



## “Reflexions on the role, diversity, conservation and management of the genetic microbial resources in Agriculture”

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### 1. Importance of soil ecology knowledge in the agroecosystems

Current worry about food production, climate change and environmental contamination, are issues of vital importance not only for human society but for the whole life in our planet. However, most of the time people forget about the importance of soil and soil microbial communities' structure and function, and as a consequence, the transcendental importance to know about ecology of the soil ecosystem and elucidate the best way to manage the soil biological and mineral resources, and understand their role in agriculture and food production, climate change and environmental contamination. It is necessary to initiate with a definition: “Soil ecosystem is a living and dynamic environment, habitat of thousands of microbial species, animal organisms and plant roots, integrated all of them in the food webs, and performing vital functions like organic matter decomposition, nutrient cycling and release, plant growth promotion. Besides, soil receive, hold and release water, transfer energy in the detritus food chain, and act as an environmental buffer (Coleman, 2013; Bardgett and van der Putten, 2014). Soil is also where plant roots productivity and their root exudates represents the main and first trophic level (producers) (Parton et al., 1987), the beginning of the soil food web and of thousands of biological and ecological interactions (Hawes et al., 1998; Walker et al., 2003; Rodríguez-Guzmán and del, 2022), which have evolved for thousands and millions of years throughout the impulse of the natural selection forces. However, soil is also built by physical and chemical components, and therefore the soil ecosystem is a living system in which interplay mineral and organic materials. Soils are built up through millions of years, from the parent rock layer to the small sand, lime and clay particles derived from physical and chemical intemperization processes, and from biological activities which perhaps be the most important factor in the soil's formation (Gadd, 2007; Rodríguez-Guzmán and del, 2022; Coyne et al., 2022)”.

Bacteria and fungi communities are the microorganisms which first

establish in the parent rock and initiate the biological intemperization process (Gadd, 2007), which in turn generate an adequate substrate for the germination and establishment of plant seeds and their progress to seedlings and young plants in time. It is important to indicate that root exudates secreted in the rizosphere by the young and adult plants will allow the establishment of mutualistic and antagonistic direct and indirect relationships with many and diverse microorganisms species and populations, among them rhizobacteria, fungi, ecto and endo mycorrhizal fungi, oomycetes, viruses, bacteriophages, protozoa, nematodes, talking only about microorganisms. Root exudates are a diverse group of compounds released by the roots throughout secretion, diffusion, or cell lysis. They are classified into two main categories: high molecular weight (e.g., mucilage, cellulose) and low molecular weight compounds (e.g., organic acids, amino acids, proteins, sugars, phenolic metabolites and other secondary metabolites). These exudates mediate interactions with neighboring plants and microbes.

Root exudates serve multiple functions, including nutrient acquisition, protection against invasion (e.g., allelopathy, and defense against root pathogens), and chemical signaling to attract symbiotic partners via chemotaxis. Additionally, they facilitate the root colonization by beneficial microorganisms (e.g., *Bacillus subtilis* and *Pseudomonas fluorescens*).

The compositions and quantity of root exudates are influenced by plant species, phenological stage, soil microbiome, and the chemical and physical properties of the environment (Bais et al., 2008). Several research have demonstrated that plant species through root exudates and soil type cooperatively shape the structure and function of microbial communities in the rhizosphere (Berg and Smalla, 2009; Amsili et al., 2021), at the same time rhizobacteria may change the plant root architecture (Khoso et al., 2024; Vacheron et al., 2013). Along with bacteria, the soil fungi and virus community participate in the geochemical cycles of N and C, and therefore in N fixation (Gadd, 2007; Williamson et al., 2017), increase the release and amount of available mineral nutrients from the soil particles. Microbiota participates in the production

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of plant growth regulators like auxins, gibberelins, cytokinin, ethylene and abscisic acid, contribute in the formation of biofilms around the plant roots, helping in the control of pathogens and the induction of systemic resistance (Khoso et al., 2024). Plant viruses have just been incorporated as another relevant element in the ecosystems (Rodríguez and Roossinck, 2012), and soil viruses as an important component of the soil biodiversity, and they function “as major drivers of microbial mortality and functioning across a wide range of spatial and temporal scales, soil viruses appear to be key regulators of cellular metabolism and microbial community properties and as well as biogeochemical processes critical to ecosystem function”) (Williamson et al., 2017; Liang et al., 2024). In this context, viruses seem to be cornerstones that catalyze the processes of evolution on the planet. Since a broad focus, we need to understand this is a tri-partite relationship among the plant (through the root exudates), the soil, and the soil microbiome community with bidirectional effects between their components, which at the same time include multiple direct and indirect effects.

