Applied Soil Ecology 145 (2020) 103345

Contents lists available at ScienceDirect

Applied Soil Ecology

journal homepage: www.elsevier.com/locate/apsoil

Review

The plant microbiome: A missing link for the understanding of community dynamics and multifunctionality in forest ecosystems

Sandhya Mishra[a,*], Stephan Hättenschwiler[b], Xiaodong Yang[a,*]

[a] CAS Key Laboratory of Tropical Forest Ecology, Xishuangbanna Tropical Botanical Garden, Chinese Academy of Sciences, Menglun, Yunnan 666303, China
[b] Centre d'Ecologie Fonctionnelle et Evolutive (CEFE), UMR 5175, CNRS – Universite de Montpellier–Universite Paul-Valery Montpellier – EPHE – IRD, 1919, route de Mende, Montpellier F-34293, France

ARTICLE INFO

Keywords:
Plant holobiont
Functional diversity
Ecosystem functioning
Tree community dynamics
Forest ecosystems
Phyllosphere
Endosphere
Rhizosphere

ABSTRACT

The global importance of forest ecosystems for essential ecosystem services, including local livelihoods and climate change mitigation, requires a detailed understanding of the major factors determining biodiversity, health, and sustainability of forests. It has long been known that forest trees are closely associated with microorganisms, but a comprehensive description of the tree associated microbiome (hereafter referred to as plant microbiome) extending beyond the relatively well-studied root mutualists, and the understanding of its functional role is largely missing. In our viewpoint, we argue that a more comprehensive consideration of the plant microbiome, especially that of the so far neglected phyllosphere and endosphere will substantially increase the understanding of fundamental ecological processes in forest ecosystems. An explicit tree community-level approach is particularly missing in the current research efforts. Because plants and their microbiome are inseparable entities forming the plant holobiont, they may collectively determine plant community assembly, diversity, functional traits, and resulting ecosystem processes to a much stronger degree than is currently acknowledged. Here, we aim to highlight the so far underestimated importance of the plant microbiome for the structure and functioning of forest ecosystems. More specifically, we emphasize the functional diversity of the plant microbiome for a better understanding of tree community dynamics and the resulting consequences for ecosystem functioning, which appears particularly important with ongoing global change. By providing a general context of the current limitation of knowledge and indicating some specific research areas that need more attention in the future, we hope that our contribution may help in identifying current research needs and stimulate future research.

1. Introduction

The world's forest ecosystems cover about 38 million km^2, thus representing the largest terrestrial ecosystem type with globally > 3 trillions of trees and contributing about 90% to the terrestrial primary production (Baldrian, 2017). Consequently, forests have a key role in the global fluxes of energy and matter. Like virtually any other complex multicellular organisms, forest trees are intimately associated with microorganisms, which contribute significantly to the trees' metabolism, ecology, and evolution. The totality of associated microbes in different plant parts such as the phyllosphere, rhizosphere, and endosphere are referred to as the plant microbiome (Turner et al., 2013; Haney and Ausubel, 2015; Rodriguez et al., 2019) and together with the host organism this microbiome constitutes the plant holobiont (Bordenstein and Theis, 2015; Sánchez-Cañizares et al., 2017). It is increasingly recognized that the holobiont as a new entity rather than the host organism alone needs to be considered for the understanding of the host's performance, fitness, and ecological significance (Hacquard, 2016). Parts of the microbiome contributing to the trees' holobiont such as mycorrhizal associations (Parniske, 2008; Bonfante and Genre, 2010; Toju et al., 2013, 2016; Taylor et al., 2016) and nitrogen-fixing bacteria (Gehring et al., 2005; Batterman et al., 2013; Taylor et al., 2017) are well studied and their critical role in the host trees' performance, tree community dynamics, and ecosystem functioning are reasonably well documented. However, a more holistic view on the holobiont beyond specific interactions with a few well-studied mutualists, and in particular including the so far largely neglected other parts of the microbiome in the trees' phyllosphere and endosphere, for example, is urgently needed for a better understanding of how the holobiont affects the structure and function of forest ecosystems.

---

* Corresponding authors.
E-mail addresses: smnbri@gmail.com, sandhya@xtbg.ac.cn (S. Mishra), stephan.hattenschwiler@cefe.cnrs.fr (S. Hättenschwiler), yangxd@xtbg.ac.cn (X. Yang).

https://doi.org/10.1016/j.apsoil.2019.08.007
Received 27 July 2019; Received in revised form 13 August 2019; Accepted 26 August 2019
Available online 06 September 2019
0929-1393/ © 2019 Elsevier B.V. All rights reserved.

