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Exploring microbiomes for plant disease management

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Abstract

Microbiome science is revolutionizing many concepts of plant biology, ecology, and evolution. Understanding plant microbiomes is key to developing solutions that guarantee crop health without impacting the environment. In this perspective article, we highlight the importance of both the structure and functions of plant-associated microbial communities in protecting their host from pathogens. These new findings have a high potential to aid biocontrol programs and to replace traditional chemical products, guiding the transition towards a sustainable production.

Keywords: microbiota; metagenomics; plant pathogen; plant protection

1. Introduction

Plants associate with a wide diversity of microscopic organisms, including archaea, bacteria, and eukaryotes, collectively called the plant microbiota. Each microbial community occupies a reasonably well-defined habitat with specific physico-chemical properties and microbial structural elements, including for example relic DNA, mobile genetic elements, and viruses (Berg et al., 2020). Plant-associated microorganisms strongly influence the fitness, phenotype, evolution, and ecology of their host plants. For example, Lau and Lennon (2012) found that plants exposed to novel environmental conditions increased their fitness when interacting with a soil microbial community that evolved under that specific environment. Also, differences in phenotype have been observed in plants of *Populus trichocarpa* inoculated with different root bacterial endophytes (Henning et al., 2016). The influence of plant-associated microorganisms on host fitness and phenotype might have driven plant ecology and evolution (Hawkes et al., 2020). Different empirical studies have also found co-diversification of host phylogeny and the structure of their associated microbial communities in different plant clades, further suggesting that plant-associated microorganisms might play a role in the evolution of their host (Abdelfattah et al., 2021; Bouffaud et al., 2014). Plant microbiome research is not only transforming the way we understand plants, but places the term “plant health” into a new perspective, where the classic disease triangle (host, environment, pathogen) is expanded to include whole plant-associated microbial communities (Bernardo-Cravo et al., 2020; Brader et al., 2017; Trivedi et al., 2020).

The microbial communities inhabiting different plant organs (e.g., leaves, roots, flowers, seeds, or internal plant tissue) are commonly referred to as the plant microbiota (Berg et al., 2016), and contain a multitude of microorganisms with different ecological roles within a defined environment. Some of these microbes can improve plant nutrition and protection or can mitigate the negative effects of different stresses. We usually refer to these microorganisms as beneficial microbes. Other microorganisms may have detrimental effects on plant fitness or cause a damage to plants. We usually refer to these microorganisms as plant pathogens. The field of plant protection focuses on these two broad categories, studying how to counteract pathogens and how to promote beneficial microorganisms. Traditionally, plant-microbe relationships have been studied by isolating single microbes *in vitro* and testing whether their presence influences plants positively or negatively. However, this field has recently expanded due to the increased affordability of high-throughput sequencing technologies, which also elicited the interest in plant-associated microbial communities. We now know that the interaction between plants and communities of microorganisms is extremely complex, and the tag “pathogenic” or “beneficial” is often context dependent.

Indeed, what we usually identify as a beneficial microorganism can have detrimental effects on some host plants (Pineda et al., 2013; Purin and Rillig, 2008), whereas those that we usually tag as plant pathogens may function as growth promoters under certain conditions (Li et al., 2021). Furthermore, environmental conditions can promote the shift of lifestyle of some microorganisms from being endophytes to becoming pathogens. For example, Álvarez-Loayza et al. (2011) found that the endophyte *Diplodia mutila* becomes a pathogen of *Iriartea deltoidei* seedlings when they are grown in presence of light, suggesting that the fungus produces hydrogen peroxide as response to light and, thus, causing the disease on plants. Also, the pathogen *Verticillium dahliae*, known to cause disease on several plant species, it has also been isolated from several asymptomatic plants, suggesting that under certain conditions it may act as an endophyte (Malcolm et al., 2013). Several studies also confirmed that even the microbiomes associated with “healthy” plants actually contain plant pathogens (Berg, 2009; Manzotti et al., 2020; Wassermann et al., 2019). Furthermore, there is a larger portion of microorganisms that do not fall within any clear classification, and their ecological role is still unknown. Despite the numerous studies defining a “healthy microbiota”, there is no clear concept from the perspective of plant protection.