## 2. Evolution of the relationship between plants and microbes

It must be noted that the relationship between plants and microorganisms, mainly bacteria, fungi and perhaps viruses, was originally established in ancient geological times, around 460 million years in the Ordovician Era (Bidartondo et al., 2011; Boer et al., 2005; P.R. Hardoim et al., 2015), during early colonization of land by terrestrial plants, and it has evolved throughout the time. These coevolutionary relationships have become necessary for both components, the plant and the microorganism, allowing both partners to develop new life strategies for their reproduction, offspring and survival under different environmental conditions (Saikkonen et al., 2004; Rutkowska et al., 2023), increasing their ecological fitness. One well known and accepted event is that without the intervention of ancient mycorrhizal fungi and perhaps bacteria (Boer et al., 2005), early plants might not be able to establish in land more than 400 million years ago (Redecker et al., 2000; Redman et al., 2001; Rodríguez et al., 2009; Bidartondo et al., 2011; Selosse et al., 2015; Rodríguez-Guzmán and del, 2022) and populate the earth. Throughout multiple symbiosis and dynamic processes in time and space (mutualist and antagonist relationships), not only with fungi but with bacteria and also with viruses (bacteriophages) (Williamson et al., 2017), plants were and are able to perform vital function like seed germination, growth, reproduction, and persistence, in natural and managed cropping systems. As a result of these biological and evolutionary relationships, some plants and microorganisms have been closely associated and co-evolved at different plant compartments: rhizosphere, caulosphere and phyllosphere (Pantigoso et al., 2022; Liang et al., 2024); even more, plant seeds also maintain a microbiome (spermosphere), without it, seeds of certain plant species will not germinate (Cordovez et al., 2019; Samreen et al., 2021; War et al., 2023). It seems that at the beginning of the terrestrial plant life in ancient geological times and until the present, soil has been an important seed bank of microbes with the soil microbiome acting directly at the rhizosphere level (Vandenkoornhuys et al., 2015; Cordovez et al., 2019). It must be noted that there are different levels of intimate relationships between plants and endophytes. Some endophytes require plant tissue to complete their entire life cycle within the plant; these are known as ‘obligate endophytes’ (e.g., fungal mycorrhiza, rhizobia bacteria, and *Epichloë/Neotyphodium* in grasses). Another group, referred to as ‘opportunistic endophytes,’ primarily proliferates outside plant tissue but occasionally enters the plant. This group includes bacterial genera such as *Pseudomonas* and *Azospirillum* and fungal genera like *Hypocrea* and *Trichoderma*. Between these two groups lies an intermediate category known as ‘facultative endophytes’ which includes the majority of plant-associated endophytes. These organisms obtain nutrients from plant tissues and, due to this behavior, are sometimes classified as mutualists (G.A. Lane et al., 2000; P.R. Hardoim et al., 2015).

This classification suggests that plant-endophyte relationships exist

on an ecological continuum, having evolved at different levels over time—and perhaps still evolving (Brundrett, 2002). However, the genetic and molecular mechanisms, DNA phylogenies between plant hosts and endophytes, and community ecology involved are only beginning to be investigated (G.A. Lane et al., 2000; Brundrett, 2002; P.R. Hardoim et al., 2015). The mycorrhiza-plant relationship is probably the most well-documented example of coevolution, particularly in the case of mutualistic, symbiotic, and obligate mycorrhizae. Nonetheless, there is no doubt that endophytes—including plant pathogens—play an intrinsic and significant role in the plant life cycle and evolution.

## 3. Importance of the dynamic evolution (Coevolution) between microorganisms and plants

As previously mentioned, microorganisms and plant host have co-evolved since ancient times. When referring primarily to bacteria and fungi, as well as viruses, it is crucial to consider the differences in evolutionary rates between plants and their microbial counterparts. Some key questions arise: How do plant physiology and phenology adjust to microbial life cycles, given that microbes have faster reproduction rates and more complex evolutionary mechanisms than their plant hosts? (de Vries et al., 2020).

To address this, several models have been proposed to explain the emergence of new pathogens in agroecosystems, including host-tracking, host jumps, host shifts, hybridization, and horizontal gene transfer (Stukenbrock and McDonald, 2008). This topic is not only relevant for understanding endophyte microbiomes but also for plant pathogens, providing fundamental ecological and evolutionary insights for their management in agriculture and natural systems. Multiple studies have demonstrated that both endophytes and plant pathogens induce significant changes in their plant hosts (Vandenkoornhuys et al., 2015; de Vries et al., 2020; El-Metwally et al., 2023). Conversely, plants also influence their microbiomes (Compant et al., 2016; Aleynova and Kiselev, 2023). These reciprocal interactions occur at various biological levels, including genetic, biochemical, cellular, physiological, individual, population, and community levels (Cahill et al., 2008; Baltrus, 2017; Cordovez et al., 2019; de Vries et al., 2020).

A relevant example of microbial communication is the ‘Quorum Sensing’, a cell-to-cell density-dependent signaling mechanism used by bacteria and some fungi (Majdura et al., 2023). This system interacts with the complex biochemical signaling networks between plants and microbes, facilitating cross-kingdom communication (Rodríguez and Roossinck, 2012; El-Metwally et al., 2023). Such communication plays a role for competing ecological niches, involving bacteria, fungi, and plants (El-Metwally et al., 2023).

Another critical but often underestimated process of plant-microbe communication and interaction is root exudation—the release of diverse biochemical compounds from roots into the rhizosphere. These root exudates and rhizodeposits mediate plant-microbe interactions (Walker et al., 2003; Chagas et al., 2018). Research has shown that plants produce specific root exudates in response to the presence of particular microorganisms, including species like *Bacillus subtilis* (Vives-Peris et al., 2020).

The processes described above provide evidence that plants and microbes have maintained close relationships over extensive geological and evolutionary periods. As Hartmann et al. (2014) stated:

“Co-evolutionary forces have endowed plants with the ability to produce signaling molecules to mimic microbial autoinducer molecules.”

