are of wide economic and scientific interest, mainly because of their application in human health and agriculture [104], as seen in Table 3. On the one hand, these bacteria are able to synthesize a wide and diverse range of secondary metabolites (more than 10,000 compounds reported) with antimicrobial, antitumor, and anti-inflammatory activity [101,105], and to promote plant growth under abiotic and biotic stress conditions, due to the synthesis of plant growth regulators (phytohormones) and organic acids [97]. In addition, *Actinobacteria* can fix atmospheric nitrogen, solubilize minerals such as phosphorus [106], produce siderophores [97] to overcome limited nitrogen, iron, and phosphorus conditions [96], and some species can produce antibiotics in situ contributing to maintain plant health.

Actinobacteria also have the ability to synthesis volatile organic compounds that diffuse into the air and soil through the pores acting as chemical agents of communication between species, suppression

of plant pathogens, formation of biofilms, indicators during differentiation, formation of mycelium, and sporulation and modification of the pH in the environment [107]. In addition, these can synthesize antimicrobial signaling peptides and quorum sensing regulators, which protect the organism from damage and facilitate interactions with the environment [104].

These bacteria play an important role in the decomposition of plant biomass, playing a vital role in the local ecology and processes, such as the carbon cycle [108]. *Actinobacteria* have a large reservoir of lytic enzymes, such as proteases, exo-, and endo-glucanases, amylases, lipases, pectinases, and xylanases, that degrade the components of the plant cell wall, facilitating the entry of the cells into the root [96,97,104,109]. They also synthesize lytic enzymes such as chitinases, dextranases, cutinases, peroxidases, and laccases, which degrade the cell wall of pathogens and are responsible for their inhibition and growth [110].

More importantly, these bacteria have the capacity to persist in the soil at a high cell density with a high rate of viability, which has led to the study of different applications in agriculture. They act either by suppressing the growth of phytopathogens and promoting growth of important crop plants, i.e., corn, tomato, and banana [111], or the ability to fix nitrogen in non-leguminous plants [97]. Nitrogen-fixing bacteria include members of the *Frankia* family, *Corynebacterium* sp., and *Pseudonocardia dioxanivorans*. Some of them are used as alternative N fertilizers [97]. Commercial products based on *Actinobacteria* have been generated, mainly from species of the genus *Streptomyces* [112], which protect plants against foliar and soil-borne diseases. These organisms can be used as insecticides, herbicides, antifungals, and biocontrol agents, as well as plant growth promoters [99].

2.4. The Microbial Consortia

Soil microbes are key ecosystem services provider and drive multifunctional processes, encompassing the interaction of different microbial communities, and the interaction of these with the other soil biota components, i.e., the micro- and mesofauna. Within this complex interconnected network, microorganisms are responsible for maintaining the energy fluxes supporting the entire ecosystem, through the recirculation of available resources [113]. However other organisms form ecological groups in the same environment and share a high multifunctionality in the ecosystem [22,114]. Soil microfauna are fundamental to the functionality of the ecosystem and any changes in these key organisms can produce changes at the vegetational, biome, and microbial level [26].

The most relevant groups of microorganisms in the soil are arbuscular mycorrhizal fungi and plant growth-promoting bacteria. These microorganisms together increase N_2 fixation and uptake, solubilize P, convert ammonium (which can be chemically bound to clay particles) into soluble, easily assimilable nitrate, protect from other pathogenic microorganisms, and even remediate contaminated soils [115,116] (Figure 1).

Arbuscular mycorrhizae, besides being related to plants, are also related to the PGPR in the rhizosphere and to the endobacteria, affecting their activity and generating a synergy in functionality [117,118]. The interactions between AMF and soil bacteria influence the expression of fungal genes. The interactions include the adhesion of bacteria to the surface of fungal spores, conidia, and hyphae, the injection of molecules into the fungal spores, the degradation of the fungal cell wall, and the production of volatile substances [119].