Another layer of complexity within microbiomes is represented by the non-linearity in the link between structure and function. Indeed, even if two microbial communities are taxonomically similar they might code for different functions, and microbiomes with different structures might code for a similar set of functions (Doolittle and Booth, 2017). Structure and function are key aspects of all biological systems, including microbiomes. The structure of plant-associated microbial communities is influenced by several factors, including plant species (Dastogeer et al., 2020; Trivedi et al., 2020; Turner et al., 2013; Wassermann et al., 2019), soil quality and management (Benitez et al., 2021; Grady et al., 2019; Malacrino et al., 2021a; Zarraonaindia et al., 2015), atmosphere (Abdelfattah et al., 2019), herbivory (Hoysted et al., 2018; Kong et al., 2016; Malacrino et al., 2021b), geographic location (Berg et al., 2016; Fitzpatrick et al., 2020), rootstock/scion combinations (Liu et al., 2018), and many others. The magnitude of change driven by each of these factors is not always clear, and few studies tried to quantify the contribution of multiple factors on structuring the plant microbiome. For example, when comparing the relative magnitude of different factors (herbivory, plant species, soil microbial diversity), Malacrino et al. (2021a) found that soil diversity was the major driver of the plant microbiome structure in potato plants, while herbivory and plant species played a minor role. Within each plant, microbial communities mainly cluster by compartment (e.g., roots, leaves, fruits), and even spatially differentiate within the same compartment (e.g., calyx vs. and stem end of fruits, endosphere vs. ectosphere) (Abdelfattah et al., 2016; Dastogeer et al., 2020; Trivedi et al., 2020). Studying the taxonomical composition of a plant microbiome can provide important information about the role of specific plant or environmental factors in influencing the microbial community. This information can also be used as a proxy to infer about the potential role of these microorganisms within the community and their relationship with the plant. For example, Benitez et al (2021) used structural equation models to predict maize and soybean responses to taxonomic changes in bacterial and fungal communities due to crop rotation. The study of the functions coded by plant microbiomes can also provide an extra layer of information to identify combinations of microbial taxa and genes that have potential for plant protection.

To date, most research work has focused on the composition of plant microbiomes. Plant microbial diversity has been promoted as a plant health indicator (Berg et al., 2017) but functional diversity seems to be even more important (Lemanceau et al., 2017). Here, we

argue that an analysis of both the composition and the functions of plant-associated microbial communities are essential for understanding the impact of microbiomes on plant health. To this aim, we review the recent insights on the structure and the function of the plant microbiome, the plant pathobiome, and the environmental microbiome (Fig. 1), analyzing their impact on plant health, and how this can be exploited to drive further advances in plant protection and biological control.

2. The plant microbiome

A wide variety of microbes, spanning several clades of the tree of life, may be present in a plant microbiome. These microbes can assemble in many ways and are responsible for a variety of functions with both positive and negative effects on plants. Thus, the study of the composition of plant microbiomes represents an important source of information about which taxa can be valuable for improving plant health. This approach sets the base for our current understanding of plant microbiomes (Abdelfattah et al., 2018; Trivedi et al., 2020), and has motivated researchers to look for new sources of potential microbes and microbial consortia to improve plant health. In this context, the microbiomes associated with wild relatives of crop plants are attracting increasing interest (Pérez-Jaramillo et al., 2018).

Plant evolution can be driven by interactions with symbiotic and pathogenic microbes and *vice versa* (Delaux and Schornack, 2021). In addition to the coevolution of natural plant-microbe interactions, the wild relatives of common crop plants were domesticated. During this process, plants have been selected to favor traits that ensure productivity and edibility, and more intensive plant breeding resulted in a reduction of crop genetic diversity. Indirectly, there are indications that the plant microbiome was influenced as well. The diversity of the plant microbiota has been shown to be reduced in several domesticated plant species when compared with their wild relatives (Escudero-Martinez and Bulgarelli, 2019; Martínez-Romero et al., 2020; Pérez-Jaramillo et al., 2018), although this might not be true for all plant clades (Chaluvadi and Bennetzen, 2018; Leff et al., 2017). We can speculate that breeding relaxes narrow-range defense mechanisms (e.g., secondary metabolites toxic to mammals) and strengthens pathways that broadly influence host-microbiome interactions (e.g., those targeted by breeders to enhance plant defenses), which can limit the interactions with a wide range of microorganisms, and lead to a decrease in microbiome diversity. This might also explain the differential patterns observed in different plant lineages, as not all crops are subjected to the same breeding strategies. Another hypothesis is that the reduction of microbial diversity is not the result of the domestication or genetic improvement processes, but the consequence of the spread of intensive agricultural practices (e.g., simplified ecosystem, use of chemical products) that indirectly influence the plant microbiome and select for a less diverse microbial community. This reduction in plant microbial diversity might cause the loss of key beneficial microbial taxa, resulting in changes in the network of interactions within the microbiome and in a higher susceptibility of diseases and stresses. Berg and Cernava (2022) proposed that different human activities are linked to a shift in the diversity and evenness of plant microbiota, a decrease in host specificity, and an increase in *r*-strategic microbes, pathogens, and hypermutators.

