the plant journal
SEB SOCIETY FOR EXPERIMENTAL BIOLOGY

The Plant Journal (2021) doi: 10.1111/tpj.15568

FOCUSED REVIEW

Sculpting the soil microbiota

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SUMMARY

Soil is a living ecosystem, the health of which depends on fine interactions among its abiotic and biotic components. These form a delicate equilibrium maintained through a multilayer network that absorbs certain perturbations and guarantees soil functioning. Deciphering the principles governing the interactions within soils is of critical importance for their management and conservation. Here, we focus on soil microbiota and discuss the complexity of interactions that impact the composition and function of soil microbiota and their interaction with plants. We discuss how physical aspects of soils influence microbiota composition and how microbiota–plant interactions support plant growth and responses to nutrient deficiencies. We predict that understanding the principles determining the configuration and functioning of soil microbiota will contribute to the design of microbiota-based strategies to preserve natural resources and develop more environmentally friendly agricultural practices.

Keywords: Assembly of soil microbiota, plant nutrition, factors that modify the soil microbiota, soil microbiota, Plant-Microbe interactions, soil health, microbe-microbe interactions.

INTRODUCTION

Soil health, defined as the ability to function as a central living ecosystem that preserves favourable interactions between plants, animals and microorganisms, is vital for maintaining life as we know it. Soil quality is directly impacted by agricultural practices and is increasingly perceived as directly related to human nutrition (Blum *et al*., 2019). Despite the importance of soils in supporting a wide range of agricultural and ecosystem services, such as food production, nutrient recycling, biodiversity and climate regulation, they have been degraded globally at a dramatic pace (Borrelli *et al*., 2020). This leads to a loss of biodiversity and organic matter and to greenhouse gas emission, with the concomitant negative consequences for food production and climate change (Borrelli *et al*., 2020). Although some sparse information on the effect of climate change or human activity on the physical–chemical properties of soil is available, little is known about the full repercussions on the ecological aspects of the soil (Guerra *et al*., 2021).

Soil health is influenced by several abiotic and biotic factors, such as its structure, temperature, pH, mineral composition, organic matter content, moisture and the organisms living within it, all of which interact with each other in intricate physicochemical and ecological networks (Figure 1). A thorough understanding of these interactions will help design holistic conservation strategies to preserve beneficial soil–crop interactions, minimize soil degradation, and rescue and preserve soil biodiversity.

In this review, we will focus on the soil microbiota, which represent an important component of soil biology. We discuss current knowledge describing how the structure and composition of free-living microbial communities are shaped by abiotic and biotic elements of the soil network, and to what extent these principles are retained during interactions between soil microbiota and plants across

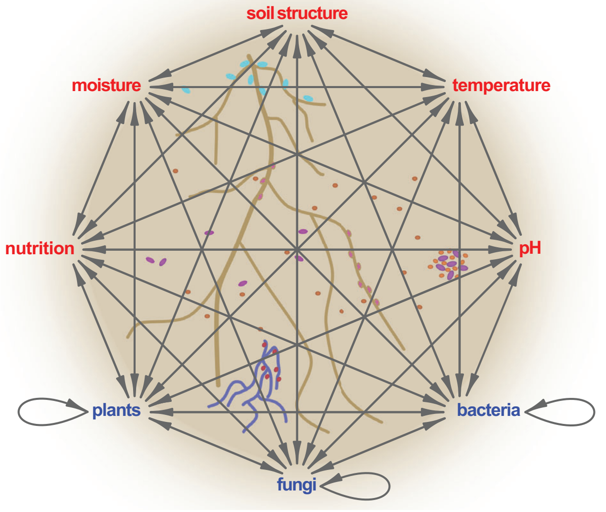

Figure 1. Schematic representation of the network of abiotic and biotic factors influencing the microbiota configuration at the root–soil interface. The soil and plant microbiota are composed of archaea, bacteria, fungi, nematodes, oomycetes, protists and viruses. In this review, and as shown in the figure, we focus on bacteria and fungi. Brown lines indicate roots and blue lines indicate fungal hyphae. The coloured dots represent bacteria. The arrows indicate interactions among abiotic (red) and biotic (blue) factors. Bacteria, fungi and plants can influence each other in a community (indicated by the looped arrows in the figure).

Box 1. Summary

- Soil health is defined as the ability of soil to function as a central living ecosystem that preserves the favourable interactions between plants, animals and microorganisms.
- Soil health is influenced by abiotic and biotic factors, such as the soil structure, moisture, mineral composition, organic matter content, pH, temperature and the organisms living in the soil, which interact with each other in complex physicochemical and ecological networks.
- A wide range of microorganisms inhabiting the soil engage in direct or indirect synergistic or antagonistic interactions that influence soil function and are of critical importance for soil health.
- Symbiotic and non-symbiotic members of the plant microbiota help plants to cope with nutrient stresses by enhancing nutrient bioavailability, influencing the root architecture and function or acting as an integral part of the plant nutritional stress responses.
- The validation of our current knowledge related to soil health in natural ecosystem contexts will help in the identification of new variables to be incorporated into models intended to predict the influence of natural or anthropogenic events on soil function.

Box 2. Open questions

- What are the most informative parameters for estimating soil health?
- What is the most appropriate strategy to integrate the different abiotic and biotic factors that modulate soil health in the design of soil recovery policies?
- How do the ecological principles driving niche colonization change at different spatial resolutions?
- How do metabolic interactions influence microbe–microbe–plant interactions in natural settings?
- How can we incorporate non-invasive high-throughput phenotyping technologies to integrate the functions of an intact microbiota with the optimization of plant performance?

the different plant compartments (phyllosphere, rhizosphere and endosphere) (Box 1). We also identify open questions that need to be answered before applying microbial-based actions to restore soil quality (Box 2).

It has been estimated that 1 g of soil harbours approximately 10^8–10^{10} microbial cells (Zhang *et al*., 2017). These complex communities consisting of hundreds to thousands of species of bacteria, fungi, archaea and viruses vary in diversity and composition across different soil types depending on soil properties. In turn, microbial activity can influence the chemical, physical and biological characteristics of the soil. Any loss of balance among factors that determine soil health, through agricultural intensification, for example, reduces the microbial diversity, compared with native soils (Roesch *et al*., 2007). This illustrates how important it is to understand the interconnectivity between elements within the multifactorial soil network as a first step towards maintaining soil quality, restoring degraded soils and designing microbial-based strategies to improve agricultural practices.

