Trends in
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Review

Microbiome selection and evolution within wild and domesticated plants

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Microbes are ubiquitously found across plant surfaces and even within their cells, forming the plant microbiome. Many of these microbes contribute to the functioning of the host and consequently affect its fitness. Therefore, in many contexts, including microbiome effects enables a better understanding of the phenotype of the plant rather than considering the genome alone. Changes in the microbiome composition are also associated with changes in the functioning of the host, and there has been considerable focus on how environmental variables regulate plant microbiomes. More recently, studies suggest that the host genome also preconditions the microbiome to the environment of the plant, and the microbiome is therefore subject to evolutionary forces. Here, we outline how plant microbiomes are governed by both environmental variables and evolutionary processes and how they can regulate plant health together.

Highlights

The environment determines the available pool of microbes available from which plants can form their microbiomes.

Plants have evolved a plethora of mechanisms to promote/restrict interactions with specific microbes from these environmental pools. These mechanisms are encoded by the genome.

The genomes of wild plants likely regulate their microbiomes for the local environment to obtain a fitness advantage and are therefore subject to natural selection. However, more studies are required to quantify the microbiome effect on wild plants within environmental settings.

The microbiomes of crops are instead driven by domestication processes, differing substantially from their wild relatives. Crop genomes could likely be manipulated to improve their interaction with microbiomes for improved nutrient and water use and resilience to abiotic stresses, but this may adversely affect yields.

Introduction

Microbes are found ubiquitously on the surfaces of plants, within many of their tissues, and even within their cells [1]. These microbes form the microbiome of the plant and certain members contribute to daily functioning to such an extent that their exclusion may significantly decrease the vitality of the plant [2]. Therefore, considering the microbiome alongside the genome will provide more information about the final phenotype of the plant in many contexts [3]. As the composition of the microbiome changes, so too does its functioning [1]. Therefore, much research has been conducted into the environmental variables that regulate soil and plant microbiomes, finding that soil conditions, climate, and geographic separation significantly affect both [1]. While soil is the primary reservoir for plant-associated microbes [4], variation in plant microbiomes occurs among plant species and populations, even when grown in the same conditions and with the same starting microbial inoculants [5–7]. Generally, this variation is much smaller than that associated with changing environments [5,6,8]. However, this has primarily been explored at a compositional (taxonomic) level and less so at a functional level. These functional studies have demonstrated that, while being subject to evolutionary forces [9], genotypic differences in plant microbiomes can have measurable effects on the plant phenotype [10,11] and surrounding ecosystem [12,13]. In this review, we outline how differences in plant microbiomes can be derived from transient environmental variation (i.e., ecological timescales) and how persistent differences in environments between plant populations lead to genotypic variation in microbiomes over evolutionary timeframes. In these instances, the host genome adapts the local microbiome for fitness advantages [5,14–16]. Further, we explore how different evolutionary processes (natural selection versus domestication processes) lead to genotypic differences in the microbiomes of wild plants and crops. Together, we provide multiple lines of evidence that point to how integrating ecoevolutionary processes can advance our understanding of plant microbiomes, and improve prediction and exploitation of crop microbiomes for sustainable agriculture.

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The microbiome affects the host phenotype

The plant-associated microbiome affects various phenotypic traits [2], including plant growth and resilience to abiotic stresses [17]. The effects of plant–microbe interactions are sometimes apparent, for example, how arbuscular mycorrhizal fungi and nitrogen-fixing bacteria improve plant biomass and nutrient content [18,19] or, conversely, the negative associations of pathogens leading to reduced biomass and growth irregularities [20]. However, such clear examples of the effects of plant–microbe interactions tend to be the exception. In reality, not only is the function of most individual plant-associated microbes unknown, but their effects are often much more subtle. Consider for example, the commensal phyllosphere species *Sphingomonas* and *Methylobacterium*. While both upregulate plant immune responses and inhibit the colonisation of pathogenic *Pseudomonas syringae*, they affect only the plant phenotype under certain conditions (i.e., where *P. syringae* is abundant) [21].

