



# Missing symbionts – emerging pathogens? Microbiome management for sustainable agriculture

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## Abstract

Plant diversification and co-evolution shaped the plant microbiome and vice versa. This resulted in a specific composition of the plant microbiome and a strong connection with the host in terms of functional interplay. Symbionts are part of the microbiota, and important for the plant's germination and growth, nutrition, as well as stress protection. However, human activities in the Anthropocene are linked to a significant shift of diversity, evenness and specificity of the plant microbiota. In addition, and very importantly, many plant symbionts are missing or no longer functional. It will require targeted microbiome management to support and reintroduce them. In future agriculture, we should aim at replacing harmful chemicals in the field, as well as post-harvest, by using precision microbiome engineering. This is because the plant microbiome is connected across systems and crucial for human and planetary health. This commentary aims to inspire holistic studies for the development of solutions for sustainable agriculture in framework of the One Health and the Planetary Health concepts.

**Keywords** Plant holobiont · Symbiosis · Anthropocene · Plant-beneficial microorganisms · Plant health · One health · Planetary health

## 1 Plants are holobionts and consist of the plant and its co-evolved microbiota

All plants are holobionts; they form a structural and functional unit with microorganisms (Vandenkoornhuys et al. 2015). Plant-associated microorganisms comprise bacteria, archaea, fungi, algae and protists, the so-called plant microbiota (Berg et al. 2020). On surfaces and within plant tissues they are the plant microbiome, which can be differentiated into the phyllosphere (above ground), rhizosphere (below

ground) and endosphere (inside tissues) microbiome. Plant microbiomes are diversified in each of these habitats and adapt to the specific conditions that require functional engagement (Cordovez et al. 2019). Moreover, they are specific for each plant species/genotype and each stage of development (Berg and Smalla 2009). This specificity is a result of plant-microbe coevolution (Delaux and Schornack 2021). Since plants colonized land, they have evolved a range of symbiotic associations with microorganisms that include protection mechanisms (Delaux and Schornack 2021). These symbiotic associations were likely required by plants to grow under harsh, nutrient-poor, and difficult conditions and involved symbiotic plant-microbe interactions resulting in survival and cooperation (Fig. 1).

Plant symbionts are part of the plant holobiont and live in relationships with plants. They have tremendous effects on plant growth, confer resistance to abiotic stresses and pathogens, aid in the accumulation of metabolites, and have crucial relationships with other plant-associated microorganisms (Yang et al. 2013). Although a long list of phylogenetically diverse plant symbionts has been reported, they mainly involve bacteria and fungi (Yang et al. 2013). The majority of plant-associated bacteria can be considered as

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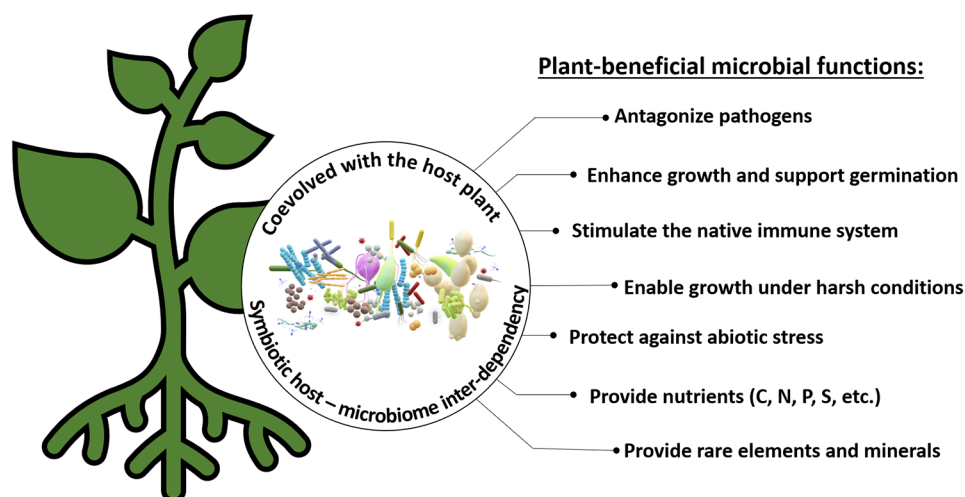
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**Fig. 1** Plants have coevolved with their microbiome, resulting in a symbiotic inter-dependency, with the microbiome providing essential functions for plant growth and survival under natural conditions