Despite advances in genomics and phylogenetics, clearly demonstrating and sustaining co-evolutionary relationships between microbes and plants remains a challenging task.

As it was said before, relationship between mycorrhizal fungi and plants is the most accepted co-evolutionary interaction between plants and microorganism. Another frequently cited example is the symbiotic relationship between nitrogen-fixing Rhizobia and leguminous plants.

However, recent genetic and ecological research suggests that this relationship may not be strictly co-evolutionary but rather a flexible symbiosis. This hypothesis is supported by findings on bacterial genetic plasticity, symbiotic replacement, easy recruitment of symbiotic bacteria by leguminous plants, and lateral transfer of symbiotic genes, all of which appear to erase the coevolutionary relationship (Martínez-Romero, 2009; Coba de la Peña et al., 2018).

A further example often classified as a oevolutionary interaction is that between *Epichloë/Neotyphodium* fungi and grasses (G.A. Lane et al., 2000). However, plant-microbe interactions become even more complex when a third or fourth component are involved; e.g., in cases like plant-microbe-insect (vector)-predator (natural enemy) systems, researchers often ask: “Who is truly leading this complex symbiosis?”. In some cases, it appears that microbes act as the primary drivers, shaping and controlling these intricate ecological networks (Blua and Perring, 1992; Redman et al., 2001; Márquez et al., 2007; Rodríguez and Roos-sinck, 2012; Sanches et al., 2023).

#### 4. Endophyte microbiome

The term endophyte was used for the first time in 1866 by Anthon De Bary, who is named the father of Plant Pathology, and he referred to any bacteria or fungi living inside the plant. Since then, this term has been modified and defined more precisely; at present ‘endophyte’, is applied to the microorganisms living inside plants without causing any damage (Wilson, 1995; Saikkonen et al., 2004). We know now that bacterial and fungal endophytes perform several important and vital functions for the host plant: growth promotion, defense against pathogens through the initiation of IAR (Induced Acquired Resistance) and ISR (Induced Systemic Resistance), defense against pest insects through alkaloid liberation, nutrient uptake, germination, resistance to biotic (plant pathogens) and abiotic stress (drought, cold and salinity), fitness and diversification (Wilson, 1995; Clay and Schardl, 2002; P.R. Hardoim et al., 2015; Rutkowska et al., 2023); some endophytic plant growth-promoting bacteria also increase the plant capacity to extract heavy metals like Cd, Zn and Pb, e.g., *Bacillus pumilis* (Ma et al., 2015; Khatoun et al., 2024).

There is research which also demonstrate that oomycetes, viruses (Márquez et al., 2007; Andika et al., 2023), and bacteriophages (Aghdam et al., 2023) can play an important role as plant endophytes. Endophyte microorganisms are acquired by the plant via vertical transmission (from parents to offspring) and also by horizontal transmission (sexual or asexual via), and act as permanent endophytes.

Endophytes enter plant tissues through natural openings in the plant: root hairs, stomata, and wounds as well as stomata, wounds, hydathodes, lenticels in the shoots and germinating radicles. Bacterial and fungal endophytes are attracted to and adhere to roots due to the rich and nutritive composition of root exudates. Once there, they may secrete cellulolytic enzymes (e.g., cellulases, xylanases, pectinases, and endoglucanases) to break down the cell walls of epidermal root cells, allowing them to enter the cortex either intra- or intercellularly. Some endophytes remain within these tissues, where they feed, develop reproductive structures (e.g., spores, hyphae, conidia), and increase in number. However, others reach the vascular tissues and migrate to different organs, including the stem, leaves, flowers (anthosphere), and fruits (carposphere) (Kandel et al., 2017; Lignon et al., 2025). Microbial endophytes are also acquired by plants through the pollen grains transported by pollinators (insects, birds) (P.R. Hardoim et al., 2015; Lignon et al., 2025). Another example of endophyte movement inside plants is seen in *Zea* (maize) seed endophytes, they can travel and colonize roots, enter the rhizosphere, and eventually reach the soil (Johnston and Raizada, 2011).

However, as mentioned before, soil is considered as the seed bank of microbes, and therefore, an important amount of soil bacteria and fungi may be acquired as endophytes from the plants roots, attracted by the root exudates present in the rhizosphere, enter through the root

epidermal cells to the cortex and to the vascular system, and acting as temporally endophytes until they are released back to the soil again, during the root senescence (Rodríguez et al., 2009; Hirsch et al., 2010; P.R. Hardoim et al., 2015). It is also important to mention that some soil microbes colonize the plant seeds, and they are important for their germination, they can readily migrate from the seeds to the roots and shoots of the germinated seedlings, producing an overall increase in the root and shoot length as it happens in the rice crop (Samreen et al., 2021; Jana et al., 2023).