Ultimately, we know that the microbiome as a whole has a sizeable effect on plant health [2], but the lack of functional knowledge of most plant-associated microbes greatly constrains the field. We also know that the composition and functioning of plant microbiomes varies with the environment [11]. However, increasing evidence suggests that genotypic variation in plant microbiomes also affects how the microbiome functions, which contributes to differences in the host phenotype [8,11,22].

Processes shaping reservoir microbiomes

In order to understand the assembly of plant microbiomes (and their subsequent effects), first, the processes shaping the environmental reservoir of microbes need to be understood. The processes regulating microbial communities differ from macroorganisms, and their fundamental ecological principles are still being established. Microbes suffer few barriers to dispersal, they have large population sizes and short reproductive cycles, and many are capable of asexual reproduction and dormancy [23]. Consequently, compared with macroorganisms, microbes more easily disperse to environments with favourable conditions where they can quickly become abundant. Therefore, environmental microbiomes may respond rapidly and (semi-)predictably to environmental changes, making them a highly dynamic source of microbes for plants. Further, environmental selection emerges as a key process for shaping microbial communities, which can be used to predict the reservoir microbiomes, and ultimately plant microbiomes [24].

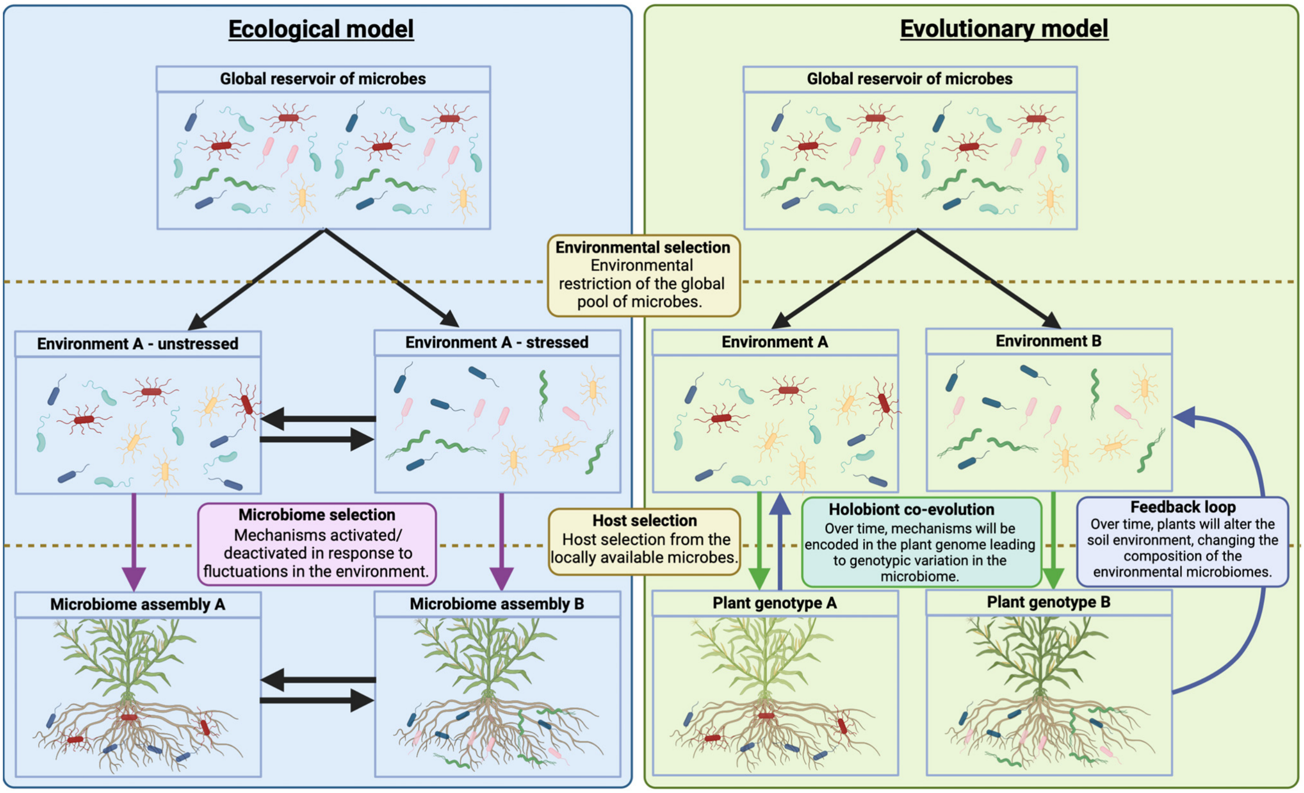
The physical environment determines environmental selection, which comprises climatic and edaphic parameters. Climatic variables are associated with large environmental microbiome variation [25]. Direct exposure to UV light is stressful for microbes. Therefore, UV sensitivity greatly affects the composition of the aboveground microbes (within the air and on the plant and soil surfaces). Additionally, temperature and precipitation (and therefore soil water content) affect the composition and functioning of microbiomes aboveground and belowground [25,26]. Edaphic factors also shape the community assembly of soil microbiomes [25,26]. Soil pH nearly ubiquitously drives the composition of the soil microbiome [25–28] and is nearly always the best predictor of it. Furthermore soil nutrients [29] and organic matter profoundly affect the composition of the soil microbiome [25,26].