Soil abiotic factors influence its microbial composition

Although we still lack a full understanding of the ecological mechanisms in soil, it appears that 80–90% of soil processes are mediated by microorganisms (Benbi and Nieder, 2003). They are involved in ecological interactions that impact the structure of the soil, the recycling of nutrients, the decomposition of organic matter, the release of mineral nutrients or the complementation of plant functions. Although these beneficial functions of the soil microbiota depend on their synergistic relationship with other soil components, the nature and dynamics of these interactions remain largely unexplored. Here, we discuss the currently available evidence for how soil properties impact

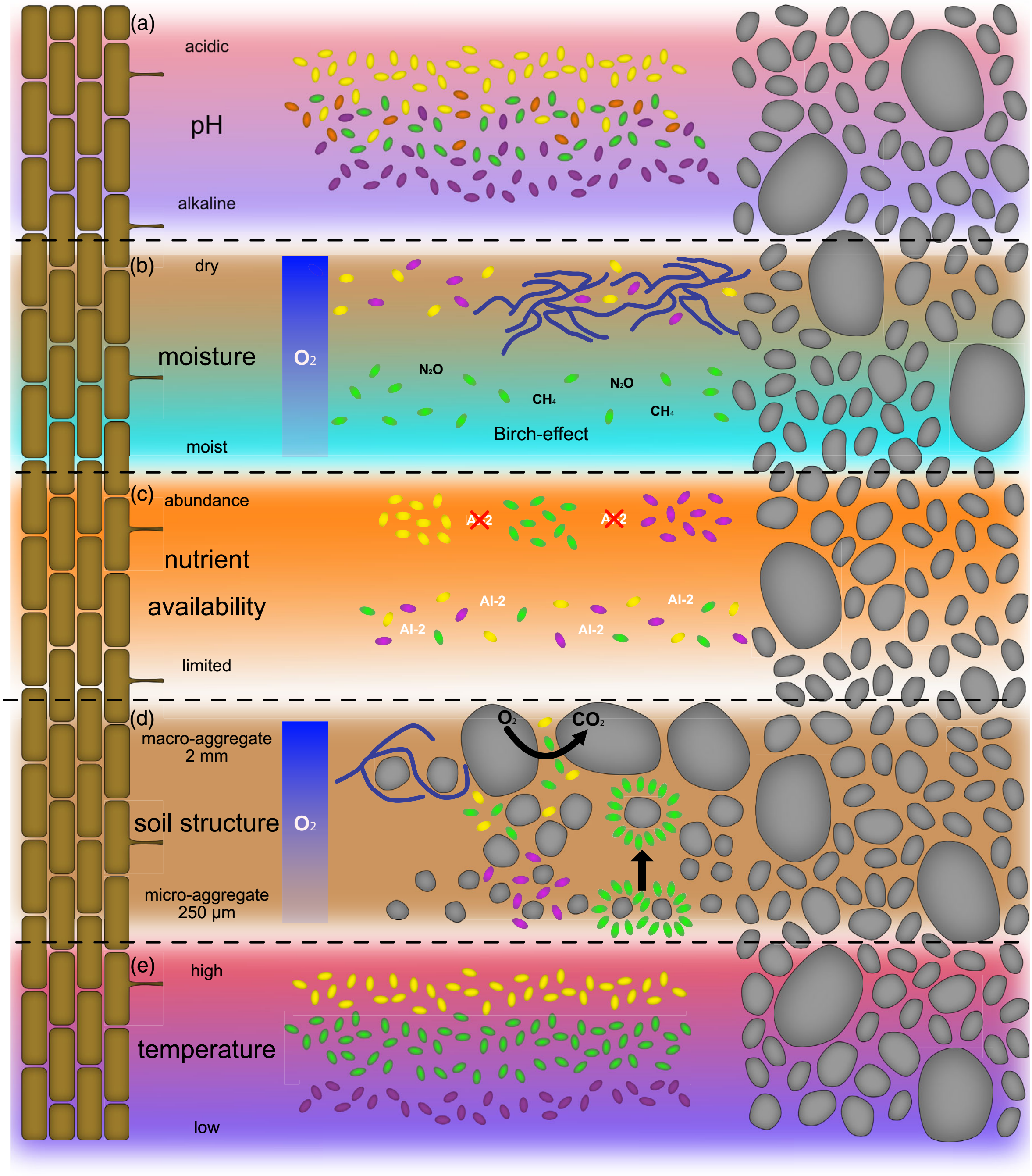

Figure 2. Abiotic factors shape soil microbial communities. (a) Soil microbial communities change according to pH. Commonly, microbial diversity is restricted at low (red) and high (blue) soil pH levels and is increased at moderate soil pH levels (Cao *et al*., 2016; Thompson *et al*., 2017; Wu *et al*., 2017). (b) Soil moisture affects the O_2 level in the soil, and thereby the activity of microbial metabolic pathways and microbial community composition. The brown colour indicates dry soil and cyan indicates moist soil. The gradient from blue to light blue symbolizes the decrease in O_2. Under dry conditions the soil harbours a broad variety of bacteria, and fungi are more successful under these conditions (de Vries *et al*., 2018). In moist conditions the composition of bacteria changes to species favoured by high humidity and that thrive at low levels of O_2. The change from dry to moist conditions can lead to the so-called Birch effect, a burst of respiration and nitrification (Birch, 1958). (c) Nutrient availability influences interactions among microbes. For example, under nutrient-limiting conditions bacteria can establish positive interactions that are coordinated via quorum sensing (through AutoInducer-2, AI-2, for instance), whereas they reduce cooperation under nutrient-rich conditions (Ranava *et al*., 2021). (d) Soil structure is determined by clusters of mineral particles (macro- and micro-aggregates). With the decrease in particle size, the availability of O_2 is also limited, favouring bacteria with anaerobic metabolism. In macro-aggregates, in which the O_2 concentration is higher as a result of the larger pore size, bacteria can adopt an aerobic lifestyle (respiration indicated by black curved arrow). Bacteria can also form filaments that can bridge and connect soil particles, thereby leading to larger soil aggregates (black vertical arrow). The abundance of fungi is positively correlated with macro-aggregate stability in the soil structure (Tiemann *et al*., 2015). (e) Soil temperature influences bacterial community composition, as different bacteria grow optimally at different soil temperatures. Red indicates high and blue indicates low temperatures. For all panels, the differently coloured bacteria indicate different bacterial genotypes (taxa, species, strains).

The Plant Journal published by Society for Experimental Biology and John Wiley & Sons Ltd.,
The Plant Journal, (2021), doi: 10.1111/tpj.15568

the diversity, structure and function of free-living microbial communities in the soil and how microbes in turn influence the soil ecosystem (Figure 2).

Soil structure. Soil structure results from structural clusters of mineral particles, encrusted organic matter, polysaccharides, plant roots and other biotic materials (Huang *et al*., 2015; Lucas *et al*., 2019; Volikov *et al*., 2016; Zhou *et al*. 2020a). These particles are classified in micro-aggregates (<250 μm) and macro-aggregates (0.25–2 mm) that contain a patchy distribution of mineral particles and nutrients (Asano and Wagai, 2014, 2015). Thus, soil aggregates form a vast range of physicochemical niches, which provide distinct microhabitats for diverse microbial communities (Fox *et al*., 2018).