The consortia (fungi and bacteria) have multiple applications to sustainable agriculture that have been reported to allow greater nutrient uptake and biocontrol of pathogens, depending on agricultural practices that allow their maintenance [120], such as practices like null or scarce tillage; use of diverse and ideally native crops covers; use of organic amendments as compost; reduction or elimination of external inputs, such as fertilizers, herbicides, and control of pests and diseases; practices that promote agroecology; organic agriculture and smart agriculture to develop a regeneration of soil microbial consortiums; and an ecological intensification of crops [2,12,53]. Likewise, different communities of soil fungi have been detected that affect soil formation or stabilization at the macro- and microaggregate scale through different mechanisms within the physical, biochemical, and biological processes [121,122].

Table 3. Beneficial effects of *Actinobacteria* in agroforestry management.

Actinobacteria Species	Crops	Beneficial Effects	Reference
Micromonospora spp.	Alfalfa (*Medicago sativa* L.)	Plant probiotic bacteria	[110]
Streptomyces spp.	Grow on cellulose, hemicellulose and potentially lignin	Biomass degradation	[107]
Streptomyces davawensis	Soil	Antibacterial antibiotic roseoflavin	[97]
Micromonospora rifamycinica	Mangrove sediment	Antibacterial antibiotic rifamycin	[97]
Streptomyces lydicus WYEC 108	Grass, ornamentals, vegetables, and forest species	Biocontrol by soil-borne plant pathogens and foliar diseases	[98]
Streptomyces avermitilis	Ornamentals, vegetables, and forest species	Biocontrol of nematodes and insects	[98]
Actinomadura spp.	Vegetables grain	Bioherbicide/biopesticide producers 2,4-Dihydro-4-(β-d-ribofuranosyl)-1,2,4 (3H)-triazol-3-one (herbicide)	[99]
Streptomyces violaceusniger YCED-9	Soil	Antifungal agent producing guanidylfungin	[99]
Micromonospora lupini Lupac 08	Nitrogen-fixing nodule of the legume *Lupinus angustifolius* L.	Plant growth-promoting bacterium	[100]
Corynebacterium spp., *Pseudonocardia dioxanivorans*, *Streptomyces* spp., *Micromonospora* spp., *Streptomyces* sp. Strain MBCN152-1, *S. lydicus* WYEC 108	Vegetables, fruits, and grains	Plant growth-promoting bacterium and nitrogen fixation. Biocontrol agent and biofungicide	[104]