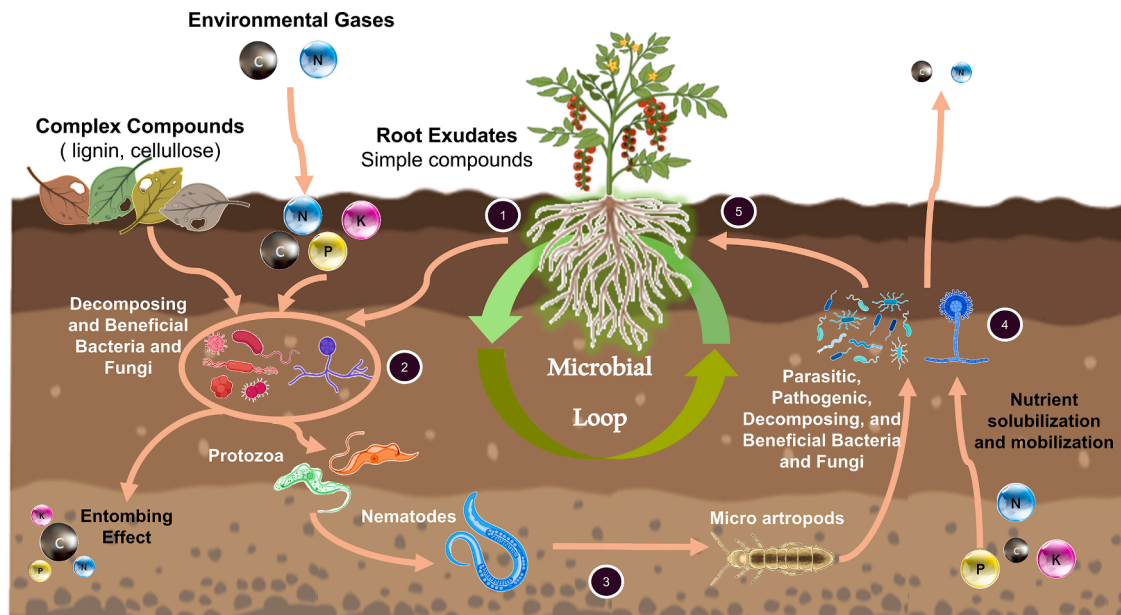
#### 5. Soil food web, microbial loop and ecological functions

Soil microbiome is a key stone in the structure and function of the soil ecosystem: plant roots, bacteria, fungi, protozoa, rotifers, diatoms, microalgae, nematodes, all of them are part of the soil food web. This food web initiates with the release of the very rich and diverse root exudates in the rhizosphere, which attract or repel a myriad of soil microorganisms in response to mutual or antagonistic interactions and functions, giving place to the ‘microbial loop’ (Fig. 1) (Bonkowski, 2004; Berg and Smalla, 2009), and later, to their connection and interaction with the mesofauna (acari, collembola, ants, termites, isopods, spiders), and the macrofauna (enchytraeids, earthworms, microarthropods, moles, shrews, small rodents) (Coleman, 2013). The microbial loop refers to the specific trophic relationships established among bacteria, fungi, bacteriophage, algae and protozoa within a trophic web (Bonkowski, 2004). Every element of the soil trophic web from the plant roots (primary producers) to consumers, decomposers, and predators of the first, second, third and fourth trophic levels are very important in order to keep structure and function of the soil food web (Fig. 2). The biodiversity of species and functional groups and therefore the complexity of the soil trophic web, affect structure, function, and dynamics of the whole soil ecosystem, driving the soil stability, nutrient cycling and reducing the possibility of invasion by foreign microorganisms like soil-borne plant pathogens (Coleman, 2013; Bardgett et al., 2005).

Microbial communities have also a transcendental role in the balance and buffering of (a healthy) soil. A healthy soil may be defined as “the continuous capacity of the soil to function as a living ecosystem that sustains plants, animals and the human being, and carry out the nutrient cycling, infiltration and disponibility of water, buffering of disturbances, physical stability, able to maintain biological activities, and therefore it is habitat for the biodiversity” (Bardgett and van der Putten, 2014; Fierer, 2017; Lehmann et al., 2020). Following this definition, soil microorganisms take part in organic matter decomposition, absorption and nutrient cycling, minerals transformations, and plant growth promotion. Nevertheless, it is important to mention that through the different trophic and non-trophic relationships (like competition, predation, parasitism, mutualism, and commensalism), established between plant-microorganisms (through root exudates) and microorganism-microorganism, it gives rise to the ecological structure, diversity and functional basis of the soil ecosystem (Rodríguez-Guzmán and del, 2022).

#### 6. Microbiome and agroecosystems

Considering all that has been discussed regarding the significance of soil food webs diversity, structure and function, and the role of the microbial communities, an important question is how the cropping systems management affect the soil ecosystem including the soil diversity and food webs? Once a plant species is established, its roots exudates vary in composition and concentration throughout its growth and development, dynamically changing over the crop’s lifetime (Chaparro et al., 2014; Zhelnina et al., 2018; Santangeli et al., 2024; Liu et al., 2024). It has been demonstrated that microbiome composition and exudation patterns also fluctuate depending on the time of day, as well as in response to abiotic or biotic stresses (McLaughlin et al., 2023).