During soil aggregate formation, microbes present in the surrounding bulk soil are enclosed within the structures of the aggregates. Once formed, the soil aggregates constitute an isolated environment that may be significantly different from the surrounding soil (Bocking and Blyth, 2018; Ebrahimi and Or, 2016; Mueller *et al*., 2012). For example, in macro-aggregate structures, microbes encounter pores with a reduced water content that allow higher oxygen diffusion rates and low organic carbon accumulation. The weakly diffusive fluxes of organic carbon resulting from the low number of water-filled pores can cause the spatial isolation of metabolic competitors within the macro-aggregates, impacting the soil microbial diversity (Dechesne *et al*., 2008). Conversely, the pores between micro-aggregates have increased water filling. Thus, oxygen diffusion rates are low and organic carbon availability is relatively high, providing an anoxic environment and enabling a more fermentative lifestyle (Neumann *et al*., 2013; Rabbi *et al*., 2016).

In response to changing environmental conditions, soil aggregates can be restructured, leading to the release of the enclosed microbial communities and enabling the colonization of new soil niches. These displaced microbial communities interact with the resident microbiota in the new soil, affect the microbial dynamics and contribute to a new cycle of aggregate formation (Cania *et al*., 2019). Prominent examples for environmental perturbations that modulate the spatial isolation of microorganisms in soil aggregates in nature are flooding or intense rainfall. With the resulting soil water saturation, microorganism-containing aggregates can be dispersed by water movement reaching new soil areas and resources (Dechesne *et al*., 2010; Ebrahimi and Or, 2015).

The impact of soil aggregates on microbial community composition have been explored in several studies (Bach *et al*., 2018; Chen *et al*., 2015; Davinic *et al*., 2012; Wu *et al*., 2019). For instance, Bach *et al*. (2018) compared soil fractions containing mainly macro- or micro-aggregates from the same agricultural soils. The micro-aggregate fraction supported a higher relative abundance of the phyla *Gemmatimonadetes*, *Actinobacteria* subdivision *Rubrobacteridae*, orders *Sphingomonadales* and *Sphingobacteriales*, the fungal orders *Onygenales* and *Chaetosphaeriales*, and the family *Trichosporonacae*, whereas the macro-aggregate fraction contained a relatively high abundance of filamentous fungi, such as arbuscular mycorrhiza fungi of the phylum *Glomeromycota* (Bach *et al*., 2018).

Thus, soil structure is an important abiotic factor that influences microbial communities through the formation of distinct niches, allowing colonization by adapted microbes. In turn, microbes constantly modulate and maintain these niches, impacting the microbial community. Therefore, the interaction of soil structure and microbes appears to be an important driving force in influencing soil microbial diversity and soil health.

Soil moisture. Depending on the geographic region, soil moisture can be more constant or highly variable as a result of weather fluctuation or changes between dry and rainy seasons. Variations in soil moisture often lead to shifts in the relative abundance of numerous bacterial and fungal taxa inhabiting the soil (Nguyen *et al*., 2018).

During drought events, the water content in soil pores is dramatically reduced, affecting the connectivity among soil areas. This lack of connectivity results in functionally disconnected resource islands across the soil structure, with low organic carbon decomposition and respiration rates (Canarini *et al*., 2017; Schimel, 2018). These changes are associated with compositional adjustments in microbial populations. As the soil dries, the bacterial abundance changes (Barnard *et al*., 2015). However, many bacteria can survive these changes by, for example, entering a dormancy state until more favourable conditions arise and growth is resumed (Jones and Lennon, 2010; Zhu *et al*., 2019).

In contrast, during rainfall, resource islands are reconnected as soil pores are filled with water. They become anaerobic, and provide conditions for methanogenesis and nitrification, and the release of CH_4 and N_2O. Furthermore, rewetting promotes a microbial activity pulse, leading to a burst of respiration and nitrification, known as the Birch effect (Birch, 1958). Many bacteria and fungi undergo cell lysis under these conditions, which probably contributes to the Birch effect through their decomposition (Blazewicz *et al*., 2014). As a consequence, the improved nutrient supply and the anoxic conditions promote the proliferation of anaerobic taxa, leading to a reduction in microbial diversity (Šťovíček *et al*., 2017).

Compared with bacteria, fungal communities are generally more successful in dealing with drought (de Vries *et al*., 2018), probably because of their ability to accumulate osmoregulators (Ramirez *et al*., 2004). Moreover, the expanded network that filamentous fungi manage to develop in the soil allows these organisms to cover a large soil volume, allowing them to reach residual humidity pockets in the soil (Amend *et al*., 2016; Manzoni *et al*., 2012). Although some fungi are efficient thriving under water deficiency, many others are highly vulnerable to high humidity. For example, ectomycorrhizal fungal communities have decreased species richness and abundance after heavy rainfall (Barnes *et al*., 2018). Interestingly, water availability impacts fungal taxa composition and biomass content (increased or decreased upon drought or irrigation, respectively) (Buscardo *et al*., 2021; del Mar Alguacil *et al*., 2012). Even with small fluctuations in soil water content, fungal communities show strong plasticity. Thus, they appear to be more sensitive indicators of soil water content than bacteria (Kaisermann *et al*., 2015).

The availability of water limits agriculture in many areas of the world. Understanding the mechanisms of how microbes cope with extremes in soil water availability may help to improve microbiota-based agricultural practices in overly dry and moist areas, thereby improving farming efficiency in these regions.

Nutrient availability in soil drives metabolic interactions. The composition of the soil microbiota is often modulated by the availability of nutrients in the soil (Fierer *et al*., 2012; Sheldrake *et al*., 2018). Fluctuations in nutrient composition and concentrations lead to complex metabolic interactions within microbial communities, resulting in a change in soil microbial composition (Leff *et al*., 2015; Rivett *et al*., 2016; Velez *et al*., 2018; Vetsigian *et al*., 2011). To avoid the complexity of studying metabolic interactions in the natural microbial communities that inhabit the soil matrix, most metabolic studies have been conducted *in silico* or under controlled conditions using a limited number of microbes and nutritional conditions.

Under *in vitro* conditions, nutrient availability changes the spatial structure and genetic diversity of microbial colonies (Mitri *et al*., 2016). In experimental mixed-genotype colonies of *Pseudomonas aeruginosa* grown with abundant nutrient resources, different bacterial lineages remained well mixed but also lost diversity as the colony expanded (Mitri *et al*., 2016). When colonies were grown under low-nutrient conditions they remained more structured into areas dominated by different genotypes, but under these conditions spatial expansion led to a loss of diversity (Mitri *et al*., 2016).