The biotechnological applications of consortia, such as the application of biofertilizers or biostimulants, is justified in agricultural soils of the Mediterranean climate that have less than 3.5% organic matter, where microorganisms can no longer perform their functions [123]. Considering that in these cases the soil microbiota must be restored with fundamental taxonomic groups or initiators, such as AMF [124], the application of microbial consortia is the preferred approach. These inoculants will have less ecological impact on the ecosystem and therefore on the environment and health [13]. Although further studies at the micro- and mesocosm level, followed by field research, will allow to assess the ability of selected AMF and bacteria to interact with native microorganisms and maintain their beneficial activities [125], the agricultural use of microbial consortia containing bacteria, fungi, and AMF is in its exponential phase [126], based on a range of evidence including wheat [127,128], Mediterranean vegetables [129], lettuce [130], vegetables [131], basil [132], tomato [133], and maize [134].
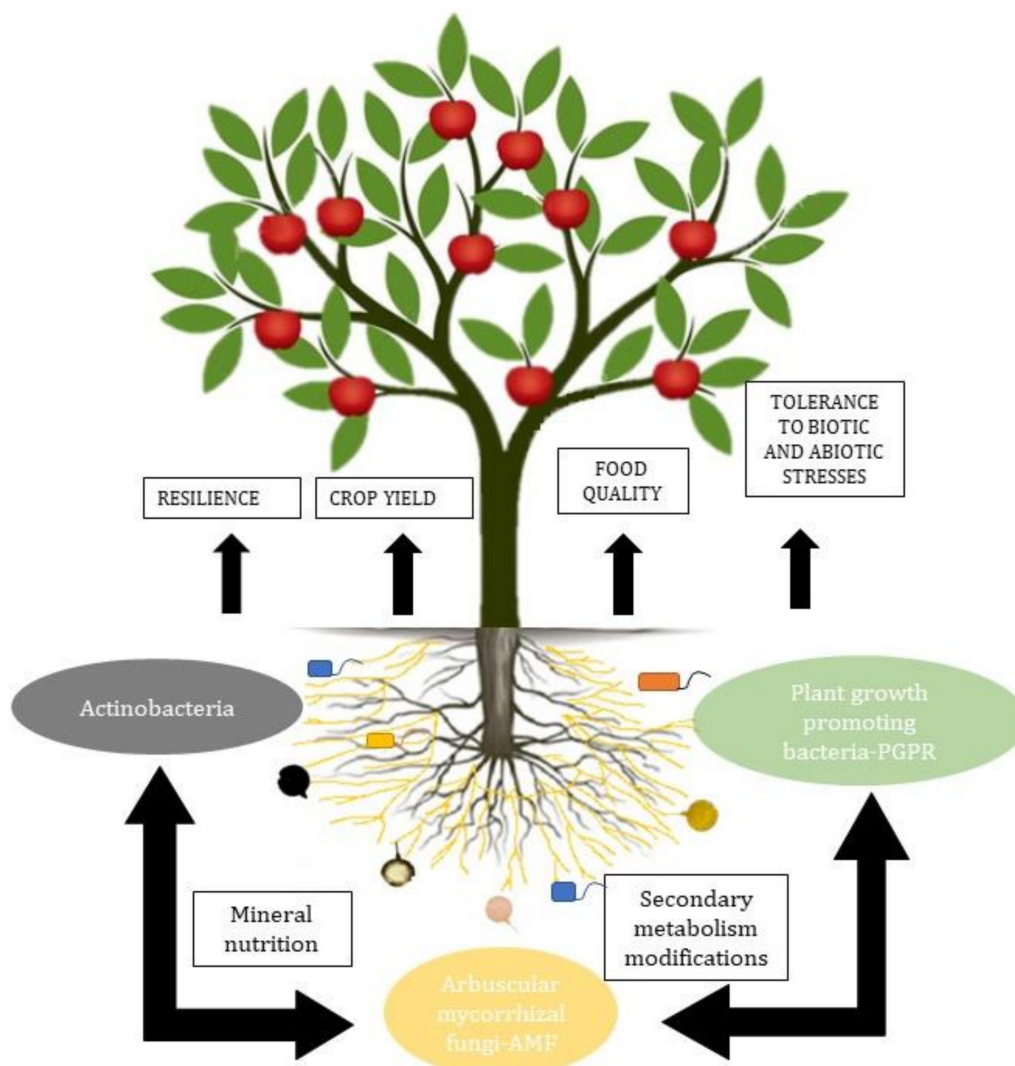

Figure 1. The ecosystem functions of microbial consortia of Actinobacteria, plant growth-promoting rhizobacteria (PGPR), and arbuscular mycorrhizal fungi (AMF) in sustainable agriculture.

Despite the demonstrated benefits produced by soil microorganisms, there is ample space for gaining further insight, especially on arbuscular mycorrhizal fungi, which are crucial for many ecosystem services, such as nutrient cycling and food production. An example is the case of Latin America [135]. In Latin America [136] and Africa, there is a need to focus on soil health and biodiversity among farmers, major agribusinesses, and policy makers, complementing the current productivity paradigm with sustainability and conservation objectives. Therefore, it is vital to describe the

development of the rhizosphere microbiome in all relevant crops, as microbial communities are deeply affected by agricultural management [137,138]. The databases of association between higher plants and mycorrhizal fungi are critical for addressing biogeographic and evolutionary issues [23]. In addition, soil biota is a key factor for the application of appropriate microbial inoculants in the field, but the genotype/genotype interactions between the microbial strain(s) and the crop cultivar(s), e.g., maize, often requires prior screening to obtain the desired results [136]; this is due to the lack of knowledge or neglect of the plant microbiome when selecting the germoplasm for higher productivity [1].