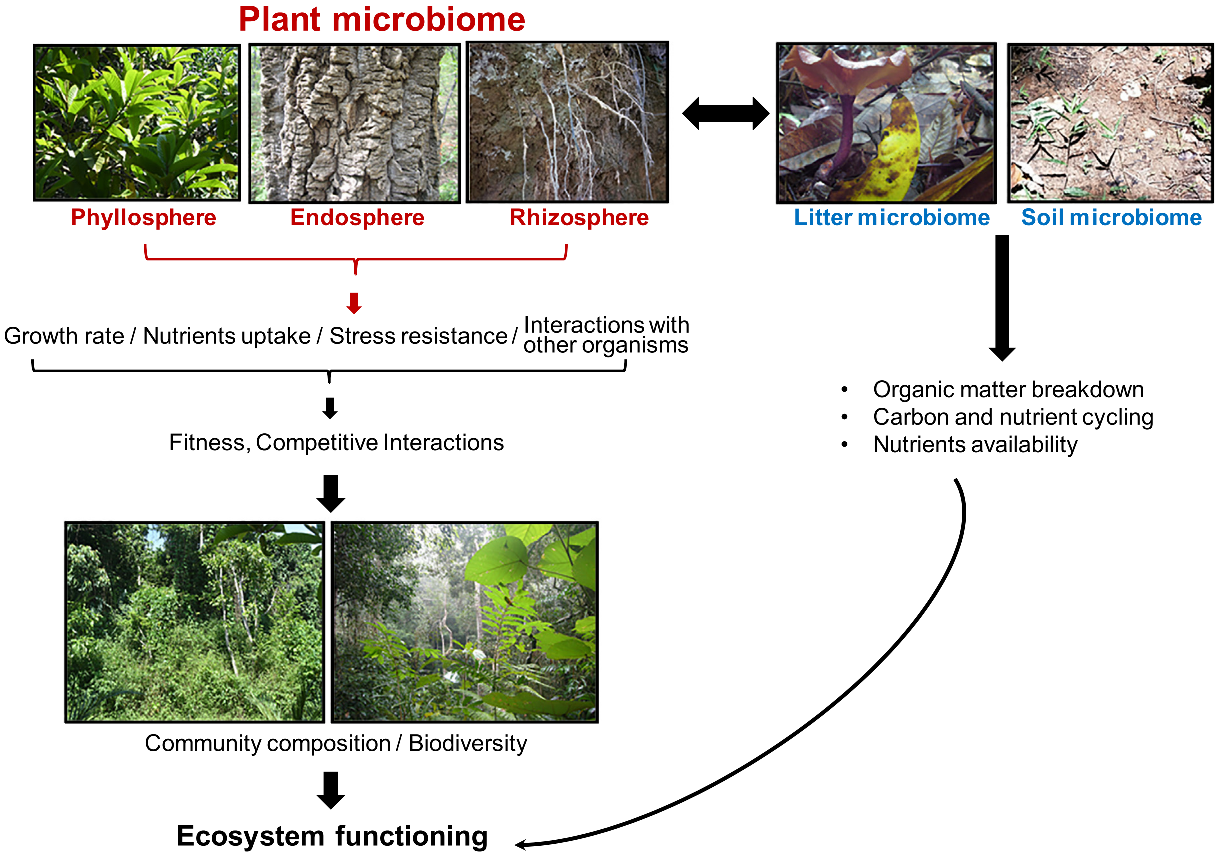

Fig. 1. A conceptual illustration of how the plant microbiome affects individual tree performance, community dynamics and ecosystem functioning. By affecting essential processes such as growth rate and interactions with other organisms at the individual plant level, which may differ among individuals and tree species, the plant microbiome continues to influence community and ecosystem level processes. The plant microbiome also interacts directly and indirectly (by influencing litter quality for example) with the litter microbiome and soil microbiome that collectively impact key ecosystem processes such as carbon and nutrient cycling and their availability for plants.

We argue that there is a strong link between the plant microbiome and key ecological processes viz. primary production, decomposition, nutrient cycling, etc. in the forest ecosystem (Fig. 1). Compared to agricultural plants , the study of the plant microbiome in forests lags behind and its ecological significance is not well understood (Vandenkoornhuyse et al., 2015; Van Der Heijden and Hartmann, 2016; Terhonen et al., 2019). This critically limits the mechanistic understanding of how forest trees cope with biotic (e.g. insect pests, pathogens, or invasive species) and abiotic stressors (e.g. increasing drought and/or temperature), and complicates the assessment of resistance, resilience, and sustainability of forest ecosystems with ongoing climate change.

Moreover, the trees and their microbiomes are evolving as a whole including plant-microbe and microbe-microbe interactions. For the understanding of the evolution of the entire holobiont the genomes of plants and associated microbiomes, together forming the plant hologenome (all genes of host plant + plant microbiome), need to be considered collectively (Rosenberg et al., 2007; Zilber-Rosenberg and Rosenberg, 2008). There is evidence that the metagenome of the microbiome (all genes of the plant microbiome) within the plant holobiont is more dynamic and shows more rapid responses to environmental change than the plant genome individually (Rosenberg and Zilber-Rosenberg, 2018). This strongly suggests that the plant microbiome is an important driver in the selection, adaptation, and evolution of the plant holobiont as a whole, thus affecting the evolutionary trajectory of the host plant. For this reason, elucidating the complexity in the structure and functions of the plant microbiome and their further characterization is a hot research topic in evolutionary ecology (Rosenberg et al., 2010). In the following sections, we discuss why we think it is important to better take into account the microbiome in studies with forest trees. We further identify some critical knowledge gaps and indicate potential ways forward for better integration of the plant microbiome approach in forest ecology.