In general, plant microbiomes can be managed either directly by applying (i) microbiota transplants, (ii) microbes with beneficial properties, (iii) microbiota-active metabolites, or (iv) indirectly by changing environmental conditions in a way that microbiomes also shift their structure and function from dysbiosis into a healthy state (Berg

et al., 2020). Wild crop relatives have high potential as a source for microbiota transplants for crop species and beneficial microbes (Pérez-Jaramillo et al., 2018). Several studies report a co-diversification of plant phylogeny and the diversity/structure of their microbiota (Abdelfattah et al., 2021; Abdullaeva et al., 2021; Bouffaud et al., 2014; Kim et al., 2020; Mazel et al., 2018; Mendes et al., 2018; Schlaeppi et al., 2014; Vincent et al., 2016). Thus, we speculate that the microbiota of wild relatives might still include microbial species that have been lost during the process of domestication, and that they might be restored in modern varieties to improve plant growth and health. This has been tested empirically by Chock et al. (2021), who inoculated plants of *Eugenia koolauensis* with microorganisms obtained from its wild relatives, and found a decrease in foliar disease caused by *Austropuccinia psidii*. Thus, the microbial diversity in wild relatives of crop species might open new paths to crop protection. We might explore the microbiomes of wild relatives and ancient heirloom breeds of crop cultivars as source of microorganisms to improve plant health and growth, in the same way we have been using wild plants to introgress genes into cultivated plants to compensate their limited genetic diversity.

Beneficial plant-associated microorganisms are involved in the germination, growth, performance, and health of their hosts. Understanding the modes of action of beneficial microbes is important for the design of promising microbial inoculants for sustainable agriculture. Plant-associated microorganisms are able to interact with their hosts and often protect the host plant against potential pathogens (Berg, 2009). Microbiome research has drastically changed our understanding of microbiome-inoculant interactions. Plant microbiome modulations are a crucial mode of action of beneficials. The microbiome can be modulated towards (i) transient microbiome shifts, (ii) stabilization or increase of microbial diversity, (iii) stabilization or increase of plant microbiome evenness, (iv) restoration of a dysbiosis/compensation or reduction of a pathogen-induced shift, (v) targeted shifts toward plant beneficial members of the indigenous microbiota, and (vi) suppression of potential pathogens (Berg et al., 2021).

Most current research describes changes in the taxonomical diversity of plant microbiome as a consequence of domestication. However, a change in microbial diversity does not mean that the functionality of the community is compromised. As suggested by Doolittle et al. (2017), the influence of selection on the taxonomic composition of a microbiome is trivial if the function is preserved. In this context, the redundancy in gene functions (Allison and Martiny, 2008) can contribute to the mechanisms of pathogen suppression exhibited by the plant microbiome. A high diversity of microbial species coding for the same function or acquiring a function by horizontal gene transfer can contribute to pathogen suppression. Thus, further research is necessary to understand the functioning of plant microbiomes.

3. The plant pathobiome

Plant diseases are a major threat to agricultural and natural ecosystems. Research has demonstrated that most of plant-associated microbial communities contain plant pathogens (Berg, 2009; Manzotti et al., 2020; Wassermann et al., 2019), suggesting that the distinction between a healthy microbiome and an unhealthy one is not solely based on the presence or absence of pathogens. This limits the “one microbe—one disease” concept. Agents of plant disease can, indeed, generate a disturbance in the interactions between the microbiome and its host, or within the microbiome itself. This disturbance can generate a microbiome that

deteriorates the host's health status, termed a "pathobiome" (Mannaa and Seo, 2021; Vayssier-Taussat et al., 2014).