**Fig. 1.** Schematic representation of the microbial loop in soil ecosystem. (1) Root exudates serve as the primary energy source for bacteria and fungi. (2) These microbes decompose organic matter, releasing nutrients, mineralizing them, and fixing environmental carbon and nitrogen, some of which is sequestered in the soil. (3) The trophic network continues as bacteria and fungi become food for protozoa, which are consumed by nematodes, and further by microarthropods. At this level, interactions become complex, as some fungi prey on protozoa, nematodes, and microarthropods, while nematodes can consume fungi, bacteria, or other nematodes. (4) Bacteria and fungi also act as pathogens, decomposers, nutrient solubilizers, and producers of secondary metabolites that influence root exudation and plant health. This microbial loop is the fundamental process that initiates crop production in agroecosystems (The figure was generated using images sourced from BioRender and BioIcons).

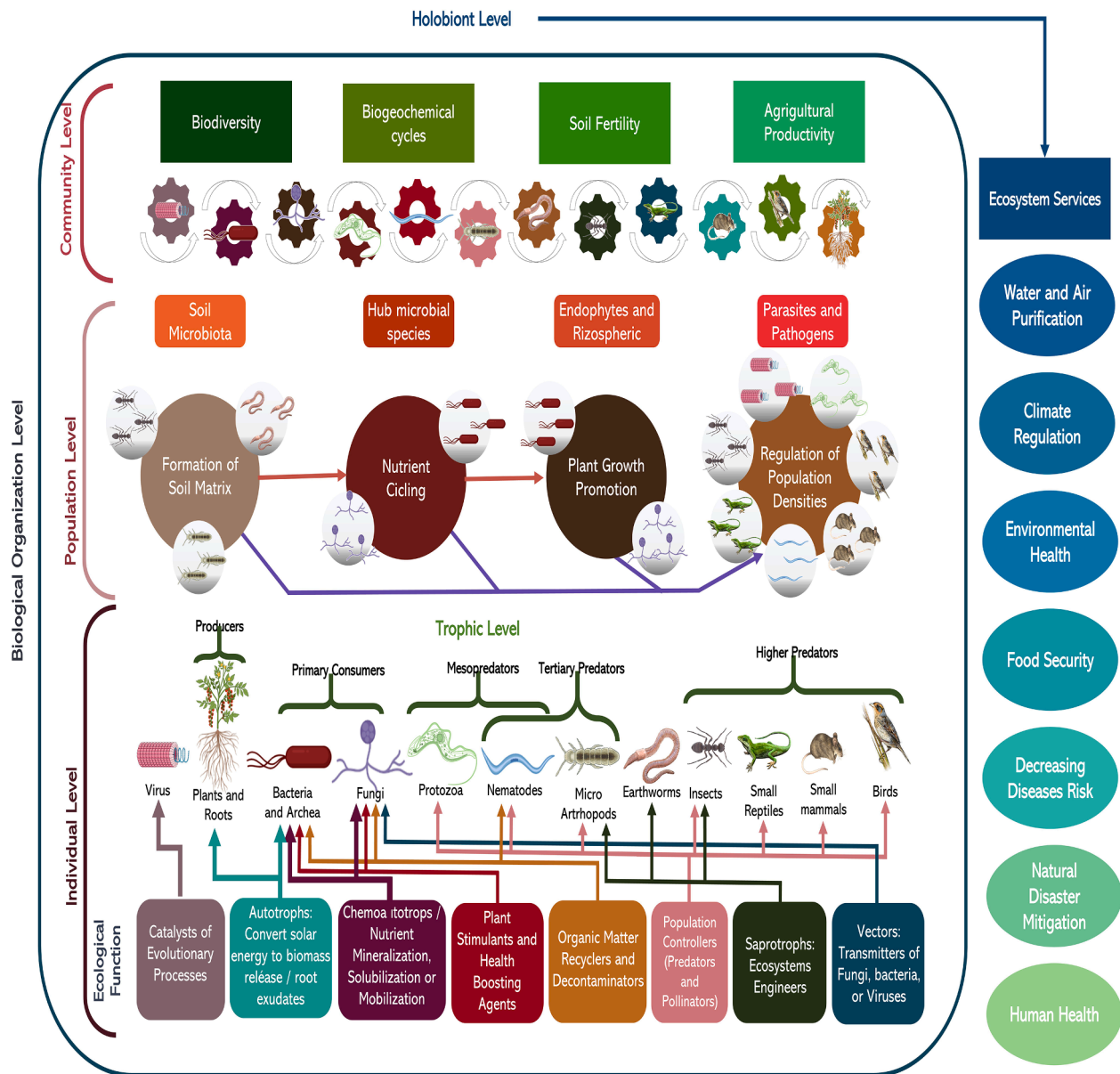
These changes affect and select the rhizosphere microbiome (Berg and Smalla, 2009), and also affect the establishment of another individual of the same plant species, and individuals of different plant species (i.e. throughout allelopathy), influencing the plant community composition, diversity, and productivity. As Van Der Heijden et al. (2008) mentions “Variations in the composition of soil microbial communities can impact ecosystem functioning”. Therefore, is expected that the different activities applied to the management of the cropping systems will decrease the diversity and change the structure and function of the soil food web, making the soil ecosystem more susceptible and/or unable to buffer perturbations and invasions. Coleman (2013), mentioned that the general conclusion is that “in conversion from natural vegetation to agriculture, the diversity of a wide range of microbial communities and faunal groups, is significantly reduced in the disturbed agroecosystems”. Nowadays we know that the change of land use from a natural ecosystem (temperate or tropical forest) to agriculture, implies above-ground perturbations like deforestation, loss of plant and animal biodiversity, water and air contamination because of the agrochemicals applied, and also belowground perturbations with loss of soil and disturbance of the structure and function of the soil microbiome (Hermans et al., 2016; Hermans et al., 2020; Yin et al., 2020; Díaz Vallejo J. et al., 2021; Navarro-Noya et al., 2022; Louissou et al., 2023). However, there are crop management strategies that causes less harmful effects on the soil microbial communities and on the soil food web, and therefore on the soil ecosystem. Some of these practices are those applied by Zhang et al. (2017), cover crops at intervals between the economic crops and minimal or no-tillage level, to assess their effect on the nematode functional groups and assemblages into the soil food web, considering the importance of the soil nematodes as indicators of the soil health and because of their different trophic habits. They took in consideration that cover crops increase the number of roots and the amount of rhizosphere exudates in the soil, which means there were “resources available to the microorganisms in the soil food web while no tillage minimizes disruption of the soil environment and the habitat provided for soil organisms” (Zhang et al., 2017). In the specific case of