2. Are forest structure and function determined by the plant microbiome?

The role of biotic factors in the distribution of plant species and community composition was traditionally underrated compared to abiotic factors like climatic parameters. A number of recent studies showed that soil microbial communities may have a greater influence on plant species distribution and co-existence in forests than climatic conditions (Walthert and Meier, 2017; Hawkins and Crawford, 2018). The importance of soil microbial communities on the composition and diversity of plant communities and ecosystem functioning is generally well acknowledged (Bever et al., 2010, 2012; Van der Putten et al., 2013; Classen et al., 2015; Delgado-Baquerizo et al., 2016, 2018; Probst et al., 2018), but it is more difficult to decipher whether these effects are direct by affecting plant physiology and development or indirect by affecting environmental conditions such as nutrient availability (Hawkins and Crawford, 2018; Bennett and Klironomos, 2019). Moreover, given that the soil microbial communities are currently assumed as the major origin of the plant microbiome (Yurgel et al., 2018; Rodriguez et al., 2019), the important question (highly relevant for the plant microbiome) is arising i.e. What factors influence the recruitment of soil microbes into the plant microbiome? While soil biota are the primary source of the plant microbiome, their recruitment into the plant microbiome and the intensity of association and specificity may be gradual. As a result of concentrated research efforts on few agricultural and model plants, the determination of associated microbial diversity has improved enormously for some selected plant species such as *Arabidopsis thaliana*, *Zea mays*, *Oryza sativa*, *Picea abies*, *Populus deltoides* (Cregger et al., 2018; Terhonen et al., 2019). Several studies reported that microbial communities contribute significantly to disease control, nutrient acquisition, and stress tolerance (Mendes et al., 2011; Lundberg et al., 2012; Berg et al., 2015; Agler et al., 2016). These are all vital functions determining also the success of tree establishment and growth, therefore affecting productivity (Schnitzer et al., 2011) and ultimately competitive interactions including exotic plant invasion (Zuppinger-Dingley et al., 2011; Mishra et al., 2013; Xiao et al., 2017), which is influencing plant community dynamics (Brandt et al., 2013) and plant species diversity (Mangan et al., 2010). However, there is only very limited knowledge about the degree of association of microbes, and the diversity and specificity of the plant microbiome for forest trees and how it may co-determine tree species composition and community dynamics in forest ecosystems and consequently their functioning. The determining impact of microbial associates on plant community composition and diversity was compellingly demonstrated in herbaceous communities for mycorrhizal fungi (e.g. Van Der Heijden et al., 1998; Van Der Heijden, 2002) and N_2-fixing bacteria (De Bruijn, 2015; Dinnage et al., 2019). These two well-documented cases of how a part of the microbiome can profoundly affect plant community dynamics also highlight the critical role of the host plant through the provision of structure and metabolites via an intimately linked physiology between plants and microorganisms (cf. Comas, 2017). Especially the allocation of carbon compounds is important, which can vary significantly among plant species, environmental conditions, plant growth stage and nutrient availability (Churchland and Grayston, 2014). Any modulation of this C exchange can modify the abundance and composition of the microbiome. In fact, the fine-tuning of the plant microbiome seems to be determined by the host plant. Moreover, the plant's capability of recruiting microorganisms into the microbiome is taxon-specific and results often from a common evolutionary history of plants and microorganisms. The establishment and identity of the microbiome may also depend on the plant's ontogeny and tissue type. However, the microbiome in plant parts and tissues other than roots remains very poorly studied, in particular for trees from natural forest ecosystems.

Generally, it is now widely accepted that plants and the associated microbiome are two vital and inseparable entities of the holobiont that collectively determine plant community dynamics and diversity (Hassani et al., 2018; Simon et al., 2019). Yet, how exactly the holobiont is determining processes at the community level and what the resulting consequences for ecosystem functioning are, is largely unknown for tree communities in natural forest ecosystems. An integrated conceptual framework across tree species and taking into account other plant parts and tissues beyond roots is missing but is urgently needed for hypotheses building and testing. Such a framework would allow a more straightforward application of the plant holobiont concept in forest ecosystem dynamics which is imperative for a mechanistic understanding of how the microbiome contributes to structuring the tree communities. In the future, a more detailed knowledge about the microbiome across tree species may then allow a more complete understanding of the drivers of tree diversity, and how functional traits and biogeography of tree holobionts are shaped.

3. Critical knowledge gaps

The recognition of the significance of the holobiont for the understanding of the physiology and ecology of an organism led to a major paradigm shift and a new research frontier. Several microbiome projects, such as the human or crop species microbiomes have been launched in the past decade, with the aim to develop microbiome-based strategies to cope with environmental challenges. In comparison, the consideration of the holobiont in forest communities, let alone its characterization, is still in its infancy. We identified two major gaps of knowledge for the development of an integrative view of the relevance of the microbiome and the resulting plant holobiont for tree communities. First, a more general appreciation of the microbiome across multiple tree species with an explicit community approach is critically missing. It seems likely that the microbiome varies substantially across tree species beyond the documented species-specific mycorrhizal associations and symbiotic N-fixation. This implies a significant share of the microbiome in the characteristics of a given tree species, co-determining its ecology including the interactions with co-occurring tree species, but also with other organisms such as herbivores, pathogens or pollinators. However, it is presently largely unknown how the microbiomes differ among and within tree species and if and how they are spatially or phylogenetically structured. How much does the microbiome differ among tree species and do these differences reflect ecological strategies, are fundamental questions to be answered. Although the tools in genomics and biostatistics exist today, this type of studies in forest ecosystems are surprisingly absent.