In terms of community structure, healthy and diseased plants often associate with distinct microbial communities, as shown in several systems (Abdelfattah et al., 2015; Bez et al., 2021; Cui et al., 2021; Diskin et al., 2017; Ewing et al., 2021; Ginnan et al., 2020; Kusstatscher et al., 2019a; Solís-García et al., 2021; Wen et al., 2020; Yurgel et al., 2018). In general, diseased plants show a higher abundance of the pathogen and an altered network of interactions within the plant microbiome. High pathogen pressure can also enrich for plant beneficial microorganisms, particularly antagonists of pathogens (Garbeva et al., 2004; Liu et al., 2021; Weller et al., 2002). This represents a chance to isolate biocontrol microorganisms that co-occur with the pathogen. This approach was originally used to recover microorganisms with biocontrol potential against postharvest rots in apple (Wilson et al., 1993). More recently, Kusstatscher et al. (2019b) employed this approach to obtain beneficial bacteria from sugar beets that were selected from fields with high pathogen pressure from *Fusarium oxysporum*, revealing that ~50% of isolated bacterial strains were antagonistic to the plant pathogen. Similarly, Zachow et al. (2011) found that ~28% of microbial strains isolated in proximity to sclerotia (dormant resting bodies) of the fungal plant pathogen *Rhizoctonia solani* had an antagonistic action against this pathogen. Sclerotia are indeed a promising source from which to isolate pathogen-antagonistic bacteria (Mehmood et al., 2020; Mülner et al., 2019). The identification of key features in the microbial community structure of healthy and diseased plants holds potential to uncover beneficial microorganisms useful to counteract the negative effects of plant pathogens.

Healthy and diseased plants also show differences in terms of microbial gene content and expression. For example, Broberg et al. (2018) found a group of 499 microbial genes upregulated in oak trees symptomatic to acute oak decline, including plant cell wall-degrading enzymes, toxins, and virulence-associated genes. Similar results were obtained by Shi et al. (2019) comparing the metagenome of potato plants grown under high or low pressure by potato common scab, and revealing that a set of microbial genes including ABC transporters, bacterial secretion systems, and quorum sensing genes, which were enriched when the pathogen was highly abundant. These results are fundamental for beginning to engineer plant microbiomes to promote plant health and growth (Ke et al., 2021). While advanced genome editing techniques like CRISPR tools are still difficult to apply in the field (Barrangou and Notebaart, 2019), the experimental evolution of plant microbiomes can also help in finding novel approaches to counteract plant diseases. For example, Li et al. (2021) evolved a plant pathogenic *Pseudomonas* into a plant mutualist within a few generations. Morella et al. (2020) used an experimental evolution approach to generate a plant microbiome that was resistant to invasion by other microbial strains. Thus, future research can combine the study of the functions encoded within the pathobiome to direct evolution experiments and generate microbial communities that can counteract plant pathogens, or to generate complex microbial consortia that can be inoculated to our crops and provide protection against agents of plant diseases.

4. The environmental microbiome

The environment in which plants grow is a continuous source of microbial inoculum (Berg and Smalla, 2009; Brown et al., 2020; Pieterse et al., 2016). Plants can drive the recruitment of beneficial microorganisms from soil through their metabolism, immune system, root

architecture, and root exudate composition (Abedini et al., 2021; Chagas et al., 2018; Jacoby et al., 2020; Park and Ryu, 2021). Thus, there is much potential to exploit the environmental microbiome to benefit plant protection.

One key example of protection against plant pathogens provided by the environmental microbiome is disease-suppressive soils. Disease suppressiveness is a unique phenomenon in soil microbial ecology, providing an immune response to the invasion by a pathogen (Raaijmakers and Mazzola, 2016). Disease suppressive soils have been shown to prevent establishment of soil-borne pathogens and/or reduce disease incidence, regardless of host susceptibility and environmental conditions conducive to disease (Bakker et al., 2018; Gómez Expósito et al., 2017; Schlatter et al., 2017; Weller et al., 2002).

Disease suppressive soils have shown diverse dynamics in relation to the structure of their microbial communities. For example, sugar beet plants grown on soils suppressive to *R. solani* show a higher abundance of members of Pseudomonadaceae, Burkholderiaceae, Xanthomonadales and Lactobacillaceae in the rhizosphere (Mendes et al., 2011). In a similar study, the rhizosphere of sugar beet plants grown on soil suppressive to *R. solani* was enriched in members of Oxalobacteraceae, Burkholderiaceae, Sphingobacteriaceae and Sphingomonadaceae when the pathogen was introduced into the system (Chapelle et al., 2016). Wheat plants grown on soils suppressive to *R. solani* showed a higher abundance of *Stenotrophomonas* spp. and *Buttiauxella* spp. in their rhizosphere, compared to plants grown in non-suppressive soil (Hayden et al., 2018). Wei et al. (2019) found an higher abundance of *Massilia*, *Dyadobacter*, *Terrabacter*, *Arachidicoccus*, and *Dyella* in the rhizosphere of tomato plants grow on soil suppressive to *Ralstonia solanacearum*. Collectively, these results suggest that the microbial communities involved in disease suppression might be unique for specific combinations of soil microbiota, pathogens, and host plants, although their function might still be conserved across different scenarios.