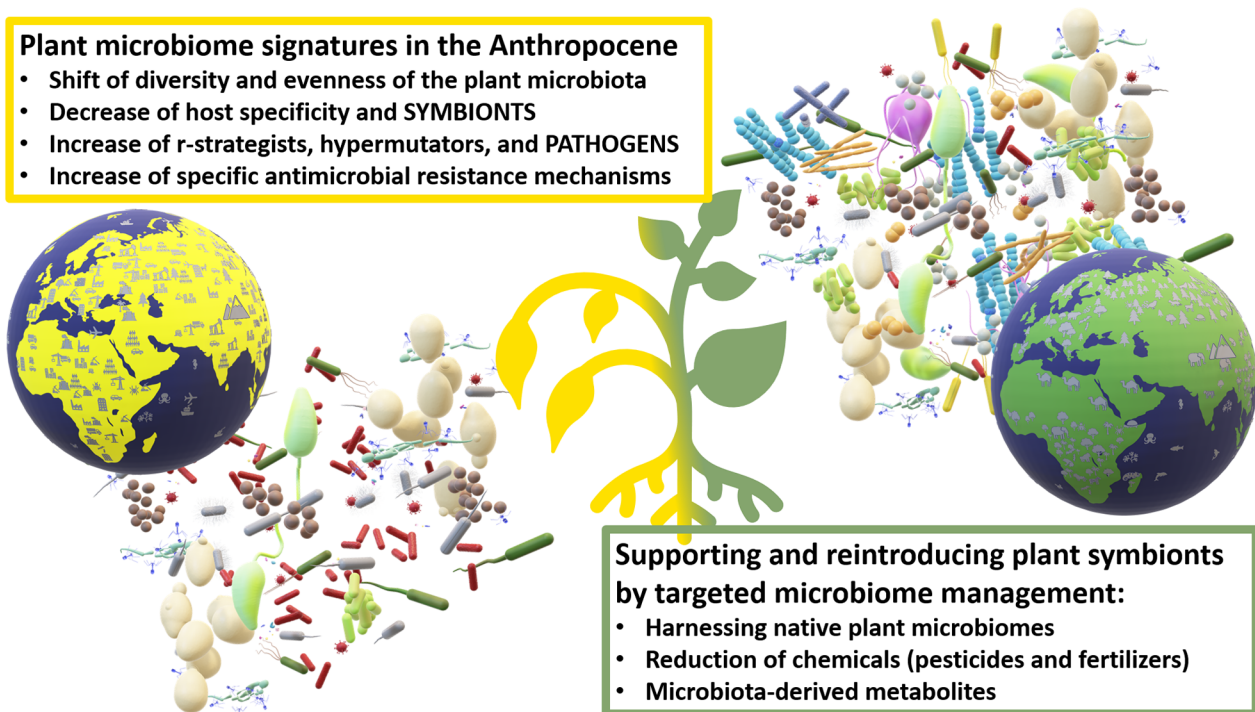
beneficial; they help to acquire nutrients, rare elements and minerals, stimulate the native immune system of plants and are able to antagonize plant pathogens (Cordovez et al. 2019; Santoyo 2022). In plant microbiomes, bacterial communities show a greater degree of specificity than the entire fungal and archaeal communities (Berg and Smalla 2009; Cordovez et al. 2019). However, symbionts from all microbial lineages show a certain degree of specificity and can be vertically transmitted (Vandenkoornhuys et al. 2015). Fungal symbionts have been classified into three types (Yang et al. 2013) (i) mycorrhizal fungi (mainly including arbuscular mycorrhizal fungi and ectomycorrhizal fungi), (ii) endophytic fungi, and (iii) specific root endophytes, e.g. *Piriformospora indica* as well as various dark septate endophytes.