A second major gap is the lack of comprehensive studies at the whole plant level extending on the current focus on root-associated microorganisms of the belowground part of plants. Work on the rhizosphere microbiome dominates the current literature discussing the plant holobiont and how it affects plant fitness and the stability of natural ecosystems (Lugtenberg and Kamilova, 2009; Berendsen et al., 2012; Trivedi et al., 2013; Almario et al., 2017), as well as community composition, ecosystem functioning, and issues related to conservation and sustainability (Teixeira et al., 2010; Philippot et al., 2013; van der Heijden and Hartmann, 2016). Compared to this root and belowground focus, the part of the microbiome within the phyllosphere and the endosphere received only little attention (Kembel et al., 2014; Laforest-Lapointe et al., 2017; Zhao et al., 2017), despite their potentially substantial contribution to the holobiont. Just by itself, the phyllosphere covers globally a total area of $> 10^8\,km^2$ and is estimated to host roughly 10^{26} bacteria (Vorholt, 2012; Kembel et al., 2014). The limited number of studies explicitly addressing the part of the microbiome within the phyllosphere showed evidence that it affects growth and fitness of their host (Meyer and Leveau, 2012; Ortega et al., 2016). Most importantly, the phyllospheric microbes are potentially involved in the defence against pathogens and contribute significantly to litter decomposition by providing inocula for initiating the first stages of degradation and affecting carbon and nitrogen dynamics (Voříšková and Baldrian, 2013; Bringel and Couée, 2015). Likewise, the microorganisms found in the endosphere were reported to influence plant physiology by enhancing plant's inherent responses against biotic and abiotic stress (Turner et al., 2013; Fitzpatrick et al., 2018). A simple literature search for papers published between 2000 and 2019 showed much less publications of research on microbial diversity in the phyllosphere or endosphere compared to that of the rhizosphere (Fig. 2). Their proportion shrinks even further when the studies on soil microbial communities without an explicit reference to the plant microbiome are considered. Overall, the studies from forest ecosystems contribute only 36% to all studies including those from agricultural systems. Despite the fact that the studies considered in these two columns (second and third from the left in Fig. 2) did not necessarily specify what plant part was included, it shows unequivocally that forest ecosystems remain understudied. Only a small fraction of investigations was devoted to the study of the plant holobiont. Collectively, there is a great need to better understand the contribution of microorganisms associated to the phyllosphere and the endosphere to the overall role of the microbiomes of forest trees and how they impact tree communities and forest ecosystems. Some relevant research questions would include: what is the relative contribution of the phyllosphere and endosphere to the overall diversity of a tree's microbiome? What are their functional roles? Do the communities overlap and if yes to what degree among rhizo-, phyllo-, and endosphere? It would also be interesting to address these questions