A recent study generalized observations made in the human gut and in oceans to soil and leaf natural microbiomes (Goldford *et al*., 2018). They found that the principles that govern large consumer–resource ecosystems include high taxonomic diversity, robust functioning at the community level, independently of species turnover, and a certain level of predictability and variability in how nutrients impact the community configuration at different taxonomic levels. In glucose-limited media, natural soil and plant communities showed similar ratios of the two dominant taxonomic families, *Enterobacteriaceae* and *Pseudomonadaceae*, across several replicate habitats, independently of the starting inoculum used to colonize each habitat. These differences can be explained as emergent metabolic self-organization between glucose (*Enterobacteriaceae*) and organic acid (*Pseudomonadaceae*) specialists (Estrela *et al*., 2020).

The metabolic coordination at the community level is also regulated by quorum sensing, a cell-to-cell communication system. The quorum-sensing signal molecule AutoInducer-2 (AI-2) is synthesized by a large cohort of bacterial species (Zhang *et al*., 2020) and allows bacteria to synchronize their physical and metabolic interactions, as in the case of the gram-positive *Clostridium acetobutylicum* and the sulphate-reducing Gram-negative *Desulfovibrio vulgaris* under sulphate starvation. In the presence of sulphate, *D. vulgaris* releases an AI-2-inhibiting compound that acts as an antagonist, shifting the interaction between the two species (Ranava *et al*., 2021).

In vitro and *in silico* experiments have helped to extract and define the principles governing microbial metabolic interactions under controlled conditions. Current efforts should focus on developing the necessary technology and methods to validate these principles in natural ecosystems, incorporating the complexity of the abiotic and biotic factors influencing soil health. This is of critical importance for the development of new strategies to preserve optimal soil function.

The pH of the soil. A global survey of soil bacterial communities has demonstrated that soil pH is a key factor shaping bacterial diversity across different terrestrial ecosystems (Delgado-Baquerizo *et al*., 2018). Whereas soils with medium pH harbour higher bacterial diversity, acidic and alkaline environments have a lower bacterial diversity (Cao *et al*., 2016; Thompson *et al*., 2017; Wu *et al*., 2017).

Soil pH induces changes in the soil microbiota by modifying the activity of specific microbial enzymes (Sinsabaugh *et al*., 2008) and by impacting nutrient availability (Lammel *et al*., 2018). By exploring the link between microbial ecophysiological traits and topsoil carbon content across a collection of geographically distinct soils and contrasting land uses, Malik *et al*. (2018) found that pH correlates with microbial mechanisms of carbon accumulation. The authors found that in soil with low pH, intensive management practices (arable fertilized croplands or intensive grasslands) that increase the pH above 6.2 provoke carbon loss via increased decomposition, which is linked to a boost in microbial growth. In near-neutral pH soils, carbon loss was associated with decreased microbial biomass and growth that was consecutively linked to trade-offs in stress response and the availability of resources. In other cases, the capacity of many microbes to change the environmental pH creates feedback loops that can affect microbial growth and survival, thereby influencing the microbiota composition (Ratzke and Gore, 2018).

Therefore, these examples reinforce the importance of integrating soil microbiome data in models designed to predict the best soil management strategies intended to reduce soil erosion in agricultural settings.

Soil temperature. Temperature is a prime factor determining the distribution of biodiversity on Earth (Peters *et al.*, 2016). How quickly and how much the temperature rises or falls in the soil depends on several biotic and abiotic factors, including soil type, environmental conditions, exposure to the sun, plant cover, water availability and organic matter content. Thus, the resistance of microbial communities to changing temperatures cannot be seen independently of these other factors (Cavicchioli *et al.*, 2019; Jansson and Hofmockel, 2020).

According to climate models, a rise in soil temperature is expected to lead to increased loss of soil organic carbon (as CO_2) through increased soil respiration (Bond-Lamberty *et al.*, 2018). In a 26-year soil-warming experiment in a mid-latitude hardwood forest, Melillo *et al.* (2017) found a four-phase pattern of soil organic matter decomposition and carbon loss to the atmosphere. This carbon-loss process associated with increasing temperature is complex and multifactorial. It is generally driven by changes in the carbon pools available to the microbes, the microbial biomass and its efficiency using carbon sources, and microbiota composition (Melillo *et al.*, 2017).

Using a collection of soils from alpine regions, a recent study found that exposing the soils to high temperature under controlled conditions promoted heat-adapted, stress-resistant and fast-growing bacteria such as *Burkholderia*, *Edaphobacter*, *Phenylobacterium*, *Pseudolabrys* and *Sphingomonas* (Donhauser *et al.*, 2020). This temperature effect on community structures was linked to the long-term climatic legacy of the soils.

Other studies in pre-alpine managed grasslands indicate that the climate change scenarios of rising temperature and atmospheric CO_2 have a reduced direct impact on the soil microbial community structure. More obvious effects of these factors on soil microbiome composition and function are predicted in the long term, likely through indirect effects on soil properties such as soil water content, nutrient availability or plant root identity (Deltedesco *et al.*, 2020).

Thus, temperature is an important factor structuring the soil microbiota in a wide range of terrestrial ecosystems, mainly influencing biogeochemical processes occurring in the soil matrix (Buzzard *et al.*, 2019). Despite recent findings in this area, a large proportion of the regulatory mechanisms that control the response of soil microbiota to temperature fluctuation remains unexplored. The consequences of the effects of temperature on soil microbiota, and on soil health in general, must be evaluated in real ecosystems through long-term field experiments. This will facilitate the scrutiny of our current reductionist knowledge in an ecosystem context and the incorporation of other variables such as microbiome traits or the carbon cycle into the models aimed at predicting the impact of global warming on the functioning of the soil.

Soil biotic factors shape its microbial populations

In a complex matrix like soil, the interaction networks established among its biotic components (e.g. bacteria, fungi, plants) absorb abiotic perturbations and adjust function in response to these changes. As a result, multi-kingdom communities with diverse nature and composition coexist in soils. Interactions between soil organisms can be cooperative, competitive or parasitic. Cooperative interactions can be further subdivided into mutualistic or commensalistic, depending on whether there is reciprocal or unidirectional benefit from the otherwise harmless relationship. However, these definitions are not always bluntly applicable (Schlechter *et al.*, 2019), as environmental conditions can dramatically change the type of interactions at play (Piccardi *et al.*, 2019).

Although important for the maintenance of the function of the soil as an ecosystem, the biotic factors that influence the function of the soil microbiota, the nature of their interactions with other biotic components, and with themselves, and the principles that govern these interactions remain elusive and poorly understood.