Less is known about archaea and protists and their beneficial traits, and interactions. Based on metagenomic mining and targeted amplicon sequencing, archaea have been identified in several plant microbiomes, especially under harsh conditions, e.g. bog ecosystems and saline soils, as well as some trees (Jung et al. 2020). They also occur at comparatively low abundances in crop plants (Taffner et al. 2020). Beneficial properties, related to phytohormone production, have been identified within such archaeal communities (Taffner et al. 2018). Interestingly, under extreme conditions like in the highly polluted, highly saline dried out basin of the Aral Sea, archaea can be the dominant structural and functional component of the plant microbiota (Wicaksono et al. 2022). Despite their different phylogenetic origin, all symbiotic associations share a number of highly conserved features, including specific plant symbiotic signalling pathways, root colonization strategies that circumvent plant immune responses, functional host-microbe interface formation, and the central role of phytohormones in symbiosis-associated root developmental pathways (Harman 2011; Yang et al. 2013). Moreover, they fulfill functions including

nutrition that usually depends on fair trade between both partners – the plant and its microbes. Thus plant-associated microbes often provide protection against biotic and abiotic stress (Cordovez et al. 2019) and resilience traits achieved by an intense metabolic interplay and exchange of (secondary) metabolites. This interplay was disentangled by Carrión et al. (2019) who showed that endophytic symbionts protected plant roots against pathogens. The resistome is a term that describes all antimicrobial resistances (AMR) within a microbiome that are encoded in antimicrobial resistance genes (ARGs) in the genome of microorganisms or on mobile genetic elements (Berg et al. 2020). In addition to AMR, the resistome mediates resilience by providing the required plasticity for the plant holobiont (Obermeier et al. 2021). Finally, native plant microbiomes often harbor a high diversity of ARGs (Berg and Cernava 2022). The functions of plant-derived resistomes remain poorly understood, and targeted approaches will be needed in the future to decipher their importance and ubiquity.

## 2 The anthropogenic impact changed the plant microbiome: more plant pathogens and less symbionts?

Anthropogenic activities have shaped our planet in such a drastic way that they have resulted in the definition of a human-dominated geological epoch, the Anthropocene (Lewis and Maslin 2015). Intense agriculture in interplay with continuous human population growth is one of the major drivers of the Anthropocene. The Anthropocene is also reflected in the planetary boundary concept. Five of the nine boundaries have already been crossed: extinction rate, deforestation, climate change, the flux of nitrogen and phosphorus, and the introduction of novel entities (Persson



**Fig. 2** The Anthropocene is shaped by human activities which have also affected the plant microbiome substantially. The incorporation of symbiotic microbial functions will be key to counteract the rising issues

et al. 2022; Steffen et al. 2015). These are all factors that influence the plant microbiota either on local scale (e.g. over-fertilization) or global scale (e.g. climate change) and are connected with changes in the environmental microbiota (Cavicchioli et al. 2019). Despite this, the impact of these anthropogenic factors on the various host-associated and inter-linked microbiomes and the consequences for our planet are not well understood (Flandroy et al. 2018). Changes on a global scale are expected to have a substantial impact on the functioning of ecosystems, which could affect the health of their inhabitants. Therefore, it will be of utmost importance to take countermeasures to maintain various microbiomes in their native state.

Berg and Cernava (2022) suggest that human activities have already substantially affected the plant microbiome (see Fig. 2). This impact is reflected by a shift of diversity and evenness of the plant microbiota, which characterized by a decrease of host specificity, and an increase of r-strategic microbes (copiotrophic, fast growing microbes according to the  $r/K$  selection theory), pathogens, and hypermutators (strains with substantially increased mutation rates) (Berg and Cernava 2022). The resistome, anchored in the microbiome, follows this shift by an increase of specific AMR mechanisms as well as an increase of plasmid-associated resistance genes. This typical microbiome signature of the

Anthropocene is often associated with dysbiosis and loss of resilience. It leads to frequent pathogen outbreaks.

