Functional Ecology

British Ecological Society

Functional Ecology 2016, **30**, 1043–1052 doi: 10.1111/1365-2435.12684

ECOSYSTEMS, EVOLUTION AND PLANT–SOIL FEEDBACKS

Giving back to the community: microbial mechanisms of plant–soil interactions

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Summary

1. The role of both plants and soil microbes on ecosystem functioning has been long recognized, but the precise feedback mechanisms between them are more elusive. Definition of these interactions is critical if we aim to achieve an integral understanding of ecosystem functioning, and ultimately explain natural, agricultural and synthetic systems.

2. Advances in genomic technologies and the development of more appropriate statistical, mathematical and computational frameworks enable researchers to almost fully describe and measure the diversity of microbial communities in soil, rhizosphere and plant tissues. Under the scaffold of community ecology, we integrate the observed patterns of microbial diversity with current mechanistic understanding of plant–microbe mutualistic and pathogenic interactions, and propose a model in which plant microbial communities are shaped by different ecological forces differentially through the plant life cycle.

3. The same genomic technologies, applied on natural and reconstructed systems, establish that plant genotype has a small, but significant, effect on the microbial community composition in, on and around plant organs. Despite these advances, technical limitations are still important and only a handful of studies exist where a precise genetic element definitively participates in these interactions.

4. Studies at the field or ecosystem level are dominated by agricultural settings, examining microbial species and communities effects on plant productivity; and conversely, that plant genetics and agricultural practices can potentially impose selective pressures on specific microbes and microbial communities.

5. Revitalized interest in plant–soil microbial feedbacks requires researchers to systematically pose and evaluate more complex hypotheses with increasingly more realistic microbial settings. Despite the advances reviewed here, most studies focus on one aspect of plant, microbe and soil interactions. Experiments that simultaneously and methodically manipulate multiple components are necessary to establish the ecological principles, and molecular mechanisms, which drive microbially mediated plant–soil interactions. This knowledge will be critical to predict how environmental changes affect microbial and plant diversity, and will guide efforts to improve agricultural and conservation practices.

Key-words: community assembly, plant microbiome, plant productivity

Introduction

Microbes possess a profound aptitude for altering their environments with their contributions impacting nutrient cycling in their environment from the local to the global scale (Rousk & Bengtson 2014). Hence, there is strong evidence that multiple microbial factors affect both plant phenotypes and ultimately genotypes through their impact on the environment (Van Nuland *et al.* 2016). The microbial metabolism responsible for these changes occurs either directly on the environment or within the context of a host, such as a plant (Bulgarelli *et al.* 2013; Rousk &

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Bengtson 2014). The resulting association between plants and microbial communities is often beneficial for the plant, promoting growth and protecting from stress, which is relevant both in the context of natural ecosystems and agricultural settings. While the microbes that colonize above-ground plant organs (i.e. phyllosphere) might be derived from a variety of sources (Vorholt 2012) below-ground, root microbiomes likely form from the incredibly diverse microbial communities in the surrounding soil (Bulgarelli *et al.* 2013). Unfortunately, growing evidence suggests that agricultural practices and climate changes will negatively impact soil biodiversity (Wagg *et al.* 2014), thereby decreasing the types of microbes available for assembly into both the epiphytic and endophytic microenvironments. Here, we review and discuss the current knowledge of plant–soil microbially mediated interactions, and the impact of improved genomic technologies on our ability to understand how these relationships impact plant performance, potentially allowing us to sustainably improve plant productivity.

Plant and rhizosphere microbial diversity throughout the plant life cycle

Plants harbour complex microbial communities inside and on every organ; their assembly depends on, among other factors, the microbial species found in the surroundings. While root and leaf communities are readily distinguishable from the surrounding soil and air communities (Bulgarelli *et al.* 2012; Lundberg *et al.* 2012; Maignien *et al.* 2014), differences in microbial composition and diversity exist between plant organs, developmental stages, plant genotypes and environments (Bulgarelli *et al.* 2013). Such differences can be explained as the result of ecological processes acting on the microbial communities. Under the theoretical framework of community ecology, the factors influencing the composition and diversity of any community can be classified into four general processes: selection, dispersal, drift and speciation (Vellend 2010; Costello *et al.* 2012) (Fig. 1). While selection and drift decrease diversity, dispersal and speciation increase diversity, and the relative contributions and interactions between these processes determine the final community assembly. Full understanding of plant–soil microbial interactions requires the knowledge of how each of these processes influences the microbial community of both plant and soil, and how these communities affect the same processes on each other over the course of the plants' life cycle and over generations of plants and microbes within an environment.

For the majority of plants, their life cycle begins with a seed, which must be dispersed from its parent. While seed dispersal is an important ecological process for the plants, its role on microbial dissemination is poorly understood. Seeds carry within them, associated microbes from their environment and parent of origin, thereby increasing the microbial diversity in their new environment (Fig. 1). Both theory and experimental data predict that the more

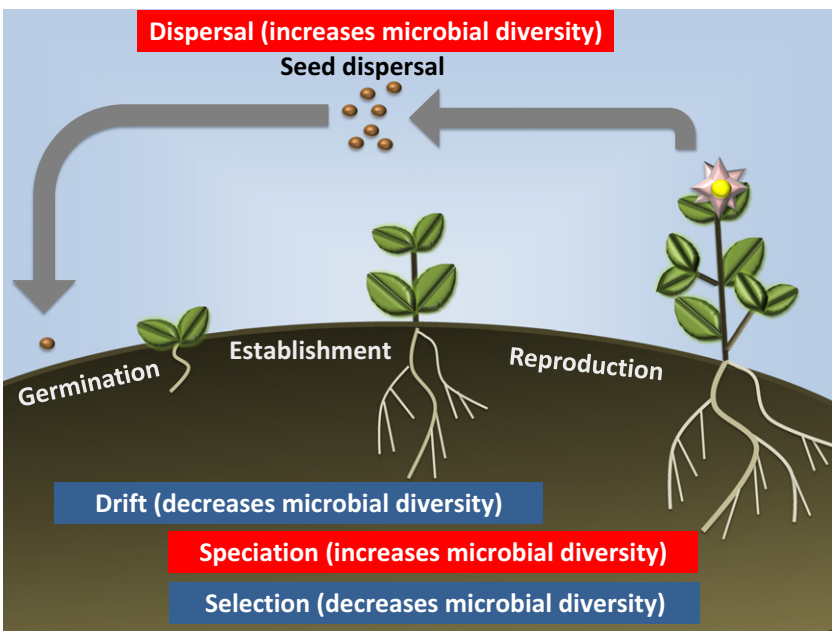

Fig. 1. Plant microbiome assembly. There is evidence for four general ecological processes to occur during the plant life cycle: dispersal, drift, speciation and selection. Microbes hitchhike in and on seeds during dispersal, effectively coupling plant and microbial dissemination and increasing diversity. This process can spread both pathogens and beneficial microbes. During germination and seedling emergence, drift becomes increasingly important; together with selection, they counteract and outweigh the effect of dispersal leading to decreased diversity in plant organs relative to the surrounding soil. The three processes continue to exert the effects in the later stages of plant development, together with microbial speciation, which might occur in any tissue after the initial colonization of communities and coupled with selection, can lead to co-evolution of plants and microbial communities (Van Nuland *et al.* 2016).

efficient the vertical transmission of a particular microbe, the stronger the tie of that microbe with plant fitness due to negative selection against virulence (Kover, Dolan & Clay 1997; Stewart, Logsdon & Kelley 2005; Pagán *et al.* 2014). Because of this, it should be expected that the microbes carried by seeds be strongly subject to (ecological) selection by the plant, and therefore more likely beneficial. While no study has systematically determined whether seedborne microbes are enriched in plant beneficial functions, there is long-standing evidence for seed-based dispersal of nodule-forming rhizobia in legume seeds (Ash & Allen 1948). More recent studies suggest the existence of surprising microbial diversity inside the seeds of maize (Johnston-Monje & Raizada 2011) and spinach (Lopez-Velasco *et al.* 2013), although they lack functional tests of those microbes. A single study profiling the fungal and bacterial seed epiphytic communities in several species of *Triticum* and *Brassica* also found a largely conserved set of micro-organisms across both genera, hinting at bacteria–fungus antagonism as an important process in determining the microbial community composition (Links *et al.* 2014). Besides these observational studies, experimental manipulation of seed epiphytes has shown that bacterial seed coatings can protect against pathogens (Wright *et al.* 2005; Hartmann *et al.* 2009) and promote plant growth (Jetiyanon, 2008). Because microbial seed epiphytes are thought to have an advantage over soil bacteria during plant colonization, seed coating methods for economically important crops are a major area of research and development with numerous patents being filed (~4000 results for 'microbial seed coating' on Google patent search), and major investment by biotechnology companies (Smith 2014). Seeds can also harbour bacterial (Gitaitis & Walcott 2007), fungal (Biswas *et al.* 2013; Maruthachalam *et al.* 2013) and oomycete (Testen *et al.* 2013) pathogens. While it has been proposed that seed dispersal is a general mechanism to escape the high density of pathogens near parents in natural ecosystems (Harms *et al.* 2000), in the agricultural world seeds act as important vectors for hundreds of diseases, and most studies point to human activities being the major factor in spreading pathogen-bearing seeds (Elmer 2001). Understanding how seedborne pathogens interact with microbial communities in the plant and soil is an essential step towards better disease control.

Following seed dispersal, during plant germination, readily dispersed microbes might gain competitive advantage over microbes that attempt to colonize after germination. At the same time, opportunistic microbes from the surrounding soil might gain access to a novel niche as the plant develops. According to this model, early colonization is a highly stochastic process, dominated by dispersal and drift (Fig. 1), which leads to 'historically contingent' plant microbial communities where the early colonizers determine the final community, mediated by microbe–microbe interactions, or by plant mechanisms reinforcing the primacy of early colonizers (Costello *et al.* 2012). Evidence for this model exists in the context of the endophytic compartment of the weedy annual *Arabidopsis thaliana* roots and leaves. Drift may be particularly important given the estimates of a total of 10^5 endophytic bacterial cells per root system (Lundberg *et al.* 2012) and 10^4 cells cm^{-2} on the leaf of the same species (Maignien *et al.* 2014). Given that hundreds of bacterial ribotypes were detected on each organ, these results imply a relatively small population of only tens to hundreds of individuals per ribotype, which greatly favours the influence of drift over other processes, and it is consistent with the observed decrease in microbial diversity with respect to soil (Fig. 1). Importantly, the 'historically contingent' model is consistent with the huge individual-to-individual variation in microbial composition found in major sequence-based surveys of the microbiome of roots in diverse species (Bulgarelli *et al.* 2012; Lundberg *et al.* 2012; Peiffer *et al.* 2013; Edwards *et al.* 2015), and the somewhat smaller but also large variation found in leaves (Redford *et al.* 2010; Maignien *et al.* 2014). While there are no experimental or observational data about the microbial communities in plants that follow alternative propagation mechanisms (e.g. rhizomes, spores, stolons, bulbs, tubers, corm or cuttings, as well as horticultural practices such as grafting), the community ecology framework predicts that these plants, which have weaker dispersion, are expected to have reduced microbial diversity (Vellend 2010). Finally, it is also relevant to define how important the primacy of early colonizers is for plants with annual vs. perennial lifestyles.

While it is well-established that plants can influence the chemical and microbial composition of the rhizosphere, which is the soil area under the root's influence, little is known about how this effect changes through plant development because most studies focus at later developmental stages, when the root system is firmly established. However, time course experiments in rice determined that the relative abundance of core bacterial taxa from inside the root peaks in the rhizosphere just 3 days after transplantation (Edwards *et al.* 2015), suggesting that plants may influence the rhizosphere microbial community very early after seedling emergence. Consistently, profiling of the bacterial and fungal communities of seedlings of the Brassicaceae family shortly after emergence shows a decrease in microbial richness, consistent with plant selection and drift happening very early (Barret *et al.* 2015). Despite these advances, a more systematic evaluation of early time points is still necessary to evaluate the effect of pre-emergence conditions, such as stratification, on microbial communities that colonize very young seedlings. The observation that the composition rhizosphere and rhizoplane bacterial communities are intermediate between that of bulk soil and those that live inside the roots (Bulgarelli *et al.* 2012; Lundberg *et al.* 2012; Peiffer *et al.* 2013; Edwards *et al.* 2015; Yeoh *et al.* 2015), has led to the hypothesis that the root microbiome is assembled in a stepwise process where microbes are first recruited to the rhizosphere and then colonize the root (Bulgarelli *et al.* 2012; Edwards *et al.* 2015). Under this working model, soil

micro-organisms that readily utilize the root exudates would have an advantage in colonizing the roots; however, this model lacks direct empirical testing so far. Another important observation is that soil bacterial composition is the major determinant of the bacterial root microbiome across a variety of plant species (Bulgarelli *et al*. 2012; Lundberg *et al*. 2012; Peiffer *et al*. 2013; Edwards *et al*. 2015; Yeoh *et al*. 2015). Interestingly, a similarly strong effect of soil has been reported for phyllosphere bacterial communities (Knief *et al*. 2010; Zarraonaindia *et al*. 2015), suggesting that a common environmental pool of microbes exists for both above- and below-ground plant organs.

Sequence-based studies indicate that the relative abundance of bacterial taxa stabilizes quickly, and it is relatively stable in roots (Edwards *et al*. 2015), but it is unknown whether this steady state is achieved through an isolation of the root microbiome from the surrounding soil, or through an equilibrium in the exchange rate of microbes between the rhizosphere and the plant. For microbes that are highly abundant or have very efficient dispersal, continual dispersal from the surrounding environment into the plant might counteract the effect of drift, as could selection to maintain them once they are established. While the current standard view is that strong colonizers both invade and persist within the plant host, the turnover rate of the plant microbiota has not been directly measured, and indirect sequence-based methods suggest that it is relatively high in above-ground organs (Redford & Fierer 2009; Shade, Mcmanus & Handelsman 2013). In any case, it is expected that during the 'establishment' phase, when the plant physiology is directed towards increasing plant biomass, the plants would achieve maximum benefit from positive associations. As such, theory predicts that the plant selection over its microbiome is the strongest during this phase (Fig. 1). The fact that reproducible enrichment of certain bacterial taxa is commonly found across diverse soils (Bulgarelli *et al*. 2012; Lundberg *et al*. 2012) and in various plant species (Schlaeppi *et al*. 2014; Yeoh *et al*. 2015) suggests that plant selection on the microbiome is stronger than ecological drift during this stage, even though it does not completely overtake the 'founders effect' that occurs during seed dispersion (Fig. 1).

Most carbon in soils is derived from plants, with individual plants releasing 5–21% of their photosynthetically fixed carbon through the roots (Marschner 1995), and global carbon release into the rhizosphere in the order of 1500–2200 kg C ha^{-1} $year^{-1}$ (Kuzyakov & Domanski 2000). The carbon released is a combination of active secretion of specific root exudates, and passive release of plant debris from both shoots and roots. This process creates a carbon-rich environment in the rhizosphere, while the surrounding bulk soils are considered to be carbon limited (Lambers *et al*. 2009); as a result, there is a higher density of bacterial cells in this region as compared to the soil, and a distinct bacterial taxonomic profile (Lu, Abraham & Conrad 2007; Bulgarelli *et al*. 2012; Lundberg *et al*. 2012; Peiffer *et al*. 2013; Edwards *et al*. 2015; Yeoh *et al*. 2015). Furthermore, stable isotope probing data indicate that carbon fixed by the plant via photosynthesis is directly incorporated by specific bacterial taxa in the rhizosphere (Hernández *et al*. 2015) and that this assimilation is dependent in close proximity to the root (Lu, Abraham & Conrad 2007).

As plants mature, the microbial communities in the root, leaves and rhizosphere may each reach its ecological climax. During this stage, plants reach their maximum photosynthesis rate (Makino, Mae & Ohira 1983) and focus their physiology into the accumulation of biomass. To achieve the maximum growth, plants must have access to enough bioavailable nitrogen and phosphorous. These two elements cannot be readily incorporated by plants from their most abundant sources, resulting in a number of exchange mechanisms between plant and microbes to access each of them. Nitrogen is the most common limiting nutrient in soils, and legumes have evolved a profound interaction with rhizobia (Wang *et al*. 2012). The exchange of specific molecular signals, plant-secreted flavonoids and rhizobia-secreted Nod factors, initiates a series of molecular responses in the other organism, leading to the formation of specialized organs in the roots called nodules, which accommodate the bacterial symbiont within the plant for nitrogen fixation, in exchange for carbon compounds (Wang *et al*. 2012). Recently, it has been observed that co-colonization of nodules by a number of other bacteria is under host genetic control (Zgadzaj *et al*. 2015), though the effect of these microbes on the legume–rhizobia symbiosis remains unknown. Other plants can form symbiotic relationships with Actinobacteria or Cyanobacteria through poorly understood molecular mechanisms (Franche, Lindström & Elmerich 2009). Although the majority of plants cannot form such tight associations with microbes, they might achieve the same success through indirect mechanism, for example through the 'microbial loop', which is a mechanism for plants to exploit predator–prey interactions ((reviewed in Bonkowski 2004)). Under this mechanism, the increased density of bacteria in the rhizosphere stimulates the activity of bacterial grazers such as protozoa and nematodes (Charholm 1985). Bacterial grazing then contributes with the excretion of one a large portion of the ingested nitrogen as ammonia, which can directly incorporated to plant or nitrified to nitrate by other bacteria before plant incorporation (Bonkowski 2004; Lambers *et al*. 2009).

After nitrogen, phosphorous is the most common limiting nutrient in soils (Schachtman, Reid & Ayling 1998). Most of the phosphorous in soil is in insoluble phosphate forms that cannot be used by plants. The vast majority of plants have overcome this limitation by evolving a mycorrhizal interaction. The most prevalent of these plant–fungus interactions is with arbuscular mycorrhizal fungi (AMF), which is estimated to interact with 80% of land plant species (Brundrett 2009) and is proposed to have

played a key role in land colonization by plants (Buscot 2015). Plants recruit AMFs by secreting compounds, such as strigolactones, that induce spore germination and hyphae formation (Schmitz & Harrison 2014). The AMF then forms a network of hyphae that is directly connected to the plant root and extends the reach and functional capacity of roots. The fungal partner solubilizes phosphate and then delivers it to the plant root, which in turn provides the fungus with a constant supply of carbon compounds (Smith & Smith 2012). The AMF hyphae not only extend the root capacity, but may also extend the rhizosphere effect. Interestingly, AMF harbours their own bacterial partners (Naumann, Schussler & Bonfante 2010; Desiro *et al*. 2014), although their effect on the root and soil bacterial communities, and on the carbon–phosphorous trade, has not been measured. Besides mycorrhizal fungi, many bacteria can also solubilize phosphate (Rodríguez & Fraga 1999), and it has been reported that, among cultivable bacteria, there is a higher proportion of phosphate-solubilizing bacteria in bulk soil than in plant tissue (Marasco *et al*. 2012). However, the importance of this process in the field is poorly understood, and inoculation of soils with phosphate-solubilizing bacteria has produced negligible differences in plant phosphate assimilation (Glick, 2012).

As plants age and enter the reproductive phase, there are substantial changes in metabolism and physiology that redirect carbon flux from the accumulation of biomass, and towards the production of reproductive organs during the sink-to-source transition (Jeong, 2004). However, in the fast-growing annual *A. thaliana*, little difference in root bacterial community was noted at two very different developmental states, before and well after the metabolic switch in carbon allocation (Lundberg *et al*. 2012). On the other hand, a finer time-scale demonstrated that different bacterial taxa preferentially colonize the apple flower at different developmental stages (Shade, Mcmanus & Handelsman 2013), suggesting that plant development may alter the selective mechanisms driving microbial succession. Further evidence for this has been found in a multiyear study of the leaf microbiome of deciduous trees where leaf age contributes more to community composition than experimental year (Redford & Fierer 2009). It is unknown how the differences in annual vs. perennial life histories influence the assembly and long-term stability of plant microbiota. To fully elucidate how the order of microbial colonization affects the plant microbiome, it would be necessary to carry out studies with time-series and crossover designs; this type of design has already been used to establish the existence of such 'order effects' in the context of colonization of the mammalian gut (Lee *et al*. 2013).

Finally, it is important to consider the possibility of co-evolution between soil and plant microbiota. Very little is known about the evolution of host-associated microbial communities, but recently, a neutral model that incorporates microbial acquisition from the environment and from vertical transmission under the Wright–Fisher genealogical model for hosts was developed (Zeng *et al*. 2015). A prediction from this model is that the least diverse microbiomes evolve from strong vertical transmission, but only a modest level of environmental contribution is required to generate high alpha diversity. While such neutral model is a useful baseline for comparison, more sophisticated models that incorporate non-neutral processes such as selection and speciation are required. It should also be appreciated that from the bacterial perspective, host colonization is a microevolutionary process, and so speciation and the processes behind it, like allopatry and resource partitioning, need to be considered. In this regard, other approaches focus on microbial dynamics and have exploited the generalized Lotka–Volterra system to identify conditions that favour community stability (Stein *et al*. 2013; Coyte, Schulter & Foster 2015). Ultimately, any theoretical framework that attempts to explain plant–soil microbially mediated feedbacks must incorporate the co-evolution of the soil, rhizosphere and host microbial communities instead of solely examining the host or microbial perspective (Van Nuland *et al*. 2016).

The genomic basis of plant–microbe interactions

To thrive in the plant tissue, a micro-organism must have the genetic determinants to access and invade at least one plant tissue and then, persist in the presence of a sophisticated immune system and a chemical composition distinct from the surrounding soil. Thus, it is expected that both plant and microbial genomes show evolutionary signatures relating to these interactions. Indeed, studies of *A. thaliana* (Bulgarelli *et al*. 2012; Lundberg *et al*. 2012) and maize (Peiffer *et al*. 2013) have shown a significant, if small, effect of the plant natural genotypes on the root microbiome with a stronger effect reported among barley cultivars (Bulgarelli *et al*. 2015). Moreover, it has been reported that there is a correlation between the phylogenetic distance and root microbiome dissimilarity in plants of the Brassicaceae (Schlaeppi, 2014) and Poaceae (Bouffaud *et al*. 2014) families. There is also evidence for plant genetic effects on the phyllosphere (i.e. aboveground) community. Poplar fungal leaf microbiome correlates with plant genotype in common garden experiments (Bálint *et al*. 2013), and a synthetic community approach with *A. thaliana* plants showed differences between accessions and comparison of mutants to wild-type plants pointed at a role for cuticle formation and ethylene signalling in shaping the phyllosphere microbiome (Bodenhausen, Horton & Bergelson 2013; Bodenhausen *et al*. 2014) and salicylic acid in root microbiome (Lebeis *et al*. 2015). Finally, a genome-wide association study in *A. thaliana* of fungal and bacterial leaf microbiome pointed at a number of plant loci that affect abundance of specific microbes and species richness; defence was the most common process associated with bacterial abundance but other processes such as cell wall integrity, trichome

branching and morphogenesis also affected the microbiome (Horton *et al*. 2014).

The emerging picture from the majority of studies is that plant loci have small and variable effects on the microbiome composition. A limitation of all of these studies is that they rely on profiling of a single marker gene to define the taxonomic composition of the plant microbiome, which means that these studies ignore the possibility that plants select at the functional, as opposed to taxonomic, level, especially if selection occurs primarily via exudation of compounds that stimulate specific microbial metabolic activities. In fact, it has been shown that bacterial strains that have the same 16S rRNA gene sequence can induce very different plant phenotypes (Blakney & Patten 2011; Haney *et al*. 2015; Timm *et al*. 2015). Importantly, these would be analogous to the observation in that the human gut microbiome has a remarkably stable functional profile despite the huge variation at the taxonomic level (Consortium, 2012). Equally important would be to extend the study of the role of plant genetic variation on the microbiome beyond the few model organisms that have been used so far. To test this hypothesis, it would be necessary to perform shotgun metagenome sequence on plant-associated microbial communities; however, the complexity of soil and technical difficulties in separating microbial- and plant-derived DNA from plant tissues have so far limited our ability to query the functional content and diversity of plant and rhizosphere microbial communities. Novel computational and experimental methods have been recently developed (Feehery *et al*. 2013; Howe *et al*. 2014) that may identify the microbial functions required for plant colonization. Despite these technical limitations, the rhizosphere metagenome has been compared between cucumber and wheat (Ofek-Lalzar *et al*. 2014), as well as among barley cultivars (Bulgarelli *et al*. 2015). Each of these studies found a signature of enriched bacterial functions in the rhizosphere although no overlap was seen between studies, possibly due to technical differences. An alternative approach to shotgun metagenomics is comparative genomics, which was used to determine that *Pseudomonas* isolates from different geographic regions are nearly isogenic to well-characterized beneficial bacteria, raising the possibility that their dispersion has been selected by the plants (Berendsen *et al*. 2015). Comparative genomics has also been used to investigate the phylogenetic distribution of bacterial genes that confer plant beneficial functions among Proteobacteria. The observed phylogenetic distributions demonstrated that plant beneficial bacteria commonly contain multiple beneficial genes, though there is no core set of plant beneficial genes, suggesting that these genes might be selected in plant-associated habitats and counterselected elsewhere (Bruto *et al*. 2014). While most comparative genomics approaches have focused on relatively narrow and well-defined bacterial clades with previously characterized functions, recent efforts to systematically sample the genomic diversity of plant-derived isolates (Bai *et al*. 2015) allow the differentiation between bacterial functions required to thrive in the plant environment, and bacterial functions that the plant may select because they provide a fitness advantage to the plant.

Studies conducted on the human gut microbiome linking disease states with different bacterial metabolic topologies (Greenblum, Turnbaugh & Borenstein 2012) suggest that microbe–microbe metabolic exchanges play a key role in structuring host-associated microbial communities. In the context of plants, correlations between bacterial, fungal and oomycete abundance were used to identify the potential keystone microbial species that drive interkingdom community assembly (Agler *et al*. 2016). Additional experiments are necessary to extend these results to the context and to demonstrate causality, in particular microcosm reconstitution experiments with complex, but well-defined, synthetic microbial communities where all the partners are well defined and tractable in isolation harness the power of reductionist science in a realistic setting. Importantly, this approach has successfully dissected the contribution of plant signalling pathways to both leaf and root colonization by bacteria (Bodenhausen *et al*. 2014; Lebeis *et al*. 2015). A complementary approach can leverage the extant publicly available bacterial genomes to perform genome-wide metabolic reconstruction. While this approach has not been directly applied to plant-associated communities, metabolic reconstruction and modelling has been used to show a high potential for the emergence of biosynthetic capacity in mixed cultures (Chiu, 2014), as well as a large number of potential metabolite exchanges among naturally co-occurring groups of bacteria (Zelezniak *et al*. 2015). Furthermore, systematic *in vitro* co-culturing of auxotroph pairs has shown a large number of syntrophic interactions, which were supported by genome bacterial genome mining (Mee *et al*. 2014; Embree *et al*. 2015). Metabolic modelling approaches depend on fully sequenced genomes and rely heavily on high-quality annotations. Thus, efforts to expand the set of reference bacterial genomes isolated from plant and rhizosphere samples, such as the study from Bai et. al, are essential building blocks. Improved annotations taking into account the ecological context are also required for modern genomic techniques like transposon insertion sequencing (Goodman *et al*. 2009) and artificial evolution (Schlötterer *et al*. 2015). In the long run, these approaches will feed statistical and population genetics models that promise to predict plant phenotypes as outputs of interactions between plants and microbial communities.

Impacts on plant performance

While pathogenic microbes decrease plant performance, plants also experience positive microbial influences on their productivity by increasing growth or by helping plants to cope with stress (Schnitzer *et al*. 2011). Hence, some microbes can produce plant growth-promoting phytohormones, such as indole-3-acetic acid (IAA), as well as can mediate acquisition by the plant of nitrogen, phosphate,

iron and nitrogen (Knief, 2012; Ofek-Lalzar *et al*. 2014; Sessitsch *et al*. 2012). Bacteria that perform one or – more commonly (Bruto *et al*. 2014) – many of these functions in the root are categorized as plant growth-promoting rhizobacteria (PGPR).

Microbes also promote plant performance indirectly by protecting against both abiotic stress and disease (Bulgarelli *et al*. 2013). In addition to the advantages microbial services provide in low nutrient environments, drought is eased by bacteria producing 1-aminocyclopropane-1-carboxylate (ACC) deaminase (Marasco *et al*. 2012), which reduces ethylene concentrations under stress conditions, by helping plants during drought stress (Cao *et al*. 2007). Protective micro-organisms in the roots may also prevent infection via immune priming (Pozo & Azcón-Aguilar 2007; Zamioudis & Pieterse 2012). Beneficial root bacteria produce induced systemic resistance (ISR), while AMF can produce mycorrhizal-induced resistance (MIR) (Pozo & Azcón-Aguilar 2007; Zamioudis & Pieterse 2012). ISR is achieved via jasmonic acid and ethylene signalling, and it is distinct from another form of systemic resistance, namely systemic acquired resistance (SAR), which is induced by leaf pathogens and mediated by salicylic acid (Conrath, 2006). MIR shares some characteristics with both ISR and SAR, and while the standard view is that fungal stimulation is directly responsible for induced resistance, it has been hypothesized that MIR is a cumulative effect of plant responses to mycorrhizal infection and ISR-inducing rhizobacteria (Pozo & Azcón-Aguilar 2007; Zamioudis & Pieterse 2012). Some rhizobacteria are capable of both plant growth-promoting activity and ISR induction. For example, *Pseudomonas fluorescens* strain WCS417 promotes growth mediated by IAA production and ACC deaminase activity, and ISR via jasmonic acid signalling (Schwachtje *et al*. 2012; Zamioudis *et al*. 2013).

Differential bacterial colonization of varying plant genotypes can occur at the community level or within a single microbial species. The latter is certainly the case with *P. fluorescens* strains (Haney *et al*. 2015), in which different ecotypes of *A. thaliana* support different levels of colonization by various strains differing in their ability to promote plant growth and protect against pathogens. Lower colonization did not correlate with higher defence response gene expression, but instead appeared to be related to some other incompatibility. Concordantly, the normal growth promotion and pathogen protection did not occur in ecotypes with the decreased levels of colonization (Haney *et al*. 2015). More recently, a genetic approach has shown that the plant defence hormone salicylic acid affects the abundance of specific bacterial groups in the root at a high taxonomic level via a combination of direct and indirect effects (Lebeis *et al*. 2015); importantly, overproduction of salicylic acid leads to the decreased biomass accumulation in plants (Bowling *et al*. 1994) Overall, these results suggested the existence of complex fitness trade-offs where the result of the plant–bacteria interaction is determined by the specific combination of plant accession, bacterial strain and plant pathogen in the environment.

Influence over plant growth may not be influenced by individual microbes, but may also be a community-level phenotype. Artificial selection experiments achieved increased plant biomass by repeatedly selecting soil microbial communities (Swenson, 2000; Panke-Buisse *et al*. 2015). As our understanding of plant–microbe partnerships improves, co-evolutionary hypotheses between plants and microbial environments become evident; in particular, it is important to understand how plant domestication has impacted the ability of plants to form microbial partnerships. Because plant domestication leads to a loss of diversity of the loci under selection, and those adjacent to them, a possible consequence is the loss of traits that were not directly under artificial selection; for this reason, it has been hypothesized that domestication has reduced the ability of plants to form beneficial associations with rhizosphere microbes (Pérez-Jaramillo, Mendes & Raaijmakers 2015). Indeed, recent studies have found that there are specific, but not overlapping, differences between wild and domesticated root microbiomes of both lettuce and barley (Bulgarelli *et al*. 2015; Cardinale *et al*. 2015). Specifically, compared to wild barley, domesticated barley grown in a common soil had increased relative abundance of the bacterial classes Alphaproteobacteria and Betaproteobacteria (Bulgarelli *et al*. 2015), which contain a number of taxa known to affect plant health, such as rhizobia. The mechanisms behind these changes might involve the microbial genes found in the core set of root micro-organisms. Thus, using shotgun metagenome sequencing of barley rhizosphere communities, it was discovered that bacterial genes related to their interactions with both plant and phage were under positive selection, promoting secretion (e.g. type 3 secretion systems), nutrient acquisition (e.g. siderophores) and stress tolerance (e.g. detoxification) (Bulgarelli *et al*. 2015). These results are strikingly similar to those from a metagenomic study performed on rice rhizospheres (Sessitsch *et al*. 2012), as well as anecdotal evidence for genes found in individual PGPR *Pseudomonas* strains (Berendsen *et al*. 2015). Together, these observations suggest that plant beneficial traits are repeatedly selected by the plants and/or indirectly by farmers and breeders during domestication.

While numerous agricultural practices could provide selective pressures that lead to differential plant microbiomes between wild and domestic crops, recent studies have highlighted that simply growing plants in monoculture instead of mixed fields significantly contributes to microbiome composition, significantly decreasing microbial biodiversity (Zuppinger-Dingley *et al*. 2014). Conversely, higher microbial diversity is correlated with increased plant height and leaf area (Zuppinger-Dingley *et al*. 2014). Negative impacts of plant monoculture in fields on microbial biodiversity might be influenced by an accumulation of plant-specific beneficial and pathogenic

microbes. While no studies have directly demonstrated whether pathogens or beneficial microbes accumulate more rapidly, a recent study with tobacco grown in a native soil demonstrated the accumulation of both within a decade of field establishment (Santhanam *et al*. 2015). It is possible that diversity plays a similar role in maintaining a healthy plant microbiome, but systematically controlling and varying diversity in microcosm reconstitution experiments is required to fully distinguish between cause and effect. Thus, conspecific fields have decreased microbial diversity with a correlating increase in diseased plants (Schnitzer *et al*. 2011). Indeed, with increasing plant diversity from 1 to 15 species, there is a decrease in non-mycorrhizal infection, while beneficial mycorrhizal infection remains constant (Schnitzer *et al*. 2011). Together these indicate that higher microbial species diversity decreases the plant–pathogen interactions leading to improved plant growth.

From an ecological perspective, the health of a community can be viewed as its ability to withstand and recover from perturbations, and low bacterial diversity in the mammalian gut has been associated with susceptibility to perturbation (Virgin & Todd 2001) and disease (Turnbaugh *et al*. 2009). Recent studies have begun to paint a picture for how the dynamics of plant microbiomes are controlled and impacted by various factors. It is vital that we understand these processes in order to effectively implement them potentially in management and agricultural practices.

Acknowledgements

S.H.P. is supported by NIH Training Grant T32 GM067553-06 and is a Howard Hughes Medical Institute (HHMI) International Student Research Fellow.

Data accessibility

This manuscript does not use data.

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Received 1 September 2015; accepted 15 April 2016
Handling Editor: Joseph K. Bailey