Bacteria–bacteria interactions. Bacteria communicate and compete through quorum-sensing signals, effectors, siderophores and secondary metabolites, which often act as antibiotics (Figure 3). The genetic potential to produce these signalling metabolites changes across the diverse phyla of soil bacteria, and also with soil depth and vegetation type within a geographic region (Sharrar *et al.*, 2020). The reconstruction of 1334 metagenome-assembled genomes from soils and saprolite samples across three sites in northern California, USA, identified diverse biosynthetic gene clusters (BGCs) for secondary metabolite production. In general, bacteria with a higher presence of BGCs were enriched in shallow soils and grassland soils, whereas the abundance patterns of the BGC type varied by taxonomy (Sharrar *et al.*, 2020). In this line, the reconstruction of hundreds of genomes from grassland soil metagenomes identified new bacteria encoding diverse polyketide and non-ribosomal peptide biosynthetic gene clusters (Crits-Christoph *et al.*, 2018). These BGCs are differentially expressed in response to environmental changes and a

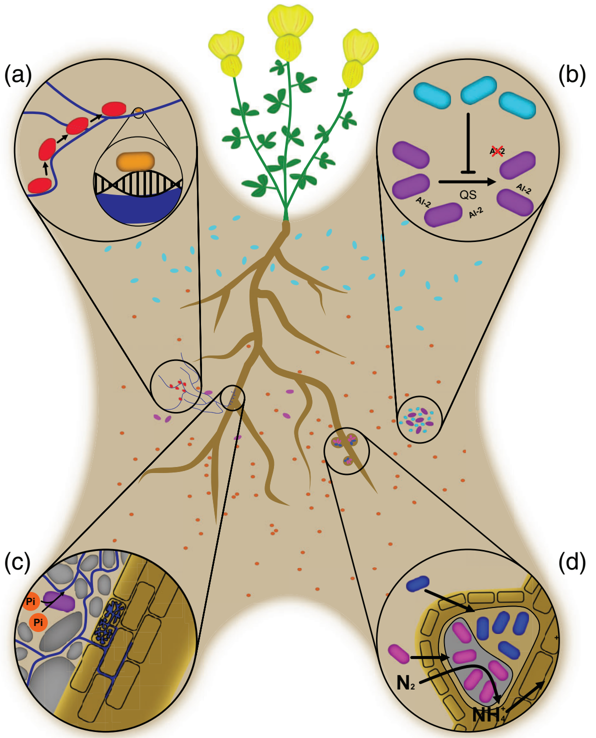

Figure 3. Examples of microbe–microbe interactions in the soil, rhizosphere and plant endosphere. (a) Bacteria–fungi interaction. Bacteria can use fungal hyphae to migrate and disperse in soil, thereby gaining access to new habitats and resources (red bacteria) (Nazir *et al*., 2014). Bacteria evolved different mechanisms to attach to the fungal hyphae; one striking example is the formation of a DNA biofilm skeleton of extracellular bacterial DNA (orange bacterium) (Guennoc *et al*., 2018). (b) Bacteria–bacteria interactions. Bacteria commonly communicate through quorum-sensing signals (e.g. AutoInducer-2, AI-2) to synchronize their metabolic activities. Some bacteria can quench this quorum-sensing signal (red cross) through enzymatic degradation of the quorum-sensing molecules, through sequestering them or through interfering with quorum-sensing receptors (Rosier *et al*., 2021). (c) Interactions between plants, fungi and bacteria. Arbuscular mycorrhiza fungi (AMF) form mutualistic symbioses with host plants. They grow into the root and form tree-shaped structures (arbuscules) inside root cortex cells, to which they provide mineral nutrients in exchange for organic carbon (Chiu and Paszkowski, 2019). Some bacteria cooperate with AMF: for example, to solubilize phosphate (Jiang *et al*., 2021). (d) Plant–bacteria–bacteria interaction. Rhizobia (pink) can colonize the inside of root nodules, and are hosted in specialized structures, the so-called symbiosomes (grey), inside the nodule cells. In these structures, they convert atmospheric N_2 into plant-available ammonia and receive space and organic carbon in return (Schwember *et al*., 2019). Some bacteria (blue) can hitch-hike along with rhizobia into the nodule where they live as endophytes, likely benefiting from plant-derived organic carbons without providing ammonia (Crosbie *et al*., 2021; Zgadzaj *et al*., 2015). Both (c) and (d) represent root endosymbioses only (arbuscular mycorrhiza and root nodule symbiosis). Currently, little is known about plant–fungal–bacterial and plant–bacterial–bacterial interactions for other types of relationships.

large percentage of them have antimicrobial activity, suggesting that a complex network of bacteria–bacteria interactions influence soil microbiome configuration in response to environmental cues.

Recently, microbial network analysis has been used to reconstruct bacteria–bacteria interaction networks in a complex microbiome background. This analysis permits to build and test hypotheses of central relevance for the understanding of microbial ecology. An example is the identification of a specific bacterium with a central position in the microbial networks, called a 'hub microbe' (Agler *et al*., 2016). These hub bacteria may represent keystone species that translate environmental changes to the rest of the microbial community via microbe–microbe interactions, sometimes impacting the growth and diversity of other microbes, even across kingdoms (Agler *et al*., 2016). These keystone species influence microbiome structure and functioning, and not only is their effect independent of their abundance in the community but their elimination can also cause a change in microbiota membership and performance (Banerjee *et al*., 2018).

Many of the bacteria colonizing the soil have the capacity to form organized supracellular structures known as biofilms. These structures are composed of bacterial cells associated with the soil surface and embedded in an extracellular polymer that promotes cell adhesion and survival (Cai *et al*., 2019). Soil biofilms are described as dynamic in space and time, promoting intensive intra- and inter-bacterial species interactions that result in increased rates of several processes, such as the degradation of soil organic matter (Balan *et al*., 2021), the exchange of signals and metabolites, and the improvement of nutrient and oxygen availability (Amaya-Gómez *et al*., 2015; Madsen *et al*., 2016).

The coordinated behaviour of the microbial community within the biofilm is a function of quorum-sensing signals, controlled by the presence of autoinducers (small signal molecules produced by several bacterial genera). This cell-to-cell communication system depends on cell density and growth stage and regulates gene expression in the microbial population. The role of quorum-sensing in biofilm formation has been highlighted in Balan *et al*. (2021). Their *in silico* docking studies of autoinducers and their receptors in different bacterial species uncovered the strength of autoinducer interactions, such as *N*-acyl homoserine lactones, with their receptors (LuxN, LuxP, LuxR), across different bacterial species. To interfere with beneficial bacteria–bacteria communication within the biofilm, other bacteria have the ability to quench the quorum-sensing activity through enzymatic degradation of the quorum-sensing molecules. For example, *Bacillus subtilis* can produce a quorum-quenching lactonase (YtnP) that cleaves the *N*-acyl homoserine lactone necessary to form the symbiotically active biofilm of *Sinorhizobium meliloti*, thus affecting the symbiotic relationship of *S. meliloti* with the host plant (Rosier *et al*., 2021). Other bacteria use a different strategy through the synthesis of quorum-sensing inhibitors such as *S*-adenosylcysteine, *S*-adenosylhomocysteine and sinefungin, which interfere with the binding of the quorum-sensing molecule to its receptors and thereby interferes with bacterial cell-to-cell communication (Rodríguez *et al.*, 2020).