Repeated small-scale and global studies have shown that microbes have reproducible patterns of variation in response to climatic and edaphic factors, and this can be used to predict the composition of environmental microbiomes (and therefore plant microbiomes). For example, lower soil pH generally favours fungal over bacterial biomass [30], while specific bacterial taxa are known to be much more UV tolerant than others (and therefore abundant within the phyllosphere) [31]. However, weather extremes, such as severe droughts and floods, occur outside expected annual cycles. Since these events are unpredictable and infrequent, they are difficult to capture within natural settings. They are, therefore, understudied, but the available results suggest that weather extremes have a large effect on soil and plant microbiomes [32,33]. Further, their effects can persist long after the extreme has subsided [34], and these legacy effects will generally be counted as unexplained variation within community analyses.

While we outline how the soil microbiome acts as a reservoir for the plant microbiome, it should be noted that plants influence the soil microbiome in a feedback loop that occurs over longer timeframes (years) (Figure 1). Plants will, over time, affect the soil organic matter and aggregate size, water retention, pH, and nutrient content [35,36]. This change in soil conditions affects the soil microbiome, ultimately affecting subsequent plant microbiomes. Therefore, plant health (and community composition) is more immediately affected by environmental microbes. However, over longer timeframes, the plant community also exerts selection pressure on the soil microbiomes.

Recruitment of plant microbiomes

Ultimately, the recruitment of microbes by plants and thus the structure of their microbiomes depends on which environmental microbes are locally available (Figure 1). However, within each



Trends in Microbiology

Figure 1. A model for the ecological and evolutionary processes governing the plant microbiome. The plant selects from the locally available microbes as proposed in the two-step model by Bulgarelli *et al.* [37] and expanded upon by Favela *et al.* [38]. Here we emphasise that variations in plant microbiomes can be derived from ecological and evolutionary processes. Environmental microbiomes change rapidly in response to stresses, such as abiotic stresses. Consequently, the plant microbiome is selected for by various mechanisms, being activated/deactivated to mitigate for these fluctuations (ecological model). Meanwhile, consistent differences between environments can lead to the mechanisms being encoded in the plant genome, thereby being constitutively expressed as part of adaptation (evolutionary model). This leads to genotypic variation in plant microbiomes being observed even within standard growing conditions.