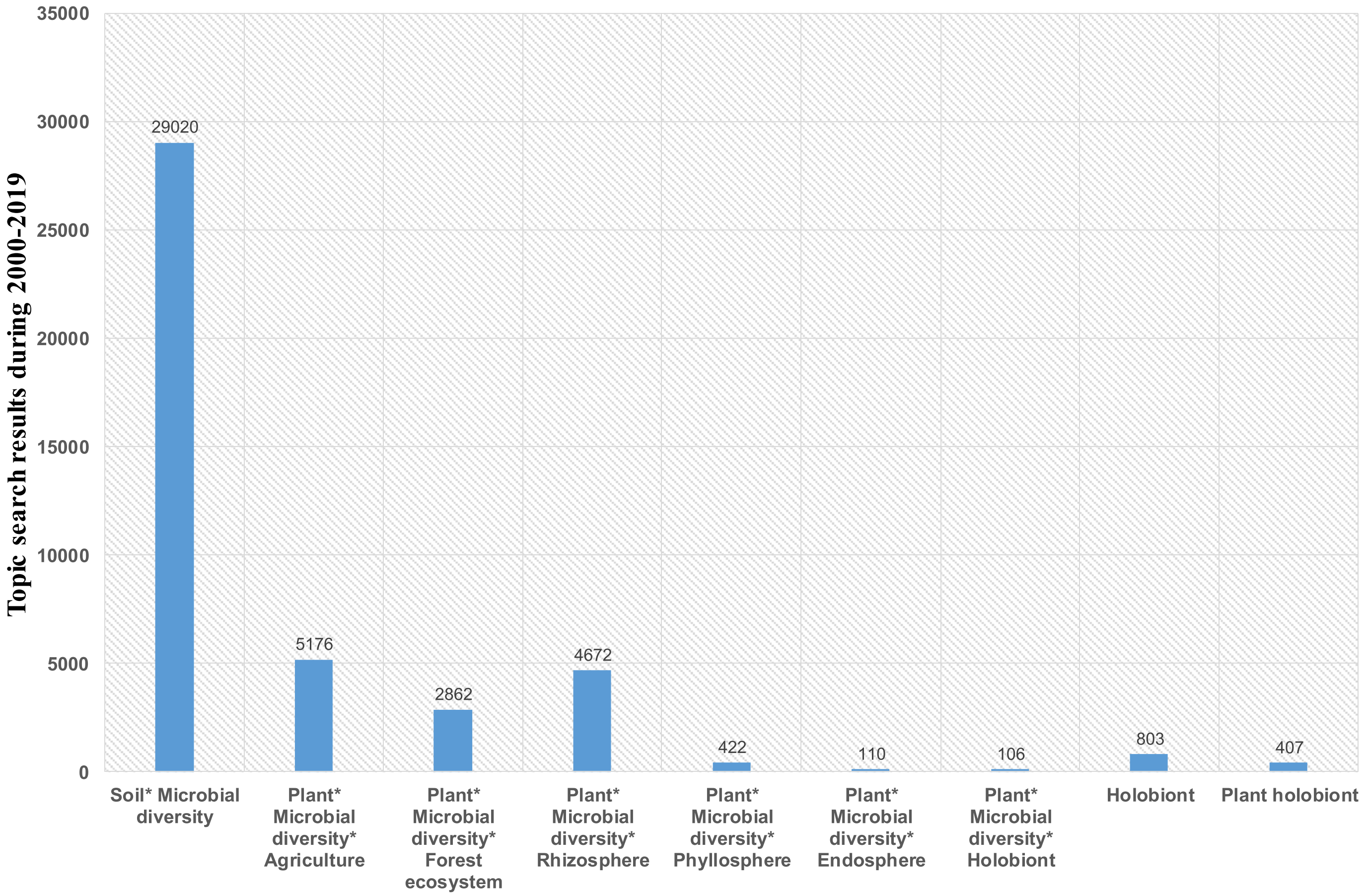

Fig. 2. Research trends showing the number of publications in related area during 2000–2019. Bar graphs were plotted based on different topics (as mentioned in x-axis) searched in the Web of Science (Clarivate Analytics) with the 27th of July 2019 as the reference date. Values over the bars represent number of hits in Web of Science.

at larger spatial scales, evaluating how environmental factors determine these patterns and how microbiome diversity is related to tree diversity in different forest ecosystems, or how dominant and rare tree species affect the observed patterns (Fig. 3). In a second time, the accumulating data could then be used to map the tree microbiome in different forest types, for example in tropical or temperate forests varying in tree species diversity, which could shed light on environmental filtering of the tree holobiont and how it affects competitive interactions, responses to herbivore and pathogen attacks and tree survival under ongoing climate change.

4. Conclusions: potential ways forward

Despite the general appreciation of the importance of the plant microbiome, its critical role in the functioning of individual plants, their interactions at the community level and the consequences for ecosystem functioning has not been sufficiently embraced for forest ecosystems. Above, we identified two major gaps of knowledge calling for more studies that describe tree microbiomes comprehensively for a variety of forest ecosystems. Ideally, this would yield a detailed picture of the genetic and functional diversity of tree species-specific microbiomes. Then, for a more mechanistic understanding of the role of these microbiomes, future studies should extend on simply describing the microbial communities by exploring how they interact across different plant compartments (phyllosphere, rhizosphere, and endosphere) and what kind of functions they have. To attain these objectives a novel focus on the functional diversity of the plant microbiome is needed. This could include the identification of specific functional genes known for their ecological relevance and allowing a connection to some key ecosystem functions, for example, related to nutrient cycling. An ambitious next goal could be the determination of the relative contribution of the genome of the microbiome and that of the host plant to some specific functions represented by the holobiont as a whole. This would ultimately allow quantifying the microbiomes' share in some key functions of particular tree species in the community. As noted above, such microbiome research in forest ecosystems should target the whole plant and not individual ‘spheres’ (Fig. 3).

In summary, we propose a set of what we think pertinent research questions that need to be addressed in future studies.

a) How do co-occurring tree species differ in their microbiome?
b) What are the differences in the microbiome among different plant compartments and how are these differences determined?
c) To what extent do the microorganisms in the different plant compartments interact?
d) What is the relative contribution of the microbiome to the overall functioning of the holobiont?
e) How do tree microbiomes contribute to tree community-level processes and does this differ among major forest ecosystems?
f) Is there any coordination in tree microbiome structure and functions across different compartments (phyllo-, rhizo- and endosphere)?
g) To what degree does the microbiome determine plant functional traits?
h) How does the microbiome vary over time?

Declaration of competing interest

None.