The disease reducing capacity of suppressive soils can be classified into two categories: general and specific suppression. All soils are virtually capable of general suppression of soil-borne pathogens if the resident microbial community outcompetes the invading pathogen. However, some soils are able to contrast the spread of specific plant pathogens (Schlatter et al., 2017). Specific disease suppression may be a product of the interaction between specific microbes (or microbial consortia) and specific pathogens, and may be caused by the release of metabolites during the interaction between the soil microbiota and the pathogen (Cha et al., 2016; Mendes et al., 2011). These metabolites, in turn, enrich for the disease-suppressive microorganisms at the expense of the pathogen (Chapelle et al., 2016). The biosynthesis of such secondary metabolites is quite complex, and it is usually under the control of clusters of genes shown to be enriched in disease-suppressive soils. For example, non-ribosomal peptide synthetases (NRPSs) gene clusters have been found enriched in soils suppressive to *Fusarium* (Tracanna et al., 2021; Zhao et al., 2018). Soils suppressive to *R. solani* were found enriched in NRPSs, polyketide synthases (PKSs) and chitinase gene clusters (Carrión et al., 2019; Mendes et al., 2011). A metatranscriptomics study found a higher expression of PKSs, terpenoid biosynthesis genes and cold shock proteins in soils suppressive to *R. solani* (Hayden et al., 2018). NRPSs and PKSs were also found enriched in soils suppressive to *R. solanacearum* (Wei et al., 2019). A wider study found PKSs gene clusters to be enriched in a wide variety of disease suppressive soils across a wide geographical range (van Elsas et al., 2008). In all these examples, NRPSs and PKSs gene clusters appear to play a major role in disease suppressive soils across a variety of systems. These gene clusters control the production of multiple secondary metabolites which are known to have

antimicrobial activity (Mousa and Raizada, 2015). Chitinase genes are also common in disease-suppressive soils (Carrión et al., 2019; Mendes et al., 2011) likely leading to chitin degradation and fungal cell wall degradation. Thus, while the taxonomical structure of disease suppressive soils seems to be quite variable, there is instead consensus on the genes that are enriched in these soils, and which represent a good target for manipulating the environmental microbiome to favor plant health.

5. Conclusions and future goals

Agriculture is still making extensive use of chemical inputs to increase crop yields and protect plants from pests and diseases. However, the shift towards a more sustainable agriculture is still slow (Siebrecht, 2020). Microbiome data are increasing our ability to understand and manipulate the interaction between plants and their associated microorganisms. Microbiome management and microbiome-based products represent one of the most promising alternatives to chemical products in agriculture. The benefits of introducing specific microbial strains into agricultural systems are widely known, and in several cases we now commonly use microorganisms to increase plant fitness and improve protection against pathogens and pests (Bashan et al., 2014; Harman, 2011). While inoculation of single strains is common, mainly because it is the easiest to implement into a commercial product, there is now an increased attention for the use of multi-strain products. The inoculation of complex microbial communities also known as synthetic communities (or SynComms), have the potential to provide higher benefits, in terms of plant growth and health, compared to the use of single microbial strains (de Souza et al., 2020; Marín et al., 2021). While we still know little about the best way to assemble these SynComms, we suggest that combining knowledge of both microbial species and their genome content will produce the most effective SynComms.

The last two decades of plant microbiome research set the baseline for the awareness of the importance of plant-associated microbial communities and their impact on plant growth and health. Here we promote extending beyond the taxonomical structure of these communities towards a deeper mechanistic understanding of their function in terms of gene content and expression. We expect that integrating both structure and function will allow us to enrich specific functions. Wild relatives, pathobiomes, environmental microbiomes, synthetic communities, experimental evolution, and microbial transplantations are all useful tools for promoting plant protection and can be integrated into a wider conceptual framework for microbiome management. Thus, the future challenge is to rethink agricultural practices to consider the power of plant and soil microbiomes. This might be one of the major ways to improve current biocontrol programs and, thus, reduce our dependence upon agrochemicals.