It has been observed that microbial communities are highly sensitive to changes in environmental properties, for example, the geographical location where the type of soil and its pH play a fundamental role in the distribution of species. In the same way, the climatic conditions and the type of vegetation determine in a dynamic interrelationship the biodiversity of the microbial communities in the different ecosystems [139,140].

Likewise, the specific inoculants of a single group of commercially produced microorganisms represent a small genetic group of fungi and/or bacteria selected to be both generalists and aggressive colonizers [13]. These traits have the potential to affect local communities of microorganisms, which may not be resistant to the introduction of other exogenous species [141]. The role of potentially invasive species in soil ecosystems has received little attention, despite knowledge of the role of soil biodiversity in ecosystem processes.

Currently, the knowledge of the identity of the species that make up a microbial community can be achieved through metagenomics. In order to be able to associate the functionality of certain taxa with the characteristics of crop productivity and resilience, it is necessary to carry on studies including the isolation and cultivation of the species [32]. In Latin America and Africa, there are still many knowledge gaps, where microbial communities are not known or are unidentified taxa [45,136]. This represents a problem when predicting changes at the ecosystem level that may be generated in the future, which is relevant in decision-making when designing public policies [23]. To protect the functionalities of terrestrial ecosystems in a productive eco-compatible modern agriculture, it is necessary to include soil microbiota and soil biota in environmental protection and impact assessment policies [22,26].

Climate change with its consequent events, such as droughts, temperature increases, and CO_2 increases, generates environmental changes that affect the microbial community and therefore the whole ecosystem. In agriculture, this presents a great challenge since there will be a significant impact on the productivity and resilience of agricultural systems [12,13]. Currently, different strategies are being developed to abort this issue, one of them being the Climatic Smart Agriculture, which seeks to develop a sustainable food system; to increase crop productivity and quality; and to reduce the impacts of climate change, through the adaptation and building of crop resilience, as well as conserving and increasing carbon stocks in soils and reducing GHGs [27].

Some examples for smart agriculture are the reported associations of the bacteria *Rahnella aquatilis*, which improves organic phosphorus solubilization, with the mycorrhizal fungus *Rhizophagus irregularis*. The association between the rhizospheric yeast fungi *Cryptococcus flavus* or *Candida railenensis* and the arbuscular mycorrhizal fungus *Rhizophagus irregularis* promotes root growth in corn plants [142]; in turn, the *Brettanomyces naardensis* yeast's association with fungi reduces the incidence of the pathogen *Macrophomina phaseolina* in sunflower plants; in addition, this association significantly improves the plant's growth parameters, such as plant height, dry weight, and number of leaves [143]. It has also been reported that consortia between filamentous fungi and PGPR stimulate the growth and yield of substances produced by plants, such as essential oils [144].

3. Conclusive Remarks

The biotechnological application of microorganisms, either through the selection and inoculation of specific microbial strains or just by promoting the activity of naturally occurring microbes, holds a great potential for sustainable agriculture, as these innovative agronomic practices have the capacity

to replace conventional agricultural practices. Beneficial microbes are multifunctional, with effects ranging from protection from pathogens to reduction of drought, stimulation of nutrient uptake, and can reproduce and be self-sufficient. In addition, microbe management can promote systems that are resilient to climate change.

When thinking about the formulation of microbial consortia, we should consider functional taxa of various species that are effective and compatible with other soil organisms, where they will be applied according to their geographical and climatic conditions. It is expected that future research related to sustainable agriculture will focus on the importance of soil (micro) biota, focusing on both the morphology of cultivable microorganisms and the metagenomics of all species found in the soil, in order to formulate distribution maps that will allow us to make informed decisions on the effect of agricultural practices on (micro) biomes.

Author Contributions: All the authors provided equal contribution to the review. All authors have read and agreed to the published version of the manuscript.

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

Abbreviations

GHG	greenhouse gases
AMF	arbuscular mycorrhizal fungi
PGPR	plant growth promoting bacteria
gibberellic acid, GA3	gibberellins
indolacetic acid, AIA	auxins
ABA	abscisic acid
ACC	enzyme 1-aminocyclopropane 1-carboxylate deaminase

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