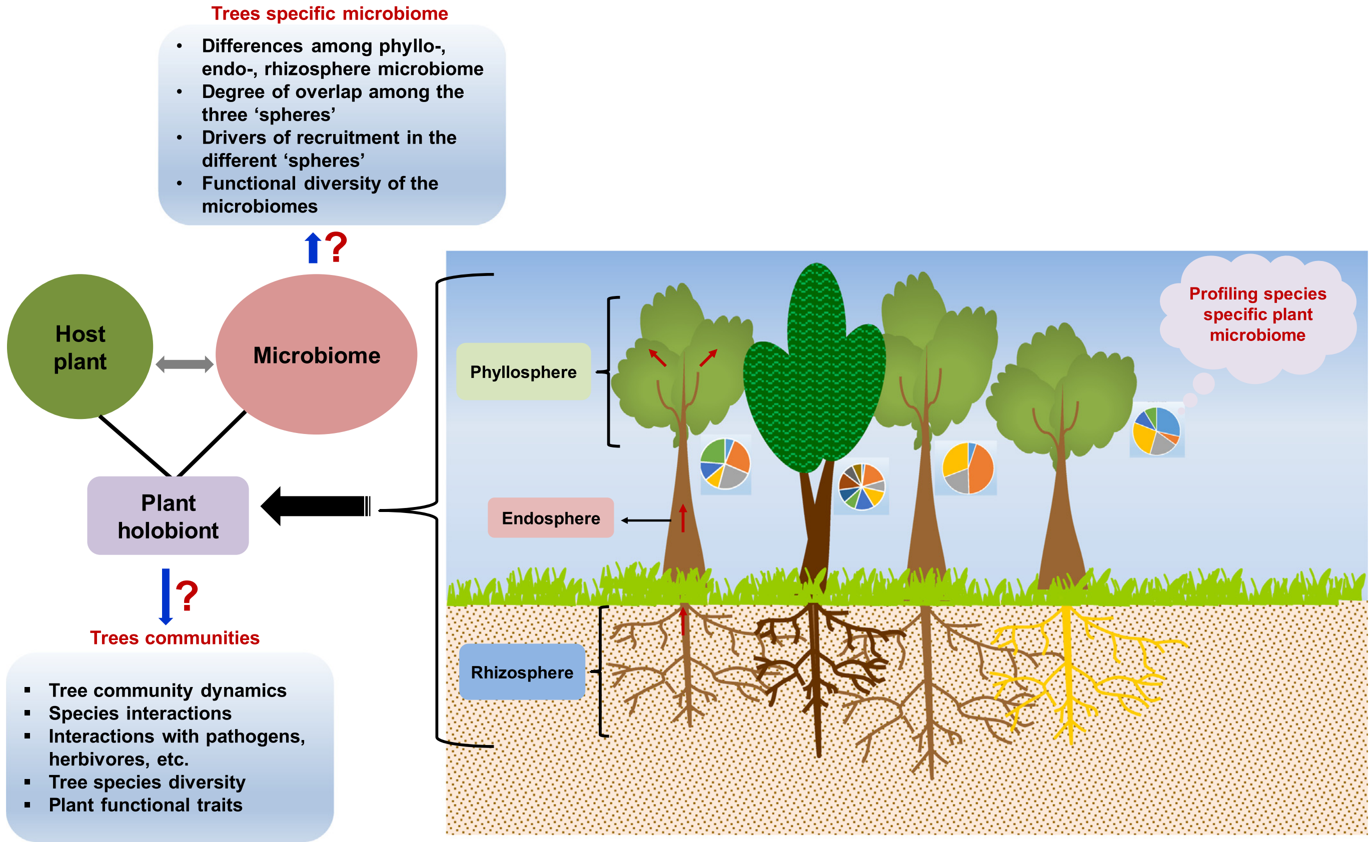

Fig. 3. A graphical overview of key elements in tree microbiome research: Major emphasis is on studying the identity, functional diversity and spatial organization of tree microbiomes aiming at a better understanding of the role of tree holobionts in community dynamics and ecosystem functioning in forest ecosystems. Different tree species are likely hosting considerably different microbiomes as indicated with the tree species-specific pie charts. The tools in genomics with high-throughput sequencing and biostatistics are now available to address the complex and data intensive questions about tree species-specific microbiomes and their functional gene diversity. The figure also emphasizes the critical importance of studying the microbiome at the whole plant level including the so far largely neglected phyllosphere and endosphere. A detailed mapping of tree microbiomes may ultimately allow to quantify microbial contributions to tree community dynamics and forest ecosystem functioning.

Acknowledgements

The authors gratefully acknowledge the financial support provided by National Natural Science Foundation of China (Grant no. 31700457), China Postdoctoral Science Foundation (Grant no. 2018M631112) and CAS President's International Fellowship Initiative (PIFI) (Grant no. 2019PC0095) awarded to Sandhya Mishra.

References

Agler, M.T., Ruhe, J., Kroll, S., Morhenn, C., Kim, S.T., Weigel, D., Kemen, E.M., 2016. Microbial hub taxa link host and abiotic factors to plant microbiome variation. PLoS Biol. 14 (1), e1002352.

Almario, J., Jeena, G., Wunder, J., Langen, G., Zuccaro, A., Coupland, G., Bucher, M., 2017. Root-associated fungal microbiota of nonmycorrhizal *Arabis alpina* and its contribution to plant phosphorus nutrition. PNAS 114 (44), E9403–E9412.

Baldrian, P., 2017. Forest microbiome: diversity, complexity and dynamics. FEMS Microbiol. Rev. 41 (2), 109–130.

Batterman, S.A., Hedin, L.O., Van Breugel, M., Ransijn, J., Craven, D.J., Hall, J.S., 2013. Key role of symbiotic dinitrogen fixation in tropical forest secondary succession. Nature 502 (7470), 224.

Bennett, J.A., Klironomos, J., 2019. Mechanisms of plant–soil feedback: interactions among biotic and abiotic drivers. New Phytol. 222 (1), 91–96.

Berendsen, R.L., Pieterse, C.M., Bakker, P.A., 2012. The rhizosphere microbiome and plant health. Trends Plant Sci. 17 (8), 478–486.

Berg, G., Rybakova, D., Grube, M., Köberl, M., 2015. The plant microbiome explored: implications for experimental botany. J. Exp. Bot. 67 (4), 995–1002.

Bever, J.D., Dickie, I.A., Facelli, E., Facelli, J.M., Klironomos, J., Moora, M., Rillig, M.C., Stock, W.D., Tibbett, M., Zobel, M., 2010. Rooting theories of plant community ecology in microbial interactions. Trends Ecol. Evol. 25 (8), 468–478.

Bever, J.D., Platt, T.G., Morton, E.R., 2012. Microbial population and community dynamics on plant roots and their feedbacks on plant communities. Annu. Rev. Microbiol. 66, 265–283.

Bonfante, P., Genre, A., 2010. Mechanisms underlying beneficial plant–fungus interactions in mycorrhizal symbiosis. Nat. Commun. 1, 48.

Bordenstein, S.R., Theis, K.R., 2015. Host biology in light of the microbiome: ten principles of holobionts and hologenomes. PLoS Biol. 13 (8), e1002226.

Brandt, A.J., Kroon, H., Reynolds, H.L., Burns, J.H., 2013. Soil heterogeneity generated by plant–soil feedbacks has implications for species recruitment and coexistence. J. Ecol. 101 (2), 277–286.

Bringel, F., Couée, I., 2015. Pivotal roles of phyllosphere microorganisms at the interface between plant functioning and atmospheric trace gas dynamics. Front. Microbiol. 6, 486.