Although these examples illustrate the importance and complexity of bacteria–bacteria interactions in the configuration of microbial communities, the breadth of the interactions, their mechanisms and their functions in soils are still not well understood. Much effort is still needed to discover the ecological principles that govern bacteria–bacteria interactions in soil before incorporating this knowledge into future soil restoration strategies.

Fungi–bacteria interactions. A wide range of fungi and bacteria engage in direct or indirect synergistic or antagonistic interactions that influence soil microbial community composition and functioning (Deveau *et al.*, 2018). Their interactions are of critical importance for supporting ecosystem function and plant health (Durán *et al.*, 2018).

The molecular mechanisms underlying fungi–bacteria interactions remain to be elucidated in the context of complex microbiomes. In more simple systems with individual bacterial isolates, actinomycetes (mostly *Streptomyces* species) were shown to suppress the plant pathogenic fungus *Rhizoctonia solani* through the production of volatile organic compounds (VOCs) (Cordovez *et al.*, 2015). In other cases, fungi colonizing the soil matrix synthetized and released compounds such as oxalic acid, which attracts soil bacteria of the genus *Collimonas* to hyphal tips, the mycelial zones most susceptible to bacterial colonization (Rudnick *et al.*, 2015).

The VOCs also mediate communication between bacteria and fungi (Deveau *et al.*, 2018). In response to VOCs from the fungal pathogen *Fusarium culmorum*, the bacterium *Serratia plymuthica* readjusts gene and protein expression associated with several important processes, such as motility, signal transduction, energy metabolism, cell envelope biogenesis and secondary metabolite production (Schmidt *et al.*, 2017). The elucidation of the molecular bases of VOC-sensing mechanisms will contribute to understanding the dynamics of multi-kingdom microbial communities in soil and to designing better microbial inocula for agricultural purposes.

Considering the large extension of fungal mycelia in soils (Ritz and Young, 2004), it is conceivable that some bacteria have evolved the ability to coexist in close association with fungi. For example *Burkholderia* spp. can colonize numerous fungal species, overcome their defence strategies, exploit the metabolites that they produce and use their hyphae to co-migrate and disperse in soil, thereby gaining access to new habitats and resources (Jung *et al.*, 2018; Nazir *et al.*, 2014; Stopnisek *et al.*, 2016). These bacteria can also assist other non-migrating bacterial species (e.g. *Dyella japonica*) to co-migrate along the fungal host hyphae (Nazir *et al.*, 2014).

The extra-radical mycelia of symbiotic ectomycorrhizal fungi (ECMF) and arbuscular mycorrhizal fungi (AMF) provide important niches for bacterial colonization because of their large surface area and release of nutritious carbon compounds (Emmett *et al.*, 2021; Guennoc *et al.*, 2018). Bacteria may use the extended hyphal network as support structures to develop biofilms. Interestingly, Guennoc *et al.* (2018) found that bacteria attach to the extraradical hyphae of the ECMF *Laccaria bicolor* through filaments of extracellular bacterial DNA, which forms the biofilm skeleton. Furthermore, although biofilm formation was observed on several basidiomycete ECMF, a number of symbiotic and saprotrophic ascomycetes did not allow biofilm formation, suggesting that these fungi might actively inhibit biofilms, for example through the secretion of DNAses (Guennoc *et al.*, 2018).

The AMF and specific rhizosphere bacteria cooperate to improve plant nutrient cycling, thus benefiting other members of the soil ecosystem (Figure 3). Recent studies describe key beneficial bacteria associated with AMF, such as: *Bacillus megaterium* or a *Bacillus* sp. associated with *Gigaspora margarita*; *Rhizobium tropici* associated with *Glomus intraradices*; *Pseudomonas fluorescens* associated with *Glomus mosseae*; and *Paenibacillus validus* associated with *Glomus intraradices* (Emmett *et al.*, 2021; Hildebrandt *et al.*, 2006; Long *et al.*, 2017; Pivato *et al.*, 2009; Tajini *et al.*, 2012). An analysis of the bacterial microbiome on the hypha of two different fungal species inoculated with soil from different geographical locations with different microbial compositions revealed that at the order level the composition of the hyphosphere microbiome was very similar across all soils, whereas differences among soils and AMF species were detected at lower taxonomic ranks (Emmett *et al.*, 2021). This suggests that AMF hyphae may provide a selective environment that enriches for certain bacterial taxa independently of the soil type and fungal species, but that there is fine-tuning on the level of individual bacterial species and strains. Similarly, Zhou *et al.* (2020b) found that different AMF co-colonizing single roots of the same *Gossypium hirsutum* (cotton) plant recruit their specific microbiota, and they hypothesized that this may be through different exudate cocktails released by the fungi.

The interaction between fungi and bacterial endosymbionts that inhabit fungal cells represents the most intimate bacteria–fungi association. Bacterial endosymbionts are present in a wide variety of fungi of broad taxonomic origins, such as ascomycetes, basidiomycetes, Mucoromycotina and Glomeromycotina (Bonfante and Desirò, 2017; Deveau *et al.*, 2018). The endobacteria, comprising Betaproteobacteria and Mollicutes, show a range of behaviours from mutualism to antagonism, and induce changes in host biology, including reproduction, metabolism and growth (Bonfante and Desirò, 2017). Although the new genome-sequencing technologies have assisted in the identification of new fungal endosymbionts in some cases, the mechanisms of host colonisation and of their effect on the host remain unknown.

Plant–microbe interactions

Plants provide organic matter that supports soil microbial activity and contributes to soil structure formation and stabilization (Adamczyk *et al.*, 2019; Philippot *et al.*, 2013). Organic compounds are exuded by roots into the rhizosphere, the soil portion surrounding the roots, or are derived from the decomposition of plant material (Mavrodi *et al.*, 2021; Moitinho *et al.*, 2018). Reciprocally, the population of soil microbes that live in close association with the root, in the rhizosphere, on the root surface or inside the root (endosphere), engage with the plant in mutualistic interactions that benefit plant growth and development. These interactions are crucial for plant competitiveness and survival in natural ecosystems.

Although plant–microbe interactions are essential for plant development, the mechanisms that operate during the recruitment of microbiota to, and into, the root remain poorly understood. Plant hosts belonging to the same taxonomic lineages share similar microbial populations. However, the microbial community structure across diverse land plants shows a marked difference according to host species (Fitzpatrick *et al.*, 2018; Kembel *et al.*, 2014; Naylor *et al.*, 2017). A comparison of the bacterial root microbiota of 30 angiosperm species growing under the same experimental conditions revealed significant variation in the root endosphere community composition across plant species (Fitzpatrick *et al.*, 2018), suggesting some level of microbial adaptation to different plant species. Recently, a clear signature of host preference among commensal bacteria of *Arabidopsis thaliana* and *Lotus japonicus* was found when the two plants were grown in a community context, suggesting that in their native host the bacteria have a competitive advantage (Wippel *et al.*, 2021). These differences in the microbiome of different plant species might be explained by the variation found, for example, in the root exudate composition, which could influence microbial colonization (Eisenhauer *et al.*, 2017). Supporting this idea, several defensive secondary metabolites, such as benzoxazinoids, secreted by the roots of cereals, affect the root microbiome composition in *Zea mays* (maize) plants (Hu *et al.*, 2018). Also, in *A. thaliana*, mutants impaired in the biosynthesis of root triterpenes, which are plant-specialized metabolites with antimicrobial activities and functions in plant defence and signalling, assembled an altered root microbiome. Thus, the composition of root exudates and, in particular, the specialized triterpene biosynthetic network might explain the microbiome differences found across distant plant species (Huang *et al.*, 2019).