environmental microbiome, plants can greatly influence the microbes that colonise them and their relative frequencies in a two-step selection model first proposed by Bulgarelli *et al.* [37] and expanded upon by Favela *et al.* [38]. As a consequence of this host selection, some microbes can be in orders of magnitude higher abundance within the plant microbiome than in their surrounding environment, while the abundance of others is greatly reduced [1]. Different crop lines or populations of wild plants promote/suppress different environmental microbes (through physical and chemical means), with many experiments demonstrating genotypic variation in plant microbiomes [15,39,40]. Until recently, the importance of this observation was mostly overlooked, partly because the effect size was so much smaller than environmental variation at a taxonomic level (of the microbiome) [11]. Further, plant microbiomes vary with host traits, such as root chemistry [41] or morphology [42], as part of adaptation to local environmental conditions, making it challenging to isolate the effects of the microbiome on the health of the plant. For example, sampling wild plant populations from different locations not only inevitably also entails sampling from different environments and, therefore, different microbial reservoirs, but also from hosts who exhibit genomic variation between populations. In these experiments, isolating the individual effects of the genome, microbiome, and environment on the plant is impossible. However, controlled experimental designs can allow for the independent manipulation of the host genome, microbiome, and the environment, thus allowing their effects to be decoupled. Consequently, studies have demonstrated that plants can manipulate their microbiomes in response to environmental changes to mitigate their effects (Figure 1 – ecological model) [17]. However, over time, consistent differences in the environment can lead to the mechanisms promoting beneficial plant–microbe interactions to become encoded in the plant genome as part of environmental adaptation (Figure 1 – evolutionary model) [8,11,18,22,43], and it is these evolutionary processes that produce genotypic variation in plant microbiomes. Interest in this genome selection has been growing exponentially within recent years since it seems that crop genomes are less selective than wild plants (in terms of recruiting optimal symbionts) [18,43], potentially due to erosion of the host genome to form optimal interactions with the microbiome × environment interactions during the domestication process, which can be improved within breeding programmes.

Mechanisms shaping plant microbiomes

To facilitate the selection (or inhibition) of environmental microbes, plants have evolved several different mechanisms to regulate their leaf and root microbiomes (Table 1) [44,45]. This includes the process of secreting exudates from aboveground and belowground tissues that serve as a pivotal energy source for microbes. Altering the total amounts of exudates allows plants to influence microbial biomass and diversity [46,47], with higher microbial diversity generally associated with improved plant health and productivity [48–50]. Root exudates alone can account for a substantial proportion of the total resources of the plant, amounting to over 10% of total fixed carbon [51], which is combined with nitrogen, phosphorus, and other more limited resources within exudates. Adjusting exudation rates therefore affects the availability of nutrients to the plant [52] and its interaction with microbiomes [53].

Plants also produce a plethora of specialised metabolites which allow them to shape their microbiome in a more targeted manner. For example, phenolics, benzoxazinoids, terpenes, and alkaloids are widely produced across the plant kingdom and have been linked to the composition of the overall microbiome and the attraction/repulsion of specific taxa [54]. For example, flavonoids in the roots of legume species initiate the process of nodulation and the recruitment of rhizobia [55]. Another example is benzoxazinoids – whose presence within root exudates is linked to the attraction of a growth-promoting *Pseudomonas* strain [56] and the suppression of pathogenic *Fusarium* strains [57] – and research is ongoing into whether benzoxazinoids can be manipulated within breeding strategies to improve crops [58,59]. Together, the quantity and composition of exudates

Table 1. Plants employ a plethora of mechanisms to influence microbes[a]

Mechanism	Examples
Morphology	• The effects of changing leaf morphology (and other aboveground structures) on the microbiome are poorly understood. • The root structure (mean root diameter, branching structure) impacts the root microbiome.
Core metabolites	• Hormones such as auxin effect both morphological structures and secondary metabolites production. • Sugars and other metabolites are used as energy sources for microbes. Their exudation rate can manipulate the microbiome.
Specialised metabolites	• Specialised metabolites can have a large effect on the composition of plant microbiomes. • They can recruit/repel specific microbial taxa. • Examples include phenolics, benzoxazinoids, terpenes, and alkaloids that are produced by many plants species.
Microbe–microbe interactions	• Microbes can interact competitively, occupying niche spaces or actively releasing compounds to inhibit competition. • Plants may manipulate the microbiome through other microbes, although this is poorly understood.

[a] Plants employ a range of mechanisms to manipulate their microbiomes in response to their environment. These can be activated and deactivated in response to environmental fluctuations. However, they can become constitutively expressed under consistent environmental pressures. This can be either through changing physical structures (morphology) [42,46,61–64], or through the synthesis of core [45,60] and specialised metabolites [54–59]. Plants may also alter their microbiome through microbial intermediaries (microbe–microbe interactions) [65–67].

represent a key mechanism by which plants can manipulate their microbiome for additional growth benefits and pathogen inhibition.