Figure captions

Figure 1. Structure and the function of the plant microbiome, the plant pathobiome, and the environmental microbiome can be studied to design synthetic communities (SynComms), which can be exploited in crop protection. Created with BioRender.com

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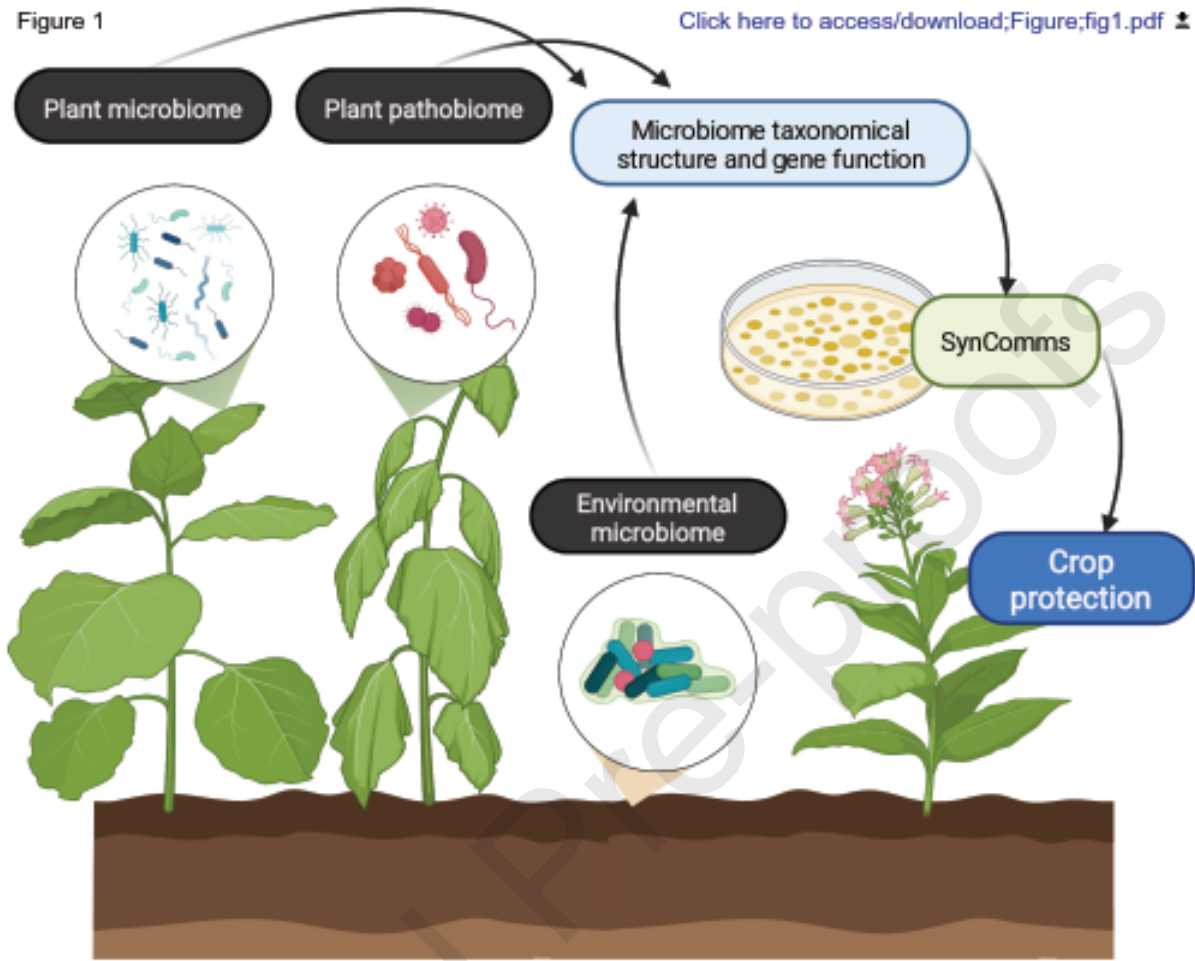
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Figure 1

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Highlights

- Plant microbiomes are essential components of plant health
- Structure and functions are important features of plant microbiomes
- Microbiome management can represent the next frontier of biological control

Author contribution

AM conceptualized and wrote the first draft of this perspective article. All the other authors contributed with ideas and to review/edit the first draft.