The plant genotype is also a factor contributing to microbiome variation in plants. Under controlled conditions, but also in multiple field locations, the microbiome of rice and *Boechera stricta* (Brassicaceae) changed according to the genotype of the plant used (Edwards *et al.*, 2015; Wagner *et al.*, 2016). In these experiments, and in many others, the major differences found in the microbial communities were in the different plant compartments (phyllosphere, rhizosphere, root endosphere) and the bulk soil, demonstrating that the plant compartment is the main driver configurating the composition of the plant microbiota.

Plants have evolved an immune system to protect themselves from invaders. Circumvention of the plant immune system is thus essential for microbes to establish synergistic relationships with plants. Microbes living in association with the plant have evolved mechanisms to deal with plant defence, activated upon the recognition of microorganism-associated patterns (MAMPs), like flagellin or chitin (Teixeira *et al.*, 2021). The activation of the plant immune system includes, for example, the induction of salicylic acid synthesis and signalling, known to influence the assembly of root microbiota (Lebeis *et al.*, 2015).

Recently, it has been demonstrated that root commensal bacteria can modulate the plant immune system by suppressing a sector of plant defence, specifically MAMP-triggered immunity. Thus, the suppressor bacteria, which are generally good root colonizers, can potentiate the colonization ability of other commensal bacteria (Ma *et al.*, 2021; Teixeira *et al.*, 2021). The capacity to evade the immune system has been associated with flg22 epitope variants at the surface of the commensal bacteria that cannot be recognized by flg22 receptors (Colaianni *et al.*, 2021). Also, the microbial ability to modify the pH of the plant growth medium through the secretion of gluconic acid, and its derivative 2-keto gluconic acid, can suppress the flg22-mediated immune response (Yu *et al.*, 2019). The evolution of these mechanisms to evade the activation of plant defence highlights the importance of the host immune system in shaping the commensal community assembly.

Despite these recent discoveries, the molecular mechanisms required for soil microbiota to colonize the root remain elusive. Levy *et al.* (2017) identified bacterial gene clusters enriched in plant-associated microbes and Cole *et al.* (2017), using a randomly barcoded transposon mutagenesis sequencing in *Pseudomonas simiae*, established a genome-wide map of bacterial genes required to colonize the roots of *A. thaliana*. A more thorough exploration and validation of the plant-associated microbial genes identified in these works is needed to gain a clearer idea of the mechanisms that microbes use to establish a synergistic relationship with plants.

The increasing understanding of the functional principles driving plant–microbiota interactions is accelerating the development of microbe-based strategies in agricultural practices; however, more efforts are needed to incorporate plant microbiota into breeding programmes or soil recovery plans.

Functions of plant-associated microbiota in nutrient acquisition

Microbes living in association with plants have central roles in plant nutrition. Symbiotic rhizobia and arbuscular mycorrhizal fungi, which colonize the inside of plant cells (Figure 3), have long been studied for their beneficial effect on nitrogen and phosphorous nutrition, and increasingly the molecular mechanisms underlying these symbiotic associations have been elucidated over recent years (Chiu and Paszkowski, 2019; Schwember *et al*., 2019).

However, other non-symbiotic members of the plant microbiota can also support plants to cope with nutrient deficiencies, by enhancing nutrient bioavailability, influencing the root architecture or acting as an integral part of plant nutritional stress responses. For instance, the role of the root microbiota has been described in the case of nitrogen (Zhang *et al*., 2019), phosphate (Castrillo *et al*., 2017; Finkel *et al*., 2019; Herrera Paredes *et al*., 2018) and iron (Harbort *et al*., 2020; Stringlis *et al*., 2018).

A disparity in nitrogen-use efficiency between the rice subspecies *Oryza sativa* (rice) ssp. *indica* and *O. sativa* ssp. *japonica* has been associated with their distinct root microbiomes (Zhang *et al*., 2019). Interestingly, bacterial taxa enriched in the *indica* variety contained more bacteria bearing genes related to nitrogen metabolism, as compared with *japonica*. This suggested that the *indica* root microbiota may improve the nitrogen metabolism in *indica* rice. In the same study, genetic approaches revealed that *NRT1.1B*, a rice gene encoding a nitrate transporter and sensor, is important for the recruitment of *indica*-enriched bacteria (Zhang *et al*., 2019).

In other cases, the capacity of the plant to establish symbiotic relationships influences the assembly of the root microbiota. Legumes such as *L. japonicus* engage in symbioses with phosphate-delivering AMF as well as with nitrogen-fixing rhizobia. Microbiome profiling of *L. japonicus* mutants perturbed in the development of root nodule or AM symbiosis showed that intact symbioses are needed to establish taxonomically diverse and distinctive microbial communities in the root and the rhizosphere (Thiergart *et al*., 2019; Xue *et al*., 2019; Zgadzaj *et al*., 2016). Interestingly, Wang *et al*. (2021b) found that in *Medicago truncatula* grown in natural soils, AM symbiosis not only shapes the bacterial rhizosphere microbiome composition in general but specifically promotes the enrichment of rhizobia in the rhizosphere, and thereby the formation of nodules. Notably, root nodules themselves are not only colonized by one rhizobial strain but host a whole bacterial community. In *L. japonicus* the nodule community composition is strongly influenced by the soil inoculum and by the nutrient status of the plant (Crosbie *et al*., 2021). Several nodule-inhabiting bacteria did not belong to the Rhizobiales and the genus *Pseudomonas* was prevalent among the non-Rhizobiales in nodules from healthy plants (Crosbie *et al*., 2021). Rhizobial endophytes, which do not fix nitrogen, colonize nodules through infection threads by hitch-hiking along with the compatible symbiont (Zgadzaj *et al*., 2015) (Figure 3). In the future, it will be interesting to elucidate which colonization route is used by other non-rhizobial nodule endophytes.