Churchland, C., Grayston, S.J., 2014. Specificity of plant-microbe interactions in the tree mycorrhizosphere biome and consequences for soil C cycling. Front. Microbiol. 5, 261.

Classen, A.T., Sundqvist, M.K., Henning, J.A., Newman, G.S., Moore, J.A., Cregger, M.A., Moorhead, L.C., Patterson, C.M., 2015. Direct and indirect effects of climate change on soil microbial and soil microbial-plant interactions: what lies ahead? Ecosphere 6 (8), 1–21.

Comas, L.H., 2017. Exploring plant root traits and fungal interactions governing plant community structure: re-focusing long standing questions. New Phytol. 216 (4), 963–964.

Cregger, M.A., Veach, A.M., Yang, Z.K., Crouch, M.J., Vilgalys, R., Tuskan, G.A., Schadt, C.W., 2018. The Populus holobiont: dissecting the effects of plant niches and genotype on the microbiome. Microbiome 6 (1), 31.

De Bruijn, F.J., 2015. Biological nitrogen fixation. In: Principles of Plant-Microbe Interactions. Springer, Cham, pp. 215–224.

Delgado-Baquerizo, M., Maestre, F.T., Reich, P.B., Jeffries, T.C., Gaitan, J.J., Encinar, D., Berdugo, M., Campbell, C.D., Singh, B.K., 2016. Microbial diversity drives multifunctionality in terrestrial ecosystems. Nat. Commun. 7, 10541.

Delgado-Baquerizo, M., Oliverio, A.M., Brewer, T.E., Benavent-González, A., Eldridge, D.J., Bardgett, R.D., Maestre, F.T., Singh, B.K., Fierer, N., 2018. A global atlas of the dominant bacteria found in soil. Science 359 (6373), 320–325.

Dinnage, R., Simonsen, A.K., Barrett, L.G., Cardillo, M., Raisbeck-Brown, N., Thrall, P.H., Prober, S.M., 2019. Larger plants promote a greater diversity of symbiotic nitrogen-fixing soil bacteria associated with an Australian endemic legume. J. Ecol. 107 (2), 977–991.

Fitzpatrick, C.R., Copeland, J., Wang, P.W., Guttman, D.S., Kotanen, P.M., Johnson, M.T., 2018. Assembly and ecological function of the root microbiome across angiosperm plant species. PNAS 115 (6), E1157–E1165.

Gehring, C., Vlek, P.L., de Souza, L.A., Denich, M., 2005. Biological nitrogen fixation in secondary regrowth and mature rainforest of central Amazonia. Agric. Ecosyst. Environ. 111 (1–4), 237–252.

Hacquard, S., 2016. Disentangling the factors shaping microbiota composition across the plant holobiont. New Phytol. 209 (2), 454–457.

Haney, C.H., Ausubel, F.M., 2015. Plant microbiome blueprints. Science 349 (6250), 788–789.

Hassani, M.A., Durán, P., Hacquard, S., 2018. Microbial interactions within the plant holobiont. Microbiome 6 (1), 58.

Hawkins, A.P., Crawford, K.M., 2018. Interactions between plants and soil microbes may alter the relative importance of intraspecific and interspecific plant competition in a changing climate. AoB Plants 10 (4), ply039.

Kembel, S.W., O'Connor, T.K., Arnold, H.K., Hubbell, S.P., Wright, S.J., Green, J.L., 2014. Relationships between phyllosphere bacterial communities and plant functional traits in a neotropical forest. Proc. Natl. Acad. Sci. 111 (38), 13715–13720.

Laforest-Lapointe, I., Paquette, A., Messier, C., Kembel, S.W., 2017. Leaf bacterial diversity mediates plant diversity and ecosystem function relationships. Nature 546 (7656), 145.

Lugtenberg, B., Kamilova, F., 2009. Plant-growth-promoting rhizobacteria. Annu. Rev. Microbiol. 63, 541–556.

Lundberg, D.S., Lebeis, S.L., Paredes, S.H., Yourstone, S., Gehring, J., Malfatti, S., Tremblay, J., Engelbrektson, A., Kunin, V., Del Rio, T.G., Edgar, R.C., 2012. Defining the core *Arabidopsis thaliana* root microbiome. Nature 488 (7409), 86.

Mangan, S.A., Schnitzer, S.A., Herre, E.A., Mack, K.M., Valencia, M.C., Sanchez, E.I., Bever, J.D., 2010. Negative plant–soil feedback predicts tree-species relative abundance in a tropical forest. Nature 466 (7307), 752.

Mendes, R., Kruijt, M., De Bruijn, I., Dekkers, E., van der Voort, M., Schneider, J.H., Piceno, Y.M., DeSantis, T.Z., Andersen, G.L., Bakker, P.A., Raaijmakers, J.M., 2011. Deciphering the rhizosphere microbiome for disease-suppressive bacteria. Science 332 (6033), 1097–1100.

Meyer, K.M., Leveau, J.H., 2012. Microbiology of the phyllosphere: a playground for testing ecological concepts. Oecologia 168 (3), 621–629.

Mishra, S., Upadhyay, R.S., Nautiyal, C.S., 2013. Unravelling the beneficial role of microbial contributors in reducing the allelopathic effects of weeds. Appl. Microbiol. Biotechnol. 97 (13), 5659–5668.

Ortega, R.A., Mahnert, A., Berg, C., Müller, H., Berg, G., 2016. The plant is crucial: specific composition and function of the phyllosphere microbiome of indoor ornamentals. FEMS Microbiol. Ecol. 92 (12), fiw173.