nematode functional groups, cover crops and no-tillage increased the number of bacterivores and fungivores but decreased the number of herbivores (plant pathogens); in general, cover crops strongly enhanced the nematode assemblages in the field soils favoring the nitrogen mineralization and therefore the ecosystem services. In another work conducted in Tlaxcala, México, with maize, comparing the effect of conventional practices (CP) and sustainable conservation agriculture practices (CA) including minimal tillage, crop residue retention and crop diversification, on the bulk soil and rhizosphere soil bacterial communities, Navarro-Noya et al. (2021), found that the agricultural practice was the most important factor in defining the structure of bacterial communities, even more than rhizosphere and plant growth stage; however, in CA the practices applied increased the diversity of soil microbial species and functions and strongly affected how they were structured compared to conventional practices. Significant research has been conducted on the effects of multiple cropping and crop rotation on the soil microbiome. In tropical and subtropical agroecosystems, multiple cropping has been a traditional agricultural strategy, particularly in Asia, Africa and Latin America (Francis, 1986). In a study conducted in a paddy field in China, multiple cropping positively influenced the soil microbiome by increasing microbial diversity, abundance, and biomass, ultimately enhancing rice crop growth and yield (Tang et al., 2024). Similarly, a 16-year field experiment in China demonstrated that diversified crop rotation improved microbial diversity and soil multifunctionality (Yang et al., 2023).

## 7. Study and application of the knowledge about microorganisms in research fields

The link between microorganisms and plants is so strong that it is impossible to study, conserve and apply them as different entities (Baltrus, 2017; Rodríguez-Guzmán and del, 2022). This is a transcendental consideration in fields of study like: a) in agriculture: plant breeding, plant tissue culture, development of plant resistance to biotic and abiotic agents, conservation of plant genetic resources (wild





**Fig. 2.** Food webs in the soil ecosystem as drivers of ecosystem services. (1) Individual level: Each microorganism has a specific function in the soil, interacting beneficially (mutualistic, symbiotic) or antagonistically (pathogenic, parasitic, predatory). (2) Population level: Groups of microorganisms with similar functions contribute to soil formation, nutrient cycling, plant growth promotion, and population control. (3) Community level: Microbial communities act like interlocking gears, enhancing biodiversity, biogeochemical cycles, soil fertility, and agricultural productivity. (4) Holobiont level (ecosystem): The synchrony of these interactions generates physiological processes that result in tangible ecosystem services (The figure was generated using images sourced from BioRender and Biolcons).

ancestors), conservation and development of suppressive soils; management of plant diseases and insect pests; b) in ecology: structure and function of communities, soil and ecosystems function and restoration, conservation 'in situ' of habitats and their microbial resources; c) in microbiology: microbial taxonomy, conservation 'in situ' and 'ex situ' of microbial genetic resources; d) in evolution: taxonomy and phylogenetics; e) in molecular biology: development of new molecular methodologies and bioinformatics; f) in medicine: development of antibiotics; g) and also in applied fields like biotechnology: obtainment of metabolites, development of bioinoculants and antibiotics. A substantial body of research has been conducted on the application of microbial inoculants, either as single strains or in combinations of two or three, sometimes referred to as a 'consortium.' These inoculants may include Plant Growth-Promoting Rhizobacteria (PGPR), such as rhizobia species or different strains of *Azospirillum*, Arbuscular Mycorrhizal Fungi (AMF) like *Glomus* spp., and well-known biocontrol agents such as

*Bacillus subtilis* and *Pseudomonas fluorescens*. Additionally, mixed inoculants combining PGPR and AMF have been explored, as described by Trabesi and Mhamdi (2013) and Naiman et al. (2009).

Overall, research findings indicate positive effects on plant growth and increased resistance to plant pathogens. However, the impact of these inoculants on the rhizosphere and soil microbial communities is not always the same; apparently, showing no a consistent behavioral pattern of the microbial communities in response to the inoculants applied. This variability highlights the need for further research involving ecological approaches at the community and ecosystem levels, integrating the microbial loop as part of the soil food web and ecological networks.