Plant regulatory elements of responses to nutrient environment appear to regulate the root microbiota. For example, the genetic network controlling the phosphate stress response (PSR) in Arabidopsis is essential for the proper assembly of a typical microbiome (Castrillo *et al*., 2017). Furthermore, PSR impairment has a significant effect on the composition of the plant microbiome in soils with different phosphorus contents, and this overrides the indirect effect of the soil phosphorus concentrations on the soil microbial communities (Finkel *et al*., 2019). *Colletotrichum tofieldiae*, an endemic endophyte fungus in natural Arabidopsis populations, transfers phosphorus to plant shoots, promoting plant growth only under phosphorus-deficient conditions. Notably, the PSR system regulates plant colonization by the fungus and is necessary for the fungal beneficial effect (Hiruma *et al*., 2016). In addition, phosphate (Pi) reallocation and homeostasis in both *Glycine max* (soybean) and *M. truncatula* root nodules are mediated by the PHR1-PSR system (Lu *et al*., 2020; Nguyen *et al*., 2021). PHR1-PSR may activate the expression of genes involved in the regulation of nodulation, reducing the number of nodules in *Phaseolus vulgaris* (common bean) and soybean under low-phosphate conditions (Isidra-Arellano *et al*., 2020). This molecular response inhibits the formation of costly nodules, when phosphate is low, optimizing the use of phosphate by the plant. The PHR-PSR system is also required for arbuscular mycorrhiza formation in *L. japonicus*, *M. truncatula* and rice (Das *et al*., 2021; Shi *et al*., 2021; P., Wang *et al*. 2021a). Rice PHR2 was described to directly regulate genes of the common symbiosis signalling network and strigolactone biosynthesis genes (Das *et al*., 2021), thereby enabling the entry of mycorrhiza into the root under low-phosphate conditions, as well as facilitating arbuscule development and function (Shi *et al*., 2021). Together, these data indicate that the phosphate status of the host plant, regulated by the PSR system, is critical to maintain the plant–microbe interactions that contribute to nutrient uptake and plant growth.

In addition to nitrogen and phosphate, the link between plant iron nutrition and the soil microbiota has been defined. Besides its role in induced systemic resistance, the root-specific transcription factor MYB72 is crucial for plant adaptation to iron deficiency (Palmer *et al*., 2013; Stringlis *et al*., 2018; Zamioudis *et al*., 2014). MYB72 regulates genes responsible for the biosynthesis of coumarins, which are prominent compounds in root exudates with an important role in iron uptake and assimilation (Fourcroy *et al*., 2016; Harbort *et al*., 2020; Schmid *et al*., 2014;

Stringlis *et al*., 2018). Interestingly, the coumarin scopoletin is dominant in root exudates and has a strong impact on the root microbiome composition (Stringlis *et al*., 2018). The secretion of scopoletin by the root exerts a selective inhibition of the soil-borne fungal pathogens *Fusarium oxysporum* and *Verticillium dahliae*, and it is innocuous to the beneficial bacteria *Pseudomonas simiae* WCS417 and *Pseudomonas capeferrum* WCS358. This suggests that coumarins have an important role in the recruitment of beneficial microbes during nutritional stress. Supporting this idea, in another study the coumarin fraxetin was shown to be required in microbiota-mediated iron uptake, and the disruption of the coumarin biosynthesis pathway was found to affect the microbiota structure and to impair plant growth under iron-deficiency conditions (Harbort *et al*., 2020).

Plants have evolved specialized root diffusion barriers at the level of specific cell layers, termed the endodermis and the exodermis. These barriers are essential to control the free diffusion of water, solutes and immunoreactive ligands. Thus, root diffusion barriers are vital in controlling the mineral nutrient homeostasis in the plant. Recently, a mechanism that coordinates the endodermal root diffusion barrier and the microbiota inhabiting the root has been characterized. Salas-González *et al*. (2021) demonstrated that the regulatory network controlling endodermal function influences the plant microbiota assembly. They characterized a regulatory mechanism of endodermal differentiation influenced by the root microbiota that largely affects the mineral nutrient balance in the plant. This mechanism is associated with the inhibition of the phytohormone abscisic acid by the microbiota and it helps the plant to cope with changes in nutrient concentration in the soil.

In general, all these studies suggest that plants and their microbiota form a highly specialized network of vital importance for plant fitness. Understanding the exact mechanisms forming and maintaining this network would be a major step in science and will open new avenues in the use of microbial-mediated actions in the agricultural sector.

CONCLUSION

In the last decade soil microbiota research and plant microbiome studies, in particular, have greatly benefitted from both technological advances and a multidisciplinary approach. Next-generation sequencing, for example, has enabled the characterization of diverse microbiomes under changing conditions, facilitating the first discoveries of the factors impacting their assembly and function. The development of large-scale whole-genome sequencing technology has complemented the understanding of microbial functions in different ecosystems, the generation of large collections of genome-sequenced isolates and the design of more realistic synthetic microbial communities. Together with the approaches adopted by the field to complement ecology, such as computational biology, statistics, synthetic biology, multi-omics and microbiome engineering, this has allowed the discovery of some molecular mechanisms and ecological principles governing the assembly of the microbiota in different ecosystems.

Despite these advances, standardized approaches and protocols are needed to increase the reproducibility and comparability of the data generated. Also, centralized and sustainable repositories of the microbial culture collections are needed to guarantee the access to these resources under high standards of quality. The expanding functional understanding of the microbiome should be accompanied by the translation of knowledge generated under controlled conditions to more complex ecological and agroecological contexts. This will facilitate the integration of the different abiotic and biotic factors modulating microbiome assembly in natural settings. More research is needed to complete, for instance, the spatial resolution of plant and soil microbiomes from single cells and tissues to soil pores and aggregates, and the definition of the metabolic interactions driving niche colonization. Likewise, we need the assimilation of non-invasive high-throughput phenotyping technologies to integrate the functions of an intact microbiota with the optimization of crop performance. This will accelerate our understanding and use of a functional microbiota to develop a more environmentally friendly agriculture and to recover eroded soils in natural and anthropogenically modified ecosystems.

ACKNOWLEDGEMENTS

We thank Dr Omri Finkel (The Hebrew University of Jerusalem, Israel) for his critical reading of the article. This work was supported by the Biotechnology and Biological Sciences Research Council and the National Science Foundation (BBSRC-NSF), grant no. BB/V011294/1, to VC and GC, and by a Nottingham Future Food Beacon of Excellence Master in Research Fellowship to VC. MG is supported by funds from the Leverhulme Trust, grant no. RPG-2019-337, and NB is supported by a Nottingham Future Food Beacon of Excellence and Rothamsted Research Fellowship. MMO is supported by the Foundation for Science and Technology (FCT; UIDB/04551/2020). CG is supported by Deutsche Forschungsgemeinschaft (DFG) SPP2125 DECRyPT (GU1423/3-1).

AUTHOR CONTRIBUTIONS

VC, MG, NB, MMO, CG and GC designed the original outline for the review. GS made the figures and legends, with input from the rest of the authors. All authors contributed to the text and corrected the different versions of the article.

CONFLICT OF INTEREST

The authors declare that they have no conflicts of interest associated with this work.

DATA AVAILABILITY STATEMENT

All relevant data can be found within the article and its supporting materials.

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