Phytohormones are core metabolites that are integral in shaping the plant morphology and immune system (i.e., secondary metabolites) [45,60]; they include auxin, ethylene, jasmonic acid, salicylic acid, and abscisic acid, and they can influence plant microbiome composition through both physical and chemical means. However, given their broad effects on the plant, phytohormones may be unlikely candidates for the host (or researchers) to use in targeted manipulations of the microbiome since many off-target changes will also occur.

Plants also manipulate microbiomes through their morphology, although it is hard to delineate whether changes in morphology directly manipulate the microbiome, or rather co-vary as morphological changes with the environment. In the phyllosphere, leaf morphology affects the composition and metabolic activity of the microbiome [61,62] but this is generally poorly understood. While the effects of root morphology on the microbiome have been explored by more studies, there is still much uncertainty. Crudely, more extensive root networks produce more rhizoexudates and promote higher microbial diversity [46,63]. Additionally, thinner roots also have higher exudation rates [64], which increases the resources available to microbes. Adjusting root thickness could be an important mechanism for plants to manipulate their root microbiomes, or simply a secondary effect of changing root morphology.

Plants may also exploit microbe–microbe interactions to regulate their microbiomes, which has downstream implications on plant health. Microbe–microbe interactions definitively contribute to the formation of plant microbiomes. For example, certain bacterial strains individually (or some in combination) inhibited leaf bacterial pathogen colonisation [65], while the presence of specific fungal root endophytes (dark septate endophytes) decreased the abundance of fungal pathogens in the roots [66]. Another study suggests that mycorrhizal fungi also further enrich plant growth by promoting bacteria on their hyphae [67]. However, it remains to be determined whether plants can deterministically manipulate their microbiome through microbial intermediaries in a targeted manner.

Importantly, many of these mechanisms are dynamic, varying as the environment (and environmental microbes) change, which allows the plant to optimise plant–microbe interactions (i.e., ecological regulation) with environmental variation. Yet these mechanisms also vary between plant species and genotypes when grown in controlled environments, translating host genomic variation into predetermined effects on plant microbiomes. Therefore, the contribution of both processes is required to fully determine the regulation of plant microbiomes.

Plant–microbe coevolution in the environment

Critically, the host genome is static throughout the lifetime of the plant. By contrast, the genes within the microbiome can change rapidly in response to environmental stressors [68], which in turn affects the functional outcomes of plant–microbe interactions (e.g., nutrient exchange and stress resilience) [69,70]. Theoretically, the plants that can manipulate their microbiome for ‘better’ gene compositions (i.e., host + microbial) under the new environment will therefore have a fitness advantage [3], for example, by using the aforementioned mechanisms to mitigate changes in the local environment [41]. However, there is further coevolution within the holobiont (Figure 1). For example, if the benefits of specific plant–microbe interactions persist over time (by a constant pressure rather than a temporary one), the mechanisms behind this interaction may become constitutively expressed and ultimately encoded within the genome (Figure 1 – evolutionary model). This is the basis of the holobiont theory, a theory that postulates that multicellular hosts work in symbiosis with their microbiome [71–73], and the contribution of the microbiome to the host needs to be considered over evolutionary space. This hardcoding of mechanisms through which plants can manipulate their microbiome may serve as part of adaptation to their environment to provide them with a fitness advantage [72,74]. Importantly, we identify several key remaining questions that challenge the importance of this host genome–microbiome coevolution. For example, it remains undetermined how quickly the microbial communities associated with plants can adapt to environmental changes, and how quickly plants can reinforce beneficial changes in their microbiomes.

The evolution of the holobiont within wild plants

Under the holobiont theory, the selection of plant microbiomes will follow natural selection. However, most studies investigating the relationship between plant genomes, microbes, and the environment have been performed on crops, which have repeatedly been shown to differ substantially from their wild relatives [40] and are likely dominated by domestication processes rather than natural selection [75]. Therefore, we urge that this distinction be considered in all future studies since it has been tacitly implied [37,38,75] but not explicitly stated.

