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Ecology and Evolution of Plant Microbiomes

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Abstract

Microorganisms colonizing plant surfaces and internal tissues provide a number of life-support functions for their host. Despite increasing recognition of the vast functional capabilities of the plant microbiome, our understanding of the ecology and evolution of the taxonomically hyperdiverse microbial communities is limited. Here, we review current knowledge of plant genotypic and phenotypic traits as well as allogenic and autogenic factors that shape microbiome composition and functions. We give specific emphasis to the impact of plant domestication on microbiome assembly and how insights into microbiomes of wild plant relatives and native habitats can contribute to reinstate or enrich for microorganisms with beneficial effects on plant growth, development, and health. Finally, we introduce new concepts and perspectives in plant microbiome research, in particular how community ecology theory can provide a mechanistic framework to unravel the interplay of distinct ecological processes—i.e., selection, dispersal, drift, diversification—that structure the plant microbiome.

Contents

1. INTRODUCTION

In the past decade, a paradigm shift in the life sciences has emerged in which microbial communities are viewed as functional drivers of their eukaryotic hosts. For plants, microbiomes can expand the genomic and metabolic capabilities of their hosts, providing or facilitating a range of essential life-support functions, including nutrient acquisition, immune modulation, and (a)biotic stress tolerance. While plant microbiomes have been proposed as a new platform for the next green revolution, fundamental knowledge of the mechanisms underlying microbiome assembly and activity is still in its infancy. Plant microbiologists have started to embrace the full breadth of high-throughput sequencing technologies to decipher the intricacies of the functional diversity and spatiotemporal dynamics of plant microbiomes. Our ability to go beyond one-microbe-at-a-time approaches has already led to a more holistic view of the plant microbiome and the discovery of taxonomically novel microorganisms and beneficial microbial consortia (27, 51, 91). Also, de novo assembly of microbial genomes from metagenome data has been leading to the identification of novel genes and pathways involved in microbe-microbe and microbe-plant interactions (4, 20, 27, 50, 65, 74, 84).

Microbiome research has also attracted the attention of various other research disciplines, including botany and plant ecology (42, 87, 100, 144), restoration and invasion ecology (64, 142), phytoremediation (119), mathematics and modelling (59, 92), and chemistry and natural product discovery (36). The striking similarities with the human microbiome (12, 43, 85) have further fueled the conceptual framework of plant microbiome research and stimulated the development of microbiome-based strategies to improve plant growth and health (34, 114, 129). For example, the colonization potential of an introduced microbial species (probiotic) is a fundamental aspect of human microbiome research and health care, but it is also a key element of the successful implementation of microbial inoculants for plant growth promotion and disease control (15). The overall results obtained so far indicate that introduced microorganisms are usually washed out and do not persist in the gut, plant, or soil ecosystem at functionally meaningful densities (39, 79, 114, 138). In this context, it is of fundamental importance to understand the coevolutionary trajectories of plant microbiomes and the mechanisms underlying assembly, activity, and persistence.

In this review, we discuss the interplay between plant genotypic and phenotypic traits, the environment, and microbiome assembly. Specific emphasis is given to the impact of plant domestication on assembly and how learning from nature can be used to reinstate the missing plant microbes, if any, in future plant breeding strategies. In addition to this walk on the wild side, we discuss how biotic stress factors (e.g., pests, diseases) urge plants to recruit or activate beneficial microbial consortia. We introduce new perspectives in plant microbiome research, in particular how community ecology theory can serve as a mechanistic framework to unravel the interplay of distinct ecological processes (i.e., selection, dispersal, drift, diversification) structuring the plant microbiome.

Spermosphere: the environment closely surrounding and influenced by germinating plant seeds

Rhizosphere: thin layer of soil closely surrounding and influenced by the plant root

Phyllosphere: the environment closely surrounding plant aerial surfaces

Endosphere: the environment inside plant tissues

Rhizoplane: the external root surface with tightly adhering soil particles

2. PLANT MICROBIOME ASSEMBLY

The transmission of microorganisms to their plant host occurs horizontally via the environment and vertically via the parents (10, 45, 116, 121). Transmitted microorganisms can move from the spermosphere to the rhizosphere to the phyllosphere and inside plant tissues, the endosphere. Hence, microbiome assembly involves dynamic changes in species composition and abundance as well as steady-state compositions of spatially different compartments. For the assembly of the rice microbiome, Edwards et al. (35) described a multistep model with three distinct but overlapping microbial communities, that is, the rhizosphere, rhizoplane, and endosphere. Each of these compartments contains a subset of the microbiome from the others, moving from the external toward the internal sections of the plant. In this context, Vandenkoornhuyse et al. (128) referred to the soil as the seed bank for root microbiome assembly, the rhizosphere as the growth chamber, the rhizoplane as a specific habitat or transitional boundary, and the endosphere as a restricted area. Indeed, bacterial communities inside plant tissues are equipped with distinct characteristics that allow them to adapt their metabolism to the physical-chemical conditions of the endosphere (38, 47, 104, 109, 125). Besides specific microbial traits such as flagella, plant-polymer-degrading enzymes (e.g., cellulases, pectinases), type V and type VI protein secretion systems, and enzymes detoxifying reactive oxygen species (ROS), plant immunity also plays an important role in structuring the endophytic community (46, 104, 115, 122).