Climate change, nitrogen, and phosphorus (over)fertilization, chemical pollution, biodiversity loss, as well as stratospheric ozone depletion have influenced the environmental microbiome in different ways, but they follow the same direction as described above (Berg and Cernava 2022; see Fig. 2). Although understanding, and predicting, the impacts of anthropogenically-driven climate change on plant-associated microbiota is important (Hacquard et al. 2022), the combined, and synergistic effects have also to be considered (Rillig et al. 2019).

Microbiota shifts have been found in studies that address the consequences of climate change. Fast selection processes were described in situations where the taxonomy of selected species showed variations, but there was also a clear tendency towards enrichment of pathogens and spore-forming organisms (Ning et al. 2020), especially when various parameters were combined (Guerra et al. 2021; Roux et al. 2021). Baldrian et al. (2022) performed a meta-study on the effect of global change including the increase of  $\text{CO}_2$  concentration, temperature, change of precipitation, and nitrogen (N) deposition on fungal species and communities in terrestrial ecosystems. They found that the plant-mutualistic fungal guilds – ectomycorrhizal fungi and arbuscular mycorrhizal fungi – appear to be especially responsive to

global change factors with N deposition and warming having the strongest adverse effects (Baldrian et al. 2022). They also reported an increase in the abundance and dispersal of plant pathogenic fungi. Thus, it can be concluded that the entire ecosystem was weakened by global change-induced phenomena, such as drought, and consequently was more vulnerable to pathogen outbreaks.

Emerging and potential pathogens have been reported in recent years. Delgado-Baquerizo et al. (2020) predicted the occurrence of new pathogens into agricultural production areas, especially fungal plant pathogens. Experimental evidence for the impact of global warming on pathogens was provided using *Prunus padua*. This study showed a significantly increased abundance of pathogenic fungi and infections (Liu and He 2021). An increase of spore-forming bacteria and pathogens was also observed after increased UV-B radiation in the peanut phyllosphere; predominant UV-tolerant bacteria were identified as *Bacillus coagulans*, *Clavibacter michiganensis*, and *Curtobacterium flaccumfaciens* (Jacobs and Sundin 2001). The increase of pathogens also involves a migration polewards and expansion of the areas affected (Bebber et al. 2013). This phenomenon will have to be given additional attention in the future to ensure the nutrition of a growing world population under increasingly adverse conditions.

In contrast, a decrease of symbionts has been reported involving decreasing diversity, abundance and functioning. For example, Carrell et al. (2019) noted a microbiome shift in *Sphagnum* connected with a decreased diversity of bacteria and diazotrophs as well as a reduced nitrogen fixation rate. Long-term warming also induced microbiome shifts and affected *nifH* gene abundance for another common moss species *Racomitrium lanuginosum* in the sub-Arctic tundra (Klarenberg et al. 2022). The excessive use of nitrogen-containing fertilizers is particularly damaging, because a substantial amount of the nitrogen, that is not taken up by plants, is transformed into nitrate which is easily leached. Moreover, N as well as P fertilizer usage results in the loss of important functions provided by the mycorrhiza and plant-associated bacteria. In forests, nitrogen fertilization has a strong effect on soil nitrogen-fixing bacterial communities (Berthrong et al. 2014). For example, in pine forests, N fertilization has a strong effect on the *nifH*-associated bacterial community structure and suppressed the diversity and abundance of N-fixing bacteria.

Babalola et al. (2022) showed that nitrogen fertilisation disrupts the temporal dynamics of arbuscular mycorrhizal fungal hyphae but not spore density and community composition in a wheat fields. On the other hand, one-time inorganic phosphate amendments caused shifts in soil bacterial and fungal communities and reduced mycorrhization rate in ryegrass (Ikoyi et al. 2018). Long-term nitrogen fertilization

was shown to affect arbuscular mycorrhizal fungal communities while long-term phosphorous fertilization limited phosphorous provision to plants (Williams et al. 2017). Thus, both, nitrogen and phosphorus fertilization consistently favour pathogenic over mutualistic fungi in grassland soils (Lekberg et al. 2021).