From the studies that have focused on wild plants, evidence for selection of microbiomes as part of adaptation is beginning to accumulate. Researchers have partitioned the effects of the host genome, the environment, and the microbiome, finding that the microbiome correlated with host genomes within controlled environments, suggesting that the host genome can predict the microbiome. This relationship was found across angiosperm species [76], specifically within lineages of *Populus* [77], switchgrass [8], and teosintes [78]. This suggests that, in general, the more similar the host genome, the more similar the microbiome is (referred to as phylosymbiosis). However, very few studies have linked genotypic variation in the microbiome with the fitness of the host [10,11,74,79]. One study of cheat grass populations (*Bromus tectorum*) suggested host adaptation to their local microbiome and their environment’s salinity [74]. Within our work on teosintes (wild maize), we found a significant correlation between the host genome and the root microbiome. Furthermore, we established that the teosinte populations taken from high altitudes were preconditioned to cultivate more microbes associated with enhanced cold tolerance [78]. However, in this work, results remained limited to correlations, not causative interactions, and in general, there remains a clear and urgent need for additional studies to go beyond correlations to confirm that genotypic variation in plant microbiomes contributes to the host's fitness [11,80].

While the ability of plants to manipulate their microbiomes is often discussed in terms of the growth benefits that microbes have, pathogens should also be considered. It has long been known that pathogen susceptibility varies between genotypes [81]. However, many pathogens exploit the same colonisation pathways as symbionts [82], suggesting a tradeoff between the benefits of beneficial microbes and the harm of pathogens. For example, it was shown that certain accessions of *Arabidopsis thaliana* were associated with higher abundances of a *Pseudomonas* strain that increased biomass [79]. However, these accessions were colonised by more *Pseudomonas* strains in general, including pathogenic ones. If this *Pseudomonas* interaction was always beneficial, it would likely spread throughout populations since it would provide consistent growth benefits, but it has not. This suggests that the benefits of increased *Pseudomonas* abundance are situational, potentially based on the ratio of beneficial to harmful Pseudomonads within the environment. Over longer timeframes, the mechanism promoting/restricting *Pseudomonas* colonisation could be encoded within the genome.

Breeding crops for better microbiomes

There is enthusiasm among researchers hoping to manipulate crop genomes to optimise microbial interactions (i.e., applying the holobiont theory), aiming to improve yields, nutrient uptake, and abiotic stress tolerances [75,83]. However, the removal of environmental pressures such as nutrient and water limitations, as well as pests, has allowed domestication processes to dominate a number of traits in crops, including the regulation of the microbiome [84,85]. Despite this, correlations have been made between the microbiomes and the genomes of sorghum [86], rice [39], maize [5], and more [40,87] (i.e., more closely related genotypes cultivate more similar microbiomes), suggesting that the genome of modern crops can be used to manipulate their microbiomes.

Importantly, studies show that modern crops are less selective and obtain fewer growth benefits from arbuscular mycorrhizal fungi (AMF) [18], rhizobia [43] and other growth-promoting microbes [88]. Further, domestication may have also increased susceptibility to existing and novel pathogens [89] and, more broadly, facilitated microbial processes with negative ecosystem effects [9,90]. For example, the root microbiomes of modern maize cultivars were found to promote denitrifying bacteria compared with older lines and teosintes [9,90], and this process likely leads to less sustainable soil nitrogen use in agriculture. These results have fuelled hopes that wild crop relatives have the genetic information to improve crop microbiomes [83].

Alternatively, early crop landraces represent an interesting source of genetic material for improving modern crop microbiomes. A study of early maize landraces (developed by Mesoamericans prior to the green revolution) showed evidence that the root microbiome was preconditioned for the local environment [11], as hypothesised for wild plant species. Specifically, the lines from low soil nitrogen environments consistently cultivated more *Massilia* species associated with resilience to low soil nitrogen [91]. Early landraces were domesticated in specific areas within lower input systems [92,93]. Based on our knowledge of their root microbiomes [9,11,90], we hypothesise that early landraces generally have more effective interactions with microbes than modern crop lines (Figure 2). Importantly, landrace genomes and physiology are more comparable with modern lines than to wild crop relatives, making them attractive to utilise within breeding programmes, if appropriate agreements can be made with relevant indigenous groups for which many have cultural significance [94].

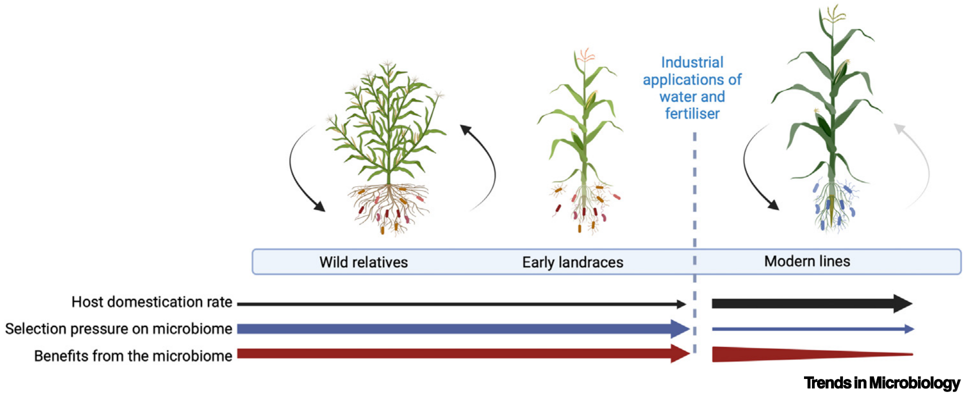


Figure 2. Theoretical model for the coevolution of the microbiome over domestication. Within wild plants, there has been coevolution between the host and microbiome within the environment. While early landraces of crops were grown with managed systems, water and fertiliser application was less intense [92,93]. We hypothesise that these are adapted to specific areas and therefore environments, allowing for the genome–microbiome interactions to coevolve. Consequently, they were subject to less domestication pressure (illustrated by the thin black line), and had a higher selection pressure on their microbiome (illustrated by the thick blue line) where they receive more growth benefits from it (illustrated by the thick red line). Modern crops are subject to less environmental selection since they generally receive excess water and nutrients, leading to diminishing growth benefits from microbes [18,43]. Future crops may be bred to interact with microbes more efficiently.

It has been previously hypothesised that the genomes of crops have been eroded during domestication so that they exert less selection on environmental microbes in forming their microbiomes [37,38]. However, crop microbiomes substantially differ from reservoir microbiomes, and genotypic effects are still observable between the microbiomes of different crop lines [39,86,87]. This demonstrates that crop genomes still exert significant selection forces, but why is not fully understood. Before breeding for better crop microbiomes can become a reality, a better understanding of how domestication processes have shaped crop microbiomes is needed (Figure 2). Currently, there are three competing hypotheses for this [75]:

(i) Evolutionary trade-offs

The application of water, nutrients, and pesticides have selected against symbioses in crops, with the nutrients spared in exudates and specialised structures invested in producing higher yields instead [95]. Here there has been the targeted selection of genes with adverse effects for the microbiome.

(ii) Co-accumulation of adverse genes

Alleles with adverse effects on the microbiome have hitchhiked alongside genes strongly selected during domestication [83,96]. These genes have become ubiquitous in crops due to their lower genetic diversity and higher linkage disequilibrium compared with their wild relatives [96].

(iii) Reduced selection

The addition of water and fertiliser has reduced the selection pressures on crop microbiomes. Consequently, the regulation of the microbiome becomes less effective with domestication (passive erosion) as alleles that would be detrimental without exogenous water/nutrients accumulate with no adverse effects [18].

Here, hypothesis (i) is the least desirable scenario, as additional growth benefits from the crop microbiome will come at the cost of yields. However, this could still be interesting for breeders to explore since there is a growing demand for lower-input agriculture for improved sustainability, and fine-tuning plant–microbe interactions could mitigate some of the growth losses associated with less fertiliser/water application. Meanwhile, under hypotheses (ii) and (iii), re-introducing alleles associated with beneficial plant–microbe interactions (or removal of harmful alleles) would improve crop yields and resilience without negative consequences. Ultimately, it remains to be determined which of these hypotheses is true. However, if selecting for 'better' microbiomes comes at the cost of yields, its feasibility will need to be carefully assessed against the savings in fertiliser, water, and pesticide application. Further, any decreases in yields will ultimately reduce the land available to natural areas [97].

Challenges in studying the plant holobiont

It should be noted that while there is growing interest in host selection of the microbiome for specific functions, the importance of this relationship remains debated, particularly as significant correlations between the host genome and the microbiome are only inconsistently found [98,99], suggesting a limited effect size. While no effect is possible, we hypothesise that inconsistent correlations between the genome and microbiome are also commonly associated with three limitations:

(i) The environment affects the plant phenotype and environmental microbiomes to a large extent [100], which can completely mask the much smaller effect of genome variation [6,40].
(ii) Host genome variation is mostly calculated as phylogenetic relatedness, often produced by a small number of barcoded regions, thereby missing causative genes [40]. More recently, this has been calculated across the entire genome (e.g. SNPs), but variation in causative regions can be overwhelmed by non-significant variation across the rest of the genome. In reality, control of the microbiome is complex (polyallelic), but these represent only a fraction of the total genome [101].
(iii) Many of these studies have been performed in domesticated crops [75] which have confounded the relationships between the genome, microbiome, and environment (discussed at length in the previous section) [102].

For future investigations of the coevolution of plants and their microbiome, we suggest conducting more studies on wild plants instead of domesticated crops since wild plants will have evolved under natural selection to their environment. Specifically, wild plants can be used to assess whether the holobiont theory is correct by demonstrating that wild plants regulate their local microbes for additional growth benefits [8,11,79]. Further, they might even help to identify microbes associated with specific traits, such as microbes that help to mitigate drought, which could be abundant in the wild plant species/genotypes from drought-prone areas. Finally, there is a need to go beyond correlating genome variation to the microbiome and identify specific genes associated with the regulation of the microbiome, for which SNP-based approaches have already yielded interesting results [11,39,103,104]. With decreasing sequencing costs and increasing computational power, future studies will be able to use whole genomes to identify the precise genomic (and epigenomic) variation associated with regulating the microbiome.

Concluding remarks

In this review, we have outlined how environmental microbiomes shape plant microbiomes. However, through evolutionary adaptations, the host also preconditions its microbiome for specific environments. We outline how plants have evolved many mechanisms by which they can achieve this. While many of these mechanisms are transient, if there is a consistent selection pressure, these mechanisms will be encoded in the genome to promote/suppress microbes for the local

Outstanding questions

Can the composition of plant microbiomes be reliably predicted from environmental microbiomes, soil properties, and climatic variables?

Can multi-omic (metagenomic, metatranscriptomic, meta-metabolomic) data be integrated to make high-quality functional predictions of the active plant-associated microbes?

Can high-throughput culture-omics methods be scaled to validate the functions of a meaningful proportion of the plant microbiome?

Can alternative methods be developed to validate the functions of unculturable plant-associated microbes?

What are the key mechanisms by which plant microbiomes affect their host health and resilience under various environmental and evolutionary conditions?

What are the primary evolutionary processes shaping variation in wild plant microbiomes across environments and species?

Do wild plants obtain more growth benefits from their microbiomes in both natural and agricultural settings compared with modern crops?

Can the microbiomes of domesticated crops be optimised without negative effects on yields?

environment. It is only with systematic explorations between the host genome, microbiome, and the environment that it is possible to demonstrate this adaptation of the microbiome for the local environment [8,11,80]. However, more studies are required to quantify the effect of these genome–microbiome interactions on plant health (see Outstanding questions box). If these processes can be better understood, they could even be exploited to breed more resilient crops [2] that are better for human health [29]. A more holistic approach to understanding plant–microbe interactions could also advance many areas of plant science, for example, identifying optimal areas to conserve threatened plant species or predicting species range changes under climate change.

Declaration of interests

No interests are declared.

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