Parniske, M., 2008. Arbuscular mycorrhiza: the mother of plant root endosymbioses. Nat. Rev. Microbiol. 6 (10), 763.

Philippot, L., Raaijmakers, J.M., Lemanceau, P., Van Der Putten, W.H., 2013. Going back to the roots: the microbial ecology of the rhizosphere. Nat. Rev. Microbiol. 11 (11), 789.

Probst, M., Gómez-Brandón, M., Bardelli, T., Egli, M., Insam, H., Ascher-Jenull, J., 2018. Bacterial communities of decaying Norway spruce follow distinct slope exposure and time-dependent trajectories. Environ. Microbiol. 20 (10), 3657–3670.

Rodriguez, P.A., Rothballer, M., Chowdhury, S.P., Nussbaumer, T., Gutjahr, C., Falter-Braun, P., 2019. Systems biology of plant microbiome interactions. Mol. Plant 12, 804–821.

Rosenberg, E., Zilber-Rosenberg, I., 2018. The hologenome concept of evolution after 10 years. Microbiome 6 (1), 78.

Rosenberg, E., Koren, O., Reshef, L., Efrony, R., Zilber-Rosenberg, I., 2007. The role of microorganisms in coral health, disease and evolution. Nat. Rev. Microbiol. 5, 355–362.

Rosenberg, E., Sharon, G., Atad, I., Zilber-Rosenberg, I., 2010. The evolution of animals and plants *via* symbiosis with microorganisms. Environ. Microbiol. Rep. 2 (4), 500–506.

Sánchez-Cañizares, C., Jorrín, B., Poole, P.S., Tkacz, A., 2017. Understanding the holobiont: the interdependence of plants and their microbiome. Curr. Opin. Microbiol. 38, 188–196.

Schnitzer, S.A., Klironomos, J.N., HilleRisLambers, J., Kinkel, L.L., Reich, P.B., Xiao, K., Rillig, M.C., Sikes, B.A., Callaway, R.M., Mangan, S.A., Van Nes, E.H., 2011. Soil microbes drive the classic plant diversity–productivity pattern. Ecology 92 (2), 296–303.

Simon, J.C., Marchesi, J.R., Mougel, C., Selosse, M.A., 2019. Host-microbiota interactions: from holobiont theory to analysis. Microbiome 7 (1), 5.

Taylor, M.K., Lankau, R.A., Wurzburger, N., 2016. Mycorrhizal associations of trees have different indirect effects on organic matter decomposition. J. Ecol. 104 (6), 1576–1584.

Taylor, B.N., Chazdon, R.L., Bachelot, B., Menge, D.N., 2017. Nitrogen-fixing trees inhibit growth of regenerating Costa Rican rainforests. PNAS 114 (33), 8817–8822.

Teixeira, L.C., Peixoto, R.S., Cury, J.C., Sul, W.J., Pellizari, V.H., Tiedje, J., Rosado, A.S., 2010. Bacterial diversity in rhizosphere soil from Antarctic vascular plants of Admiralty Bay, maritime Antarctica. ISME J 4 (8), 989.

Terhonen, E., Blumenstein, K., Kovalchuk, A., Asiegbu, F.O., 2019. Forest tree microbiomes and associated fungal endophytes: functional roles and impact on forest health. Forests 10 (1), 42.

Toju, H., Yamamoto, S., Sato, H., Tanabe, A.S., 2013. Sharing of diverse mycorrhizal and root-endophytic fungi among plant species in an oak-dominated cool-temperate forest. PLoS One 8, e78248.

Toju, H., Yamamoto, S., Tanabe, A.S., Hayakawa, T., Ishii, H.S., 2016. Network modules and hubs in plant-root fungal biomes. J. R. Soc. Interface 13, 20151097.

Trivedi, P., Anderson, I.C., Singh, B.K., 2013. Microbial modulators of soil carbon storage: integrating genomic and metabolic knowledge for global prediction. Trends Microbiol. 21 (12), 641–651.

Turner, T.R., James, E.K., Poole, P.S., 2013. The plant microbiome. Genome Biol. 14, 209–215.

Van Der Heijden, M.G., 2002. Arbuscular mycorrhizal fungi as a determinant of plant diversity: in search of underlying mechanisms and general principles. In: Mycorrhizal Ecology. Springer, Berlin, Heidelberg, pp. 243–265.

Van Der Heijden, M.G., Hartmann, M., 2016. Networking in the plant microbiome. PLoS Biol. 14 (2), e1002378.

Van Der Heijden, M.G., Klironomos, J.N., Ursic, M., Moutoglis, P., Streitwolf-Engel, R., Boller, T., Wiemken, A., Sanders, I.R., 1998. Mycorrhizal fungal diversity determines plant biodiversity, ecosystem variability and productivity. Nature 396 (6706), 69.

Van der Putten, W.H., Bardgett, R.D., Bever, J.D., Bezemer, T.M., Casper, B.B., Fukami, T., Kardol, P., Klironomos, J.N., Kulmatiski, A., Schweitzer, J.A., Suding, K.N., 2013. Plant–soil feedbacks: the past, the present and future challenges. J. Ecol. 101 (2), 265–276.

Vandenkoornhuyse, P., Quaiser, A., Duhamel, M., Le Van, A., Dufresne, A., 2015. The importance of the microbiome of the plant holobiont. New Phytol. 206 (4), 1196–1206.

Vorholt, J.A., