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MICROBIOMES

Curating communities from plants

Large-scale cultivation and genome sequencing of the bacteria that inhabit the leaves and roots of *Arabidopsis* plants have paved the way for probing how microbial communities assemble and function.

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Vast networks of microorganisms live in our soils, seas and bodies. These microbiomes also develop in intimate association with plants, in which they can enhance nutrient uptake, growth and tolerance to pathogens, pests and environmental stresses. Recognition of the fundamental role of microbes in the health of plants and animals, and the centrality of microbes in many ecological processes, has led to recent proposals for international[1] and US-based[2] microbiome initiatives. These proposals have highlighted a key need to develop collections of cultured organisms for experimental enquiry into the function and assembly of native communities[1]. In a paper online in *Nature*, Bai *et al.*[3] describe genome-sequenced bacterial culture collections that represent most of the species in native root- and leaf-associated microbiomes of *Arabidopsis thaliana* plants. They show that these collections can be used to reproducibly establish communities that resemble those found naturally on wild plants.

High-throughput genomic sequencing is enabling the characterization of microbiome profiles based on nucleic-acid signatures and the total gene content of a community (metagenomics). The breadth and depth of this profiling is increasing with the affordability of sequencing. Because this approach does not require the microorganisms to be cultivated, it has transformed our understanding of the taxonomic composition and gene content of animal- and plant-associated microbiomes. For example, cultivation-independent profiling of the root microbiota of the model flowering plant *Arabidopsis* has highlighted compositional consistencies not only across soils from multiple continents[4,5], suggesting that these microbiomes share common assembly processes, but also across multiple *Arabidopsis* lineages[6], suggesting their evolutionary conservation.

However, uncovering the microbiome assembly mechanisms requires the ability to manipulate microbial communities, including engineering and perturbing synthetic communities. Thus, experimental enquiry into microbiomes requires more than sequence data — it needs microbial cultures (Fig. 1).

Bai and colleagues amassed and identified almost 8,000 bacterial isolates from the roots and leaves of *Arabidopsis* plants grown in the field or in the laboratory in soils taken from the field. These collections included representatives of most bacterial species that have been identified in *Arabidopsis* microbiomes by cultivation-independent profiling[4–8], which suggests that most bacteria associated with *Arabidopsis* leaves and roots are readily cultivated. This culturability of plant-associated bacteria contrasts sharply with the historic inability to culture the vast majority of bacteria in soil and aquatic habitats[9], and it probably results from root and leaf habitats being rich in organic compounds and oxygen. The finding that these communities can be so well represented by culture collections highlights the value of plant microbes as models for investigating the mechanisms of microbiome assembly and function.

Bacteria associated with the roots and leaves of terrestrial plants generally fall into only a few phyla that are shared between these plant tissues[4–8]. By generating taxonomically representative culture collections of microbes from roots (194 isolates) and leaves (206 isolates), Bai *et al.* established that bacterial families in these phyla are generally found on both tissue types. However, the function of microbiomes, particularly with regard to their impact on the host plant, is probably strongly rooted at the species, subspecies and strain level, and information at these levels is captured by sequencing whole genomes.

The authors generated high-quality draft genome sequences of their 400 root and leaf isolates, as well as 32 soil isolates, and examined how the phylogenetic and functional diversity among isolates within microbial families correlates with their origins in roots or leaves. They found some evidence for microbial specialization to either the leaf or root niche: a few phylogenetic clusters were found only or primarily in one niche, and certain functional characteristics — such

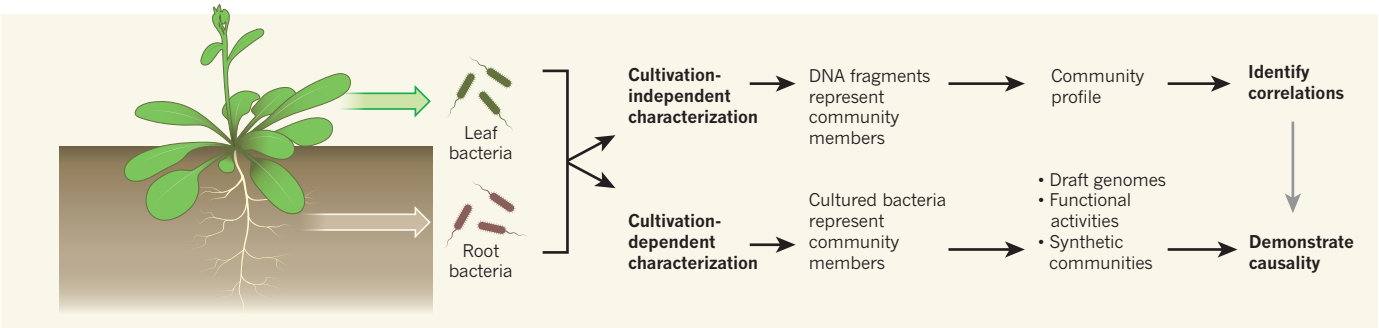

Figure 1 | From correlation to causation. Cultivation-independent profiling of microbial communities involves sequencing DNA fragments amplified from cells to generate a comprehensive picture of the community members. These profiles can be used to identify correlations, such as the presence of specific microbes on leaves versus roots, and to evaluate the extent to which culture collections represent the complete community. Bai *et al.*[3] generated large collections of bacteria associated with the leaves and roots of *Arabidopsis thaliana* plants and found them to be highly representative of the species present in cultivation-independent profiles. The authors used these culture collections to derive draft genomes, evaluate potential functional activities and create synthetic communities that, when applied to initially microbe-free plants, allowed experimental evaluation of factors that drive the assembly of leaf- and root-associated microbial communities.

as the degradation of foreign chemical substances — were enriched in one niche more than the other. However, the taxonomy of the isolates predicted their functional diversity much better than did their origins on roots or leaves. The authors' recognition of prominent family-level differences in functional diversification demonstrates a need for studies into how distinct taxonomic groups contribute to microbiome function.

Synthetic microbial communities can be used to systematically query natural microbiome processes. Bai *et al.* introduced synthetic communities of 188 and 218 representative isolates from root (or soil) and leaf communities, respectively, onto gnotobiotic *Arabidopsis* plants — plants that were microorganism-free before inoculation with known microorganisms. They then evaluated the communities that assembled by sequencing genes that help to identify the taxa (the 16S ribosomal RNA genes). These synthetic communities yielded assemblages on gnotobiotic plants that had consistent compositions, showing reproducibility in microbiome assembly processes; moreover, their composition resembled the native bacterial microbiomes found on wild *Arabidopsis* plants. Surprisingly, the resulting communities were not influenced by the relative proportion of the applied strains, indicating that community assembly is a robust process.

The synthetic communities were also instrumental in teasing apart two of the drivers of community assembly on *Arabidopsis* leaves: the source of the isolates (roots or leaves), and their arrival through the air or the soil. These findings demonstrate how synthetic communities can serve as windows on the origins and development of the bacterial component of plant microbiomes.

We are at a crucial juncture in microbiome research, transitioning from cataloguing microbes and genes to executing hypothesis-driven experiments. Bai and colleagues have provided resources that will speed this transition for plant research, including a large culture collection, complex synthetic communities with sequenced genomes and a gnotobiotic reconstitution system. Together, these resources enable recapitulation of the assembly of native bacterial communities on *Arabidopsis* plants, facilitating studies that provide ecologically relevant answers to questions about the establishment, dynamics, resilience, function and evolution of plant microbiomes. The mechanistic understanding derived from these synthetic communities is an excellent step on the road to understanding how the sustained health and productivity of our agricultural and natural systems are influenced by plant microbiomes and, more broadly, by phytobiomes — the networks of bacteria, fungi, oomycetes, viruses, nematodes, insects and other animals that affect plants. ■

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