Chemical pesticide treatments were also shown to affect plant symbioses. For example, neonicotinoid seed treatments induced shifts in the phyllosphere and soil microbial communities in soybean-corn agroecosystems. The microbiota shifts were reflected by a decline in the relative abundance of some potentially beneficial soil bacteria (bacteria involved in the N cycle) in response to pesticide applications (Parizadeh et al. 2021). The engineered nanomaterials SiO<sub>2</sub>, TiO<sub>2</sub>, and Fe<sub>3</sub>O<sub>4</sub> induced a reduction of N-fixing bacteria and iron-redox bacteria in the maize rhizosphere along microbiome shifts; however, the occurrence of plant growth promoting bacteria was enhanced (Zhang et al. 2020). These disruptions must be more considered in the future when fertilization and plant protection strategies are developed.

The seed microbiome is of special importance because it mainly consists of a core of plant beneficial bacteria (Bergna et al. 2018) and can be vertically transmitted symbionts (Gundel et al. 2017). The composition of the seed microbiota reflects the anthropogenic impact as well. Especially breeding activities were previously shown to have changed the composition and abundance of native microbial communities (Kim et al. 2020; Matsumoto et al. 2021; Rybakova et al. 2017). Moreover, chemical seed treatments were found to reduce bacterial diversity even before the onset of germination (Chen et al. 2020). Counteracting such changes could facilitate sustainability in agriculture.

### 3 Symbionts—the key for sustainable agriculture?

The plant microbiome, is already affected by the Anthropocene, and has led to missing symbionts in modern crop varieties that require targeted microbiome management strategies. There is a need for the development and application of microbiome-based products. The latter would help to replace harmful agrochemicals in the future for a more sustainable agriculture. This is not only a vision, it's a strategic aim of the European Green Deal, and anchored in the WHO Global Strategy for maintenance of antimicrobial resistance and the UNO Sustainable Development Goals.

In general, microbiomes can be managed directly by applying (i) microbiome transplants, (ii) microbes with beneficial properties, or (iii) microbiota-active metabolites, or 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). Studying native symbioses is a key to understand a healthy plant microbiome and its functioning, but can also help to isolate microorganisms with unique traits, design microbial transplants or microbiota-derived metabolites for use in sustainable agriculture (Fig. 2).

Native plants are a reservoir for plant-beneficial bacteria. This was demonstrated for *Sphagnum*, identified as rich source for plant-beneficial microbes, as well as many other microorganisms, and a new model for climate change studies on plant holobionts (Carrell et al. 2019; Hingley 1993, 1999). This plant has an extraordinarily high proportion of plant-beneficial microbes (Opelt et al. 2007a), that are species-specific, independent of the site (Opelt et al. 2007b). Vertical transmission of a beneficial core microbiota described by (Bragina et al. 2012), provides plant-beneficial properties within the moss metagenome (Bragina et al. 2014). The observation that mosses are an important reservoir for plant-beneficial microorganisms was applied by (Shcherbakov et al. 2013) to isolate plant growth promoting bacteria, which are now commercialized for sustainable agriculture. The distinct trait of the moss-associated microbiota to withstand abiotic stress has been exploited by Zachow et al. (2013) to isolate and design stress-protecting agents, which are commercialized. *Sphagnum* is only one example but there are exploitable symbiont reservoirs within the large group *Bryophyta*, which comprises liverworts, mosses and hornworts. Mosses were early land colonizers on Earth. Most of them depend on specific symbionts such as mycorrhiza and/or nitrogen-fixing cyanobacteria (Delaux and Schornack 2021), their potential as a source for plant-beneficial microorganisms is mostly untapped.

Composts serve as traditional microbial transplants that are still of great importance, especially in organic agriculture. Composts can substantially vary in their composition of microorganisms and other materials. However, for the enrichment of soil biodiversity, this is an advantage. Vermicompost is a specific type of compost produced by earthworms. Its high microbial diversity makes it suitable for a very broad range of crop species and cultivars, which can be selected to benefit best from this compost (Wolfgang et al. 2020). Suppressing soils also showed promising results from compost applications and researchers generally differentiate between natural and acquired suppressiveness. The former, can be found in diverse native ecosystems while the latter can spontaneously establish after several years of monoculture. Establishment of such soils mostly relies on microbial diversity and antagonism that the taxonomically different microbes mediate.

Plant microbiota assembly can result from vertical and/or horizontal transmission (Abdelfattah et al. 2021). As a result of a survey with native Alpine seeds, we know that

a highly diverse core of the microbiome of these plants is vertically transmitted and actively colonizes newly emerging seedlings upon germination (unpublished results). This reinforces the observation that the seed is an important carrier for beneficial symbionts in sustainable agriculture (Berg and Raaijmakers 2018). Interestingly, vertical transmission of microbial symbionts seems to be a frequent phenomenon (Bright and Bulgheresi 2010).

What are currently the biggest hurdles for microbiome management and microbiome-based products? Humankind requires further intensification of agriculture. Microorganisms provide the means to achieve this in a sustainable way (Basu et al. 2021). However, only a small proportion of the plant-associated microbial biodiversity can be cultured despite progress in analyzing the plant microbiome based on meta-omics technologies. There are interesting examples where keystone species were discovered by high-throughput sequencing and bioinformatic tools, and subsequently verified by isolating and applying the identified candidate (Matsumoto et al. 2021). They led to the first discoveries of disease-preventing microorganisms, so-called “sotero-bionts” (Cernava and Berg, 2022). However, cultivation-based approaches have to be further expanded and better integrated, because there are many ways in which microorganisms can positively influence plants (Vessey 2003). Only a small proportion of the plant-associated microbial biodiversity is currently exploited. Missing fermentation and formulation methods, especially for Gram-negative bacteria, are reasons for this bottleneck. Spore-forming bacteria like *Bacillus thuringiensis* and *B. amyloliquefaciens* and their relatives currently prevail in the commercially available products. While there are new formulation methods on the market (Berg and Müller 2018), strain-specific production methods have to be developed. Developments are still hampered due to inconsistent results and effects under field conditions. Modelling and machine learning can offer new solutions (Corander et al. 2022). For example, the optimization of synthetic microbial communities (SynComs) (Vorholt et al. 2017) from *Arabidopsis* has been selected by a computational approach and successfully employed against the plant pathogen *Pseudomonas syringae* (Vogel et al. 2021).

#### 4 The plant microbiome is embedded in one health and planetary health issues

The role of the microbiome for plant health is widely accepted, but the importance of inter-linked microbiomes, especially those associated with plants, for health issues of other organisms is less of a research focus. The connection of human, animal and plant microbiomes is evident in

**Fig. 3** Plants are the centerpiece of One Health components, and their growth and productivity are directly linked to the microbiome. Targeted microbiome management, that supports native functions of symbionts and reintroduces them where depleted, will improve sustainability and planetary health



the “One Health” concept of the World Health Organization (WHO), In addition the “Planetary Health” concept includes environmental health and its relationship to human cultures and habits (Flandroy et al. 2018). The signatures of the plant microbiome in the Anthropocene in relation to the inter-connected microbiome may result in intensified shifts, and result in a global microbiome imbalance. The absence of important symbionts in crop plants is recognized, missing microbes in native plants or wildlife are currently less considered. Peixoto et al. (2022) argued for microbiome stewardship for these organisms because they harbor great potential for restoration of endangered ecosystems.

## 5 Conclusion

The shift from symbionts to pathogens is one of the most visible signatures of the plant microbiome in the Anthropocene. The main drivers of this shift that act synergistically, have to be evaluated, changed and/or stopped. The plant microbiome is responsible for plant health, but due to the microbiome interconnectivity is also involved in “One Health” and “Planetary Health” concepts. These observations support the need for action in terms of targeted microbiome management strategies improving abundance and functioning of symbionts (Fig. 3). We have to close scientific knowledge gaps, and improve our understanding of (i) the filtering between interconnected microbiomes, (ii) interactions, communication and cooperation within the entire microbiome including viruses, and (iii) the microbial networks involving symbionts. Finally, we have to improve public perception of the importance intervention strategies. An example of one way to do this is the MOOC (massive open access online course) “Microbiome & Health” that

provides basic and applied knowledge about the microbiome (<https://imoox.at/course/microbiome>) to a very large audience.

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