Research on the microbiome and microorganisms is crucial due to their profound evolutionary and ecological interactions within any ecosystem -be it soil, plants, animals or humans. Given the potential long-term cascading effects these interactions may have, as noted by

Cahill et al. (2008), its imperative that researchers and technicians across all disciplines adhere to ethical standards in their work. This is more than a request, is a demand (Rodríguez-Guzmán and del, 2022). Perhaps in the field of biotechnology is more relevant and easier to make some important ethical questions, like: Do bioinoculants must be developed and applied as only one microbial species, or as a consortium of species? How is it decided what microbial species conform the consortia? Biotechnological enterprises made research to define their bioinoculants under scientific (ecological and evolutionary) basis? Since an ethical research point of view is important to consider the mutualistic and antagonistic evolutionary relationships established between plants and microorganisms?

## 8. Relevant approaches and considerations in the research, conservation and management of the genetic resources of microorganisms

Microbial genetic resources play a crucial role in ecosystem functionality and health, including agricultural systems from which humanity derives food (Zelaya-Molina et al., 2024). The aforementioned discussion clarifies that food production is a result of biotic interactions that have coevolved over time. These interactions involve the soil, the microorganisms and macroorganisms within it, and their intricate interactions with plants and their exudates, all influenced by environmental factors (Bender et al., 2016; Fierer, 2017; Chávez-Díaz et al., 2019; Delgado-Baquerizo et al., 2020; Cruz-Cárdenas et al., 2021). This complex molecular dialogue among biotic and abiotic components of agroecosystems orchestrates productivity. Considering this knowledge, the pathway to sustainability becomes evident. It requires the transformation of agricultural practices to embrace technologies that enhance biodiversity, foster interactions, support the soil biogeochemical cycles and the soil resilience ability from disturbances, thereby ensuring sustainable high-yield production.

Effective management, conservation, and utilization of microorganisms, informed by an understanding of agricultural ecosystems, should be a medium-term goal for humanity. Knowledge gathered from molecular and genetic technologies since 1985 should now be harnessed to develop tools that address critical questions: How can we identify and harness key species in agroecosystems? How can humanity develop technologies for the effective long-term preservation of these species *ex situ*? How can humanity conserve environments that support the coevolution of crops and their microbiomes despite climate change? Additionally, how can we create microbial-based technologies to enhance food security and resilient economy? (Sessitsch et al., 2018; Trivedi et al., 2020).

The development of such technologies should not overlook bioethical considerations and should adhere to principles such as doing good, not causing harm, respecting others, and acting justly (Lange et al., 2022). These technologies should also comply with equitable frameworks for access and benefit sharing, such as the Nagoya Protocol (Sessitsch et al., 2018).

On the other hand, it is crucial to raise awareness about the differences between chemical and microbiological inputs. While chemical inputs are generic and can be applied broadly, inputs based on native and exotic microorganisms do not seem to work the same. Native microbiological inputs often yield better responses, suggesting that agricultural productivity may be closely tied to what we could describe as 'soil microbiological sovereignty.' This concept is supported by numerous observations showing that native microorganisms are better adapted to the crops and environmental conditions with which they have coevolved, thereby establishing more efficient interactions than introduced exotic microorganisms. Thus, the food production phenomenon is the result of millions of years of coevolution, as documented by researchers such as Bakker et al., 2012; Chaparro et al., 2012; Vacheron et al., 2013; Pérez-Jaramillo et al., 2016, and many others. It raises a critical question: could the long-term use of exotic microorganisms

negatively affect the microbiological sovereignty of the soil, and what repercussions might this have? Is there a risk that, after 50 years, we might face a scenario similar to the current issues with agrochemicals?

## 9. Insights from co-occurrence analysis: conclusive observations

To construct this article, predefined search terms were used as search engines in the PubMed, Elsevier, Scopus, and Google Scholar databases. These search terms included 'Agroecosystems and Microbiome,' 'Endophytes,' 'Plant Holobiont,' 'Ethics in Microbiome Management,' 'Microbiomes in Plant Domestication,' 'Microbial Competition and Fitness,' 'Microbial Consortia,' 'Plant-Microbial Coevolution,' 'Rhizosphere,' 'Soil Biodiversity,' 'Soil Food Web,' 'Microbial Loop,' 'Microbial Resilience,' 'Soil Viruses,' 'Agroecosystems Evolution,' and 'Conservation of Microbial Genetic Resources.' After conducting the search, a total of 82 relevant publications were retrieved.

The retrieved articles were managed in Zotero (Takat et al., 2023), and a .RIS file was generated for further analysis using VOSviewer. A co-occurrence map was created using the full counting method, analyzing terms from the titles, abstracts, and keywords. A total of 2403 unique terms were identified, of which only those with a minimum of 10 co-occurrences were retained, reducing the set to 75 terms. Using VOSviewer's predefined algorithms, a relevance score was calculated, and the top 60% most relevant terms were selected, resulting in 45 terms. After filtering out unrelated terms ('context,' 'factor,' 'number,' and 'year'), the final co-occurrence map was constructed with 42 terms, employing the association strength normalization method (Perianes-Rodriguez et al., 2016).