The large fluctuations in abiotic conditions throughout day and night, such as temperature, moisture, and radiation, lead to less diverse but more dynamic communities in the phyllosphere than in other plant compartments (61, 77, 122, 132). Taxonomic and genomic analyses of large culture collections of *Arabidopsis thaliana* showed specific functional categories for the root and leaf microbiome but also considerable functional overlap between these two communities (4). Whether this functional overlap is due to transmission of microorganisms from root to leaf and vice versa or is typical for plants that form a leaf rosette that is in direct contact with the same soil microbial seed bank still remains to be elucidated.

2.1. Allogenic and Autogenic Factors Governing Microbiome Assembly

Soil type is the major allogenic factor shaping the root microbiome (18, 78, 93, 101, 110, 112, 134, 146). As indicated by Schlaeppi et al. (110), the soil defines not only the microbial inoculum but also the nutrient availability for plants, which in turn affects plant growth, root structure and exudation, and microbiome assembly (18). This is well exemplified in studies of land-use conversion where changes in soil management practices affected not only plant diversity and growth but also soil properties such as moisture, texture, pH, and nutrient availability (66, 82). For example, the conversion of the Amazon rainforest into agroecosystems led to an increase in soil carbon and pH, altered microbial diversity, and a decrease in the relative abundance of *Acidobacteria* species (106).

Within a microbiome, autogenic factors such as microbe-microbe interactions play important, yet often overlooked, roles in structuring the overall microbiome assembly. To illustrate that, using a simplified maize root community consisting of seven species, Niu et al. (91) elegantly explored how bacterial interspecies interactions affect microbiome assembly. They showed that removal of only one species, *Enterobacter cloacae*, led to the dominance of *Curtobacterium pusillum* and a significant decrease of the other five members of the community, suggesting that *E. cloacae* is a key player influencing community assembly. The seven microbiome members together showed better protection of the maize roots against infection by the fungus *Fusarium verticillioides* than the individual members, confirming and extending earlier observations that microbial community diversity and interactions affect the invasion of pathogenic microorganisms (9, 80, 127).

2.2. Host Signature Effects on Microbiome Assembly

The impact of plant genotype and developmental stage on microbiome assembly has been reported for the model plant *A. thaliana* (18, 78, 110), numerous crop species (2, 23, 35, 112), and several wild plant species (17, 94, 118, 134, 148). Plant genetic variation affects morphological characteristics such as root growth, architecture, and exudate composition, which in turn impact microbiome assembly. For example, Legay et al. (70) showed that root diameter, root dry matter content, and root C/N ratio were significant predictors of the variation in microbiome composition. The strong influence of root traits on microbiome structure is likely due to the quantity and quality of plant carbon and nitrogen released from the roots into the surrounding soil. The chemically diverse constituents of root exudates enrich for specific microorganisms by stimulating their growth and/or by inducing or repressing specific microbial functions that have an important role in plant-microbe and microbe-microbe interactions (5, 21, 32, 44, 54). Interestingly, phylogenetically diverse bacterial taxa that are consistently found in association with plants share functions that enable them to adapt to the plant environment (74). More specifically, genomes of plant-associated bacteria encode important carbohydrate metabolism functions and fewer mobile elements than genomes of related bacterial genera not associated with plants (74). Among these functions, protein domains characteristic of the LacI transcription factor family, which regulates sugar catabolic operons in response to carbon, are enriched in plant-associated bacteria (74). By integrating microbiome, comparative genome, and exometabolome analyses, Zhalnina et al. (149) further showed that the exudation properties and microbial substrate uptake traits collectively contribute to a metabolic synchronization during rhizosphere microbiome assembly. Following these findings, further optimization of methods to identify exudates released by plants in situ will be needed for an in-depth understanding of the spatiotemporal metabolic dynamics in the rhizosphere, phyllosphere, and endosphere.

2.3. Genetic and Chemical Basis of Microbiome Assembly

Experiments with mutant plants and genome-wide association studies (GWAS) are beginning to shed light on the genetic and chemical basis of microbiome assembly (16, 28, 33, 137). Studies with *A. thaliana* mutants deficient in hormone-regulated defense responses pointed to the involvement of the plant immune system in microbiome assembly in the rhizosphere, endosphere, and phyllosphere (6, 49, 62, 67). Lebeis et al. (67) showed that *A. thaliana* mutants, in which salicylic acid (SA) signaling was either constitutive or disrupted, displayed significantly different root bacterial communities. Subsequent experiments with a 38-member synthetic community (SynCom) showed that isolates absent in the majority of the samples from wild-type plants were abundant in samples from SA-deficient mutants. These results suggested that SA modulates the overall structure of

the root bacterial community by differentially affecting the growth of specific rhizobacterial community members. In another study with *A. thaliana* mutants compromised in jasmonic acid (JA) signaling, changes in the species abundance were associated with shifts in the concentration of specific root exudates (21). The authors showed that JA-mutant plants released higher concentrations of 1-deoxy-erythritol and glycerol-gulo-hepto, which were positively correlated with higher relative abundances of members of the *Clostridiales* and *Pseudomonadales*. Also, higher concentrations of fructose, glyceric acid, isoleucine, and 2-hydroxy valeric acid for the *Arabidopsis* mutants were positively correlated with higher relative abundances of *Paenibacillus*, *Lysinibacillus*, and *Bacillus* species. If and how specific plant hormones or other alterations in root exudate composition in these plant mutants drive the selection and activities of these groups of root-associated bacteria remain to be validated.

For phyllosphere microbiome assembly, GWAS pointed to plant loci associated with defense and cell wall integrity (52). More specifically, plant genes encoding different ABC transporters were associated with the abundance of *Mycosphaerella* and *Sphingomonas*, whereas pectin-related enzymes were associated with *Sphingomonas*, *Chryseobacterium*, and *Xanthomonas*. Using a SynCom and a set of 55 *A. thaliana* mutants, Bodenhausen et al. (13) showed that mutants in the cuticle synthesis genes *lacs2* and *pec1* harbored a higher bacterial abundance and a different microbiome composition than wild-type plants. They hypothesized that the increased bacterial abundance for the *lacs2* mutant was due to increased leaching of nutrients compared to the wild type and *pec1* mutant.

Badri et al. (3) were among the pioneers to demonstrate the impact of changes in rhizosphere chemistry on microbiome assembly. *A. thaliana* mutants disrupted in the ABC transporter *abcg30* (*Atpdr2*) showed increased exudation of phenolics, decreased secretion of sugars, and a less diverse bacterial community (3). The authors hypothesized that these changes in exudation led to a more specialized community able to resist or degrade the phenolic compounds enriched in the exudates of *abcg30* plants. Also for poplar, accumulation of phenolic compounds in seedlings silenced in cinnamoyl-CoA reductase (CCR) led to distinct community structure and functions of the endosphere microbiome (7). In a recent study, Stringlis et al. (117) revealed the involvement of the root-specific transcription factor MYB72 of *A. thaliana* in the excretion of the coumarin scopoletin, an iron-mobilizing phenolic compound with antimicrobial activity. By coupling microbiome and root exudate analyses of wild-type and mutant plants, the authors nicely demonstrated the impact of scopoletin on root microbiome assembly. Intriguingly, Hu et al. (53) revealed that indole-derived benzoxazinoids (BXs) released by maize roots in the surrounding soil can even influence the microbiome composition of the next generation of maize plants growing in the same soil. The authors highlighted that BX-mediated alteration of the root microbiome composition in a BX-deficient maize mutant affected plant growth and resistance against insect herbivores aboveground.

2.4. Stress-Induced Microbiome Assembly

Plants are able to recruit (micro)organisms that alleviate biotic stress both above- and belowground (29, 124). One of the first hallmark studies on "cry for help" belowground was carried out by Rasmann et al. (103), who showed that maize roots damaged by insects emit the volatile compound (E)-β-caryophyllene, which attracts entomopathogenic nematodes. Since then, several other studies have described changes in root microbiome composition upon insect (63, 68, 145) and pathogen (5, 113) attack. Rudrappa et al. (107) showed that *A. thaliana* leaf infections by *Pseudomonas syringae* pv. tomato (Pst) induced root exudation of malic acid that selectively recruited the beneficial *Bacillus subtilis* strain FB17. The higher malic acid concentrations stimulated attachment

of this rhizobacterium to the plant roots, followed by biofilm formation. In a recent study, leaf infection of *A. thaliana* by Pst also led to higher amounts of amino acids and long-chain organic acids (LCOAs) but lower amounts of sugars and short-chain organic acids (SCOAs) compared to noninfected plants (147). The authors further showed that plants grown in soil containing a mixture of LCOAs and amino acids or in soils successively cultivated with Pst-infected plants displayed significantly lower disease incidence. Using a split-root bioassay, Jousset et al. (55) revealed that infection of barley roots by the oomycete pathogen *Pythium ultimum* led to enhanced exudation of vanillic, p-coumaric, and fumaric acids in noninfected parts of the root system. These exudates did not adversely affect the growth of the pathogen directly but increased the expression of *phlA*, a gene involved in the biosynthesis of the antifungal compound 2,4-diacetylphloroglucinol (2,4-DAPG) by *Pseudomonas fluorescens*. Among the plant exudates, the BXs have been long implicated in direct plant defense against pests and diseases above- and belowground (141). In addition, particular attention has been given to the effects of 2,4-dihydroxy-7-methoxy-2H-1,4-benzoxazin-3(4H)-one (DIMBOA) released by maize roots on chemotaxis by the beneficial *Pseudomonas putida* strain KT2440 (89). Root colonization by this strain further primed hormone-mediated defense mechanisms in wild-type maize but not in BX-deficient mutants (89). Collectively these studies suggest that the root microbiome of plants changes upon infections above- and belowground, leading to enrichment or activation of specific beneficial microorganisms and microbial traits, presumably to assist plants to counteract subsequent infections.

The enrichment of protective root-associated microorganisms following infections has been well documented for soils that are suppressive to soilborne plant pathogenic fungi, oomycetes, bacteria, and nematodes (41, 111). Soil physicochemical properties can modulate the onset and extent of disease suppressiveness, but the suppression that operates in suppressive soils is in most cases microbiological in nature (41). For example, taxonomic analyses of the rhizosphere of sugar beet seedlings grown in a soil suppressive to the fungal root pathogen *Rhizoctonia solani* revealed several bacterial genera that were consistently associated with the disease-suppressive state (84). When plant roots were challenged with the fungal pathogen, stress-related genes were upregulated in bacterial families that were significantly more abundant on roots of plants grown in the suppressive soil (24). Based on these findings, the authors postulated that the invading fungal pathogen triggers, directly or via the plant, stress responses in the rhizosphere microbiome that in turn lead to compositional shifts and activation of specific antagonistic traits that restrict pathogen infection (24). Subsequent isolations and functional analyses of specific bacterial genera from the *Rhizoctonia*-suppressive soil showed that *Pseudomonas corrugata*–like species hinder pathogen infection via the production of the chlorinated nine–amino acid lipopeptide thanamycin (84, 126, 135). Strikingly similar results were found for *Pseudomonas* species isolated from a Greenland soil suppressive to potato scab caused by *R. solani* (86). Also, *Streptomyces* and *Burkholderia* species were shown to contribute to *Rhizoctonia* suppressiveness via the production of specific antifungal volatiles (20, 26). *Streptomyces* species have also been described to have a critical role in a *Fusarium*-suppressive soil via the production of the thiopeptide conprimycin and the class II lantipeptide grisin (22, 57). Collectively, these studies highlight the importance of microbial metabolites in stress-induced microbiome assembly and plant protection.

3. A WALK ON THE WILD SIDE: IMPACT OF DOMESTICATION ON MICROBIOME ASSEMBLY

Plant domestication and the agricultural revolution provided a more continuous food supply to early human hunter-gatherers and were key drivers of stable human settlements (99). Domestication was accompanied by progressive changes in the habitat and crop management practices to

promote high yields and protect plants against (a)biotic stress (96). Plant phenotypic modifications associated with the domestication process include larger seed size, loss of dispersal mechanisms, and determinate growth (11, 48). Domestication not only altered phenotypic traits but also reduced plant genetic diversity. How this so-called domestication syndrome (31) affects the plant microbiome is currently being addressed for several plant species to obtain insights into potential mechanisms underlying microbiome assembly and activity. The initial studies focused on differences between ancestors, landraces, and modern crop genotypes to sustain symbiosis with mycorrhizae and nitrogen-fixing rhizobia (reviewed in 96). For example, pea and broad bean were less able to interact with symbionts than their wild relatives (88). Kiers et al. (56) showed that newer cultivars of soybean had lower seed yields as compared to older cultivars and also that the yield difference ratio (i.e., the ability of cultivars to reach their full symbiotic potential in the presence of mixed rhizobial strains) was higher for older than for newer cultivars. Extending beyond symbiotic root-associated microorganisms, Zachow et al. (148) revealed that wild sugar beet plants (*Beta vulgaris* ssp. *maritima*) grown in soil collected from their natural habitat harbored a more diverse rhizosphere community than modern cultivars. Similarly, Coleman-Derr et al. (25) observed lower bacterial and fungal diversity in the rhizosphere and phyllosphere of cultivated *Agave tequilana* than of the native species *Agave salmiana* and *Agave deserti*. For barley, Bulgarelli et al. (17) showed a significant domestication effect on the diversity of root-associated bacterial communities. Opposite results were obtained by Cardinale et al. (19) for *Lactuca sativa* cultivars and the wild ancestor *Lactuca serriola* and by Leff et al. (69) for sunflower. In a later study, they observed no effect of the sunflower genotype on rhizobacterial microbiome assembly (69). Instead, a domestication effect was observed for the fungal rhizosphere microbiome with unclassified *Chaetomiaceae*, *Olpidium*, and *Mortierella* at higher relative abundances on roots of wild sunflower while modern sunflower accessions had higher relative abundances of *Pleosporales*, *Preussia*, unclassified *Thelebolaceae*, *Fusarium*, and *Conocybe* species. In most of these studies, the mechanisms involved in differences in community structure between wild relatives and domesticated cultivars are not yet fully understood. Pérez-Jaramillo et al. (94) revealed significant correlations between the rhizosphere microbiome composition and root architectural traits of domesticated and wild common bean accessions. Also, in an earlier work by Szoboszlay et al. (118), a higher number of very fine and thick roots were observed for teosinte, the wild ancestor of maize, than for the domesticated maize cultivars. How these changes in root architecture affect microbiome composition was not investigated in these studies.

Although our knowledge of the impact of plant domestication on the microbiome is still fragmented, several bacterial taxa appear to be consistently associated with roots of wild plant relatives. In particular, members of the *Bacteroidetes* were found at higher relative abundances in the rhizosphere of wild plant species and wild crop relatives, whereas *Actinobacteria* and *Proteobacteria* were more abundant on roots of the domesticated accessions (95). Pérez-Jaramillo et al. (95) postulated that the enrichment of *Bacteroidetes* on roots of wild relatives may be due to their ability to degrade complex biopolymers available in the root exudates. Whether a higher abundance of *Bacteroidetes* on plant roots affects plant fitness and health remains to be investigated. Most studies to date have also pointed to a lower microbial diversity in domesticated plants, but it is not yet known whether the missing or depleted plant microbes constitute a functionally important component of the microbiome of wild plants in their native habitats. The concept of missing microbes was first introduced by Blaser (12) for the human microbiome, where antibiotic overuse and modern lifestyle are proposed to have caused a loss of several members of the gut microbiota. Whether the same principle applies to the plant microbiome is still controversial. Plant domestication is accompanied by progressive habitat changes and overuse of pesticides and fertilizers to promote high yields and to protect domesticated crops from biotic and abiotic stress factors (96) (**Figure 1**). Hence, the

Landrace: Dynamic population(s) of a cultivated plant that has historical origin and is locally adapted to traditional farming systems

Symbiotic potential: the ability of a microorganism to engage in symbiosis with its host plant

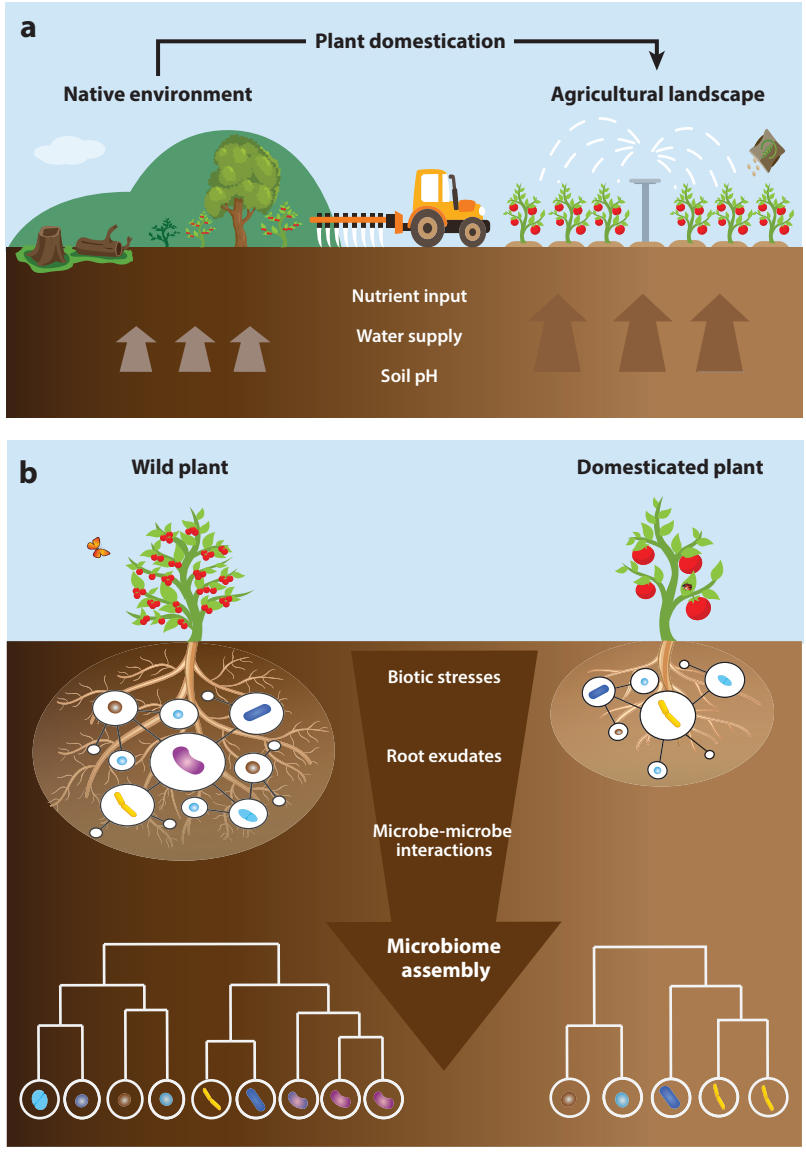

Figure 1

Impact of plant domestication on plant microbiome assembly. (*a*) During domestication, management practices drastically changed soil chemical and physical properties (e.g., nutrients, water, pH), which altered soil microbiome composition and functions. Plants were moved from their native habitat to agricultural soils, where they were bred for higher yields and resistance against biotic and abiotic stresses. (*b*) The plant phenotypic and genotypic changes impact root morphological traits and exudation, which in turn influence microbiome assembly. Domesticated plants may harbor fewer associations with symbionts and less diverse microbial communities than their wild relatives. In addition to these allogenic factors that impact microbiome assembly, competition and cooperation between microorganisms, biotic stresses (above- and belowground), and plant development also determine rhizosphere microbiome assembly.

transition from native habitats to agricultural soils may have led to a depletion of coevolved beneficial microorganisms and functions. For example, long-term nitrogen fertilization resulted in the evolution of less-mutualistic rhizobia (136) and suppressed soil respiration and microbial biomass, promoting copiotrophs such as *Actinobacteria* and *Firmicutes* while reducing the abundance of oligotrophs such as *Acidobacteria* and *Verrucomicrobia* (102). It has also been shown that the occurrence of *Bacteroidetes*, known for the degradation of complex organic matter, is negatively affected by agricultural management practices (140). Some recent studies, however, point to an opposite direction, i.e., that through plant domestication and resistance breeding, plant breeders may have unintentionally co-selected for plant traits that support microorganisms that protect plants from infections (83). Therefore, adopting the back-to-the-roots approach (96), where the microbiome of indigenous plants and their native habitats are explored for the identification of complementary plant and microbial traits, holds the potential to unravel the mechanisms involved in microbiome assembly and to integrate microbiome research into future plant breeding strategies.

4. INTEGRATING COMMUNITY ECOLOGY IN PLANT MICROBIOME RESEARCH

Most microbiome studies to date attempt to address the questions of who is there; what are they doing, when and where; and which microbial consortia respond to and confer tolerance to a particular (a)biotic stress. We propose that future efforts in plant microbiome research should also be directed toward understanding how well-defined ecological processes govern plant microbiome assembly and functionality. Ecological theory, including a recent conceptual synthesis in community ecology (130, 131), and metacommunity theory (71), offers the theoretical foundation for studying plant-associated microbiomes (**Figure 2**). In his monograph "The Theory of Ecological Communities," Vellend (131) proposed that any given ecological community is structured by an interplay of four main ecoevolutionary processes, two of which are responsible for the input of organisms within a community context, i.e., dispersal and diversification, and two of which regulate species relative abundances, i.e., selection and drift. An optimum appreciation of Vellend's theory can be achieved by considering the importance of metacommunity theory (71), which integrates local- and broad (regional)-scale processes that influence community assembly. Metacommunity theory assumes that a given community structure (e.g., rhizosphere/phyllosphere/endosphere microbiomes) is a result of specific processes that occur within the local community, i.e., biotic interactions and/or abiotic constraints, and the process of dispersal that links communities (71). Moreover, metacommunity theory explicitly considers that static snapshots of plant microbiomes are not solely results of processes that operate at a local scale at a given point in time. But, instead, the microbiome structure emerges as a result of multiple-scale processes that dynamically interact in the system and that collectively account for the community historical contingency, i.e., the effect of the order and timing of past events on community assembly (37). In the following sections, we describe how plant microbiome assembly and dynamics can be viewed in light of the aforementioned four processes of community assembly. We do not discuss the quantitative methodological aspects, as they have been recently reviewed (150).

4.1. Dispersal

Dispersal: the movement of individuals across environments

Perhaps the most notable illustration of the importance of dispersal in plant microbiome assembly and functionality was recently provided by Niu et al. (91). By studying the role of the root microbiome in protecting maize plants against the pathogenic fungus *Fusarium verticillioides*, they narrowed down the complexity of the microbiome composition to a simplified consortium

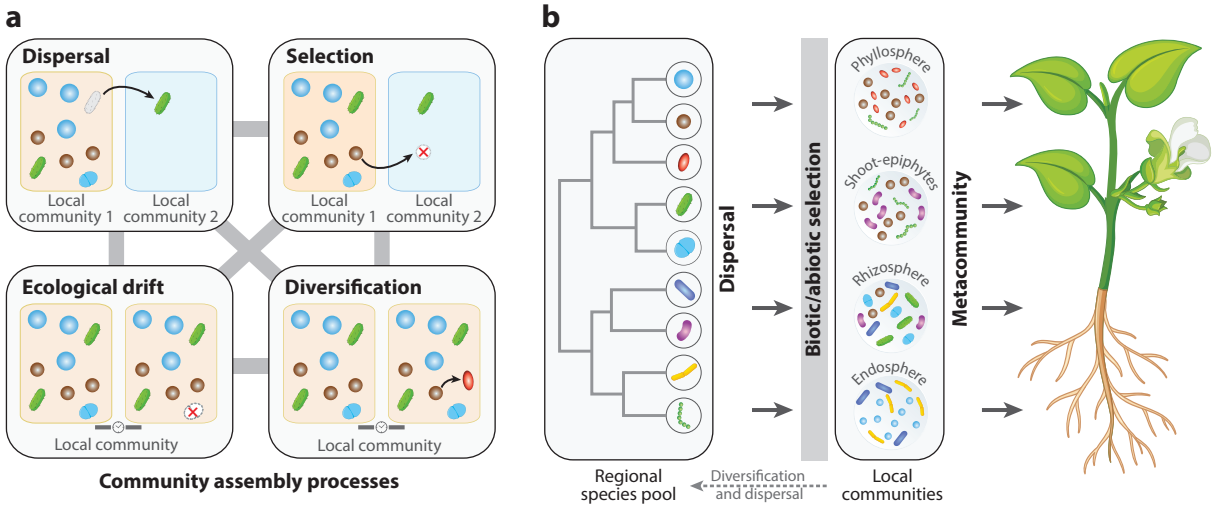

Figure 2

Ecological processes involved in plant microbiome assembly. (*a*) Details of how the four ecoevolutionary processes structure community assembly. Dispersal is illustrated as the movement of microorganisms between local communities. Selection is shown here as the result of abiotic conditions affecting the establishment of a microorganism within a community. Ecological drift is the result of stochastic changes in population sizes that, in this case, resulted in the extinction of a particular microbial taxon. Diversification is the process that generates genetic variation, here illustrated within a local community. The X symbols indicate unsuccessful establishment or organismal removal. (*b*) A general scheme of the interactions between the regional species pool and the metacommunity. Local communities are initially colonized by dispersal from the regional species pool and biotic/abiotic selection. This in turn leads to the assembly of distinct local communities (collectively called a metacommunity). Eventually, diversification that takes place in the metacommunity can enrich the diversity of the regional species pool through dispersal (*dashed arrow*).

consisting of only seven bacterial strains. They elegantly showed that not only the composition of this simplified microbiome consortium matters but also the order by which each individual strain was introduced onto the plant surface. This notion of how orderly microbial individual taxa arrive in the system and how the individual taxa exert lasting impacts on the diversity, composition, and function of communities is referred to as priority effects. Priority effects can operate via facilitation of inhibition, through mechanisms known as niche preemption (i.e., early colonizing species depleting resources) and/or niche modification (i.e., early colonizing species physically/chemically modifying the local niche) (37). Toju et al. (120) recently used priority effects and mechanisms to develop new lines of research strategies aiming at optimizing microbiome functions in agroecosystems. In brief, they theoretically enumerated how predefined core taxonomic units in early stages of plant development can be used to engineer and manipulate the dynamics of soil and plant-associated microbiomes.

Given the small size, high abundance, and relatively short generation time of most microorganisms, dispersal is notoriously difficult to directly quantify in microbial systems. However, as illustrated above, dispersal is a process that can be easily manipulated through controlled experimentation. To further illustrate its importance, Toju et al. (120) manipulated the dominance of particular microbial taxa (i.e., *Neokomagataea* bacteria and *Metschnikowia* yeasts) in nectar microbial communities in field settings. They reported distinct priority effects and showed that their respective influences on microbiome assembly persisted over multiple floral generations. In an earlier study, Adame-Alvarez et al. (1) showed that endophytic colonization by diverse fungal strains was able to protect bean plants when these were later exposed to the bacterial pathogen *P. syringae*

pv. syringae. However, no protection by the endophytic fungal consortium was observed when plants were exposed to the bacterial pathogen first. In another study on the association of *Medicago truncatula* with two distinct species of arbuscular mycorrhizal fungi (AMF), Werner & Kiers (139) advocated the importance of priority effects for AMF inoculation of seedlings. The authors highlighted that the strengths of these effects on AMF seem to be dependent on the length of the head start, and their persistence is likely associated with the composition and abundance of indigenous AMF.

Selection: environmental selection is the result of biotic and abiotic effects causing fitness differences across individuals or species

Ecological drift: random changes in population sizes via stochastic birth and death events that occur irrespective of species identity

4.2. Selection

Selection has been predominantly used in plant microbiome studies to explain patterns in assembly (e.g., selection by plant genotype, exudation profile, developmental stage, stress; see above). Conceptually, environmental selection is defined as the result of biotic and abiotic effects causing fitness differences across individuals or species. In line with this definition, it is important to consider that at least a fraction of the microbial taxa in plant microbiomes may not be assembled as a direct outcome of selection. This occurs because selection needs time to structure microbial abundances toward a stable state. It is possible that in the plant microbiome, both above- and belowground fractions are constantly exposed to environmental changes such as those imposed by agricultural practices (e.g., ploughing, irrigation) and variations in climatic conditions (e.g., UV radiation, temperature, wind, rain). These disturbances exert different selective impacts on the plant microbiome and also contribute to the passive dispersal of microbial taxa. If dispersal is high, the distinct local communities in the soil and plant microbiomes can be homogenized, thus weakening the effect of selection. Second, as selection operates by filtering out less fit viable taxa, microorganisms that are able to enter a stable state of dormancy [a common trait observed in soil microorganisms, albeit not yet investigated for the plant microbiome (72)], can bypass environmentally imposed selection. As a result, these taxa can indiscriminately persist within a local community even under inhospitable/harsh environmental conditions without being affected by selection.

4.3. Ecological Drift

The effect of ecological drift on community assembly is pronounced under conditions where selection is weak and overall population size and diversity are low. Because low abundant taxa are more prone to going extinct (90, 131), it is possible to envision the importance of drift for plant microbiome assembly, in particular for the endosphere and phyllosphere. Endophytic microbial communities are known to have relatively lower cell densities and diversity than those found in the rhizosphere, and their establishment largely depends on the plant physiological status and developmental stage (see above). In addition, despite some microorganisms successfully colonizing the endophytic compartment through the course of plant development, this effect of dispersal or internalization often occurs at relatively low cell densities and by a small fraction of the overall root-associated microbial taxa. As such, it is likely that drift can play an important role in structuring the endophytic community, alongside priority effects imposed by early colonizing species. Microbial colonization in the phyllosphere occurs in scattered patches (or aggregates), often in surface depressions formed at the junctions of epidermal cells (123, 132). Interestingly, the assembly of the phyllosphere microbiome is largely dependent on passive dispersal, which occurs through the action of rain, wind, or insects (73, 75). The combined effects of continuous dispersal with daily exposure to environmental stresses (e.g., UV radiation, highly fluctuating water availability) can likely result in a differential impact on population sizes and, as a result, increase the relative influence of ecological drift.

4.4. Diversification

Diversification: generation of new genetic variation in a population

Diversification is perhaps the most neglected process structuring the plant microbiome. This is due to our limited understanding of how scales influence microbial diversification, and how to study this process empirically at the community level. Diversification is often used to study adaptive mechanisms that confer beneficial traits to a particular population that colonizes and thrives in a given plant compartment. For example, distinct epiphytic strains affiliated with *P. syringae* have been reported to endow UV tolerance through UV-inducible plasmid-borne *rulAB* genes, which are known to confer DNA repair (58). These genes provide a critical adaptive trait on plasmids, and their maintenance likely represent an important mechanism by which endophytes evolve and diversify in the phyllosphere (77). In addition, diversification has also been used to explain streamlined cells and their small genome sizes. Streamlining refers more generally to diversification imposed by selection that favors the shrinking of cell sizes and complexity, particularly in nutrient-poor environments. This occurs because reducing metabolic costs increases fitness and evolutionary success once the local environmental selection is homogeneous or lifted (40). Genome diversification and streamlining are prone to occur in microbial taxa strictly inhabiting the plant endosphere, for instance, through coevolutionary dynamics (30, 81, 97). Particularly for plant endophytes, mounting evidence has supported the role of diversification in shaping genome evolution and architecture that further result in significant changes in organismal lifestyles (43, 60, 74, 143). To illustrate that, Xu et al. (143) highlighted the roles of both internal genetic mechanisms (e.g., gain or loss of function, DNA duplications, transposable elements) and external factors (i.e., interaction with the host plant responses) in shaping the evolutionary transition of the fungus *Harpophora oryzae* from a strict plant pathogen to a mutualistic endophyte.

It is also important to note that diversification that takes place in the bulk soil might account for the genetic variation reflected in the plant microbiome. In this context, a recent perspective article discussed the potential role of soil aggregates as evolutionary incubators for microbial taxa (105). If that is the case, not only intimate associations between the host plant and particular microbial taxa can lead to coevolution, but also the ongoing diversification processes that take place in the microbial seed bank pool account for evolutionary dynamics in the system. Here, it is possible to assume that microbial dormancy might play an important role in imposing variation in evolutionary rates over time. For instance, dormancy allows genetic variation to persist in an environment even by being decoupled from the recent community history and local selective pressure. As a result, dormancy increases the genetic diversity within community members, which can ultimately influence evolutionary processes. Moreover, microorganisms can rapidly evolve through horizontal gene transfer (HGT). This also characterizes a trait that can decouple evolution and time. For example, Pinto-Carbó et al. (97) illustrated the role of HGT in leaf-nodulating *Burkholderia*, in which the acquisition of key secondary metabolisms allows a relatively short-time-scale transition of this bacterium from a facultative/commensal lifestyle toward obligate symbiont. Last, it is important to emphasize that some specific bacterial taxa can rapidly generate genetic diversity in biofilms, particularly when exposed to inhospitable conditions. This occurs through a combined effect of mutation and HGT, with direct implications on evolutionary rates (14).

5. CONCLUDING REMARKS AND FUTURE PERSPECTIVES

Despite the increasing recognition of the importance of the microbiome for plant growth and health, harnessing its genomic potential as a new platform for improved stress resilience of future crop production in a changing climate is one of the greatest challenges for the coming decade. To this end, we need a fundamental understanding of (*a*) plant traits and mechanisms involved in

recruitment and activation of their microbial partners and (*b*) the biosynthesis and regulation of microbial traits that confer improved plant growth and stress resilience/resistance. Understanding and engineering microbiome assembly and activity require diverse complementary approaches, including mathematics, ecology, modelling, high-throughput plant phenotyping, microbiology, and molecular biology to identify the functional basis of beneficial interactions at the molecular and (bio)chemical levels in both plants and microbes. Several strategies have been proposed to optimize plant microbiome composition and functionality. In particular, the design of assemblages of different microorganisms with complementary or synergistic traits has been advocated to provide a more effective and consistent effect on plant growth and health. Examples of effective microbial consortia are presented in the study by Santhanam et al. (108) on protection of *Nicotiana attenuata* against sudden-wilt disease, in the study by Niu et al. (91) on protection of maize against *Fusarium verticillioides*, and in the study by Berendsen et al. (8), where a consortium of three bacterial species promoted growth and induced systemic resistance of *A. thaliana.* Also, the recent work of Herrera Paredes et al. (51) nicely showed that, in the context of alleviating phosphorus starvation of *A. thaliana*, studying a subset of bacterial communities is sufficient to anticipate the outcome of novel combinations. This study indicated that it is possible to deduce causality between microbiome composition and host phenotypes in complex systems.

The concept of so-called reconstructed microbiomes or SynComs is gaining momentum, but to find or select the right players of a consortium requires in-depth understanding of the network formed by the root microbiome, the underlying communication, and traits. Several factors need to be considered when designing SynComs, including (*a*) division of labor among the consortium members, (*b*) their spatial and temporal organization, and (*c*) functional redundancy across genomes to minimize competition among consortium members for specific resources (76, 133). In this context, Poudel et al. (98) developed a framework for the interpretation of microbiome networks, illustrating how network structures could be used to generate testable SynComs that affect plant growth or health. Briefly, this framework included four types of network analyses (98): General network analysis identifies candidate or keystone taxa for maintaining an existing microbial community; host-focused analysis includes a node representing a plant response such as yield, identifying taxa with direct or indirect associations with that node; pathogen-focused analysis identifies taxa with direct or indirect associations with taxa known a priori as pathogens; and disease-focused analysis identifies taxa associated with disease (positive or negative associations with desirable or undesirable outcomes).

In most plant microbiome studies to date, however, there is a lack of evidence for the contribution of the microbiome to a particular plant phenotype. Therefore, Oyserman et al. (92) proposed the so-called microbiome-associated plant phenotypes (MAPs)-first approach, a theoretical and experimental roadmap that involves quantitative profiling of MAPs across genetically variable hosts first before assessing the microbiome composition and functions. Once a particular plant phenotype has been associated with a particular subset of the microbiome, it will be feasible to develop modular microbiomes—microbial consortia that are engineered in concert with the host genotype to confer different but mutually compatible MAPs to a single host or host population (92). Besides designing modular microbiomes, other exciting new avenues can be taken to harness the functional potential of microbiomes for plant growth and health. These include (*a*) strain improvement via experimental evolution, (*b*) optimization of the host plant by genotype selection or by genetic modification for specific root traits (e.g., exudation, architecture) that maximize microbial recruitment and plant beneficial activity, and (*c*) synbiotics, which involve the combination of a beneficial microbial strain or consortium with specific substrates that selectively stimulate their growth, colonization, and beneficial activities. With this latter strategy, it may be possible to engineer the microenvironment of seeds, roots, or leaves at prescribed times and with well-defined

rates to ensure functionality of introduced microbial strains or to activate indigenous beneficial microbial consortia for a particular plant phenotype.

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3. Pioneering work on the impact of changes in rhizosphere chemistry on microbiome assembly.

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