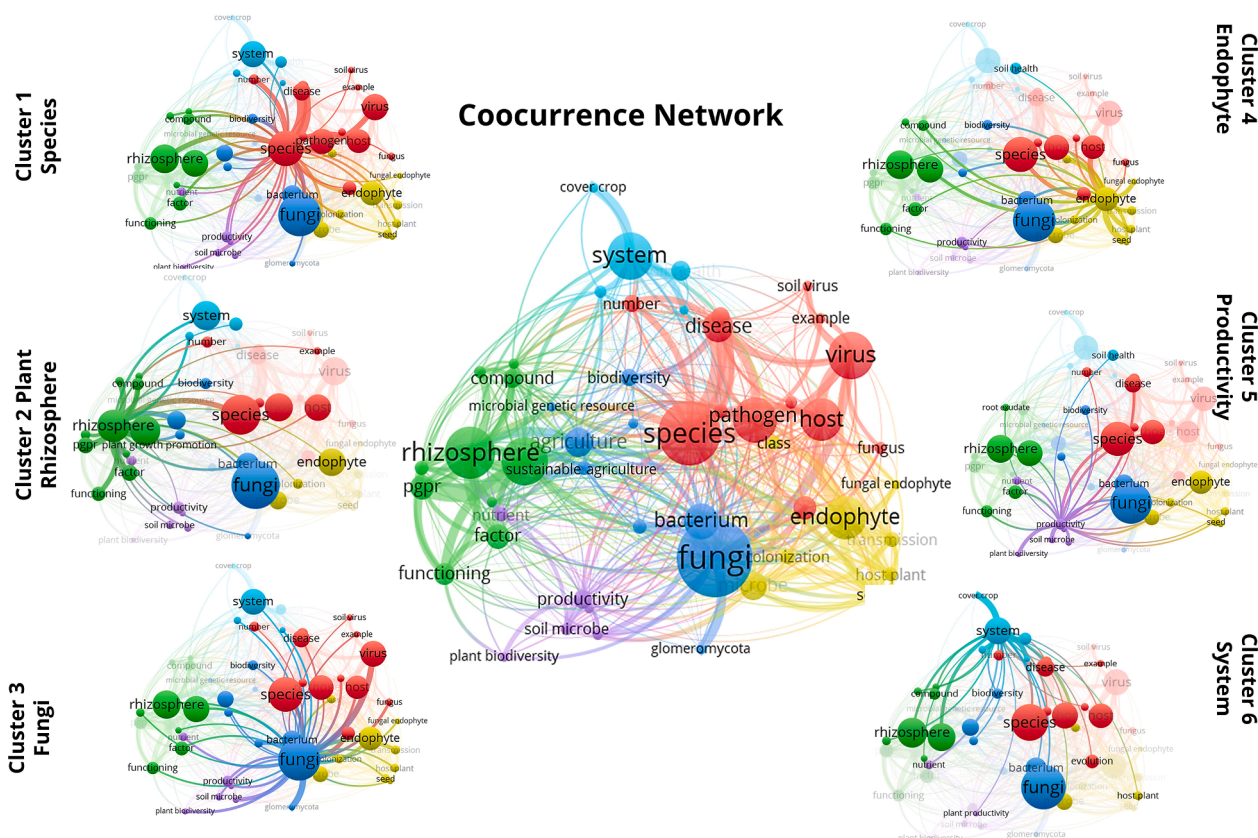
The obtained co-occurrence network is divided into six clusters, representing the critical terms that the referenced research in this review focuses on, thus enriching the discussion (Fig. 3).

The first cluster, 'species,' highlights the ongoing debate on soil biodiversity and its fundamental role within agricultural systems, emphasizing the importance of native microbial communities and their co-evolutionary interactions with crops. The second cluster, 'rhizosphere,' reflects the interactions at the root-soil interface, mediated by root exudates and microbial molecular mechanisms, and their impacts and responses within the agricultural system, conceptualized as a holobiont.

The transition to the third cluster, 'fungi,' underscores the critical role of fungi in ecosystems, particularly their symbiotic relationships with plants and bacteria that are central to nutrient cycling. The fourth cluster, 'endophyte,' highlights how endophytes, the internal colonizers of plants, significantly contribute to the nutrition, health, and productivity of crops. Collectively, these four clusters illustrate that food production is fundamentally an eco-physiological and biological phenomenon. Understanding this complexity and respecting the 'microbiological sovereignty' of the soil are essential for fostering sustainable and productive agriculture, which in turn is pivotal for environmental and human health.

The fifth cluster, 'productivity,' explicitly connects agricultural productivity to the interactions among plants, microorganisms, and the environment, emphasizing their collective impact on health and ecosystem services. The sixth cluster, 'system,' likely represents the systematic approaches that facilitate the exploration of biotic and abiotic interactions, crucial for enhancing food security.

The term co-occurrence network analysis facilitated a conclusive section, reinforcing the manuscript's advocacy for holistic understanding and management of complex systems to promote sustainable agricultural practices. The insights derived from the analyzed manuscripts constitute a body of scientific evidence paving the way for a new generation of understanding and managing microbial genetic resources within the framework of sustainable food production.



**Fig. 3.** Term co-occurrence network generated with VosViewer. The image displays a complex network of terms from the titles, abstracts, and keywords of the articles cited in this manuscript. The network is organized into six clusters of related terms, each differentiated by color. The size of the spheres varies according to the frequency of term co-occurrence, while the thickness of the lines indicates the strength of the relationships between terms.

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## Declaration of competing 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 manuscript.

## Data availability

Data will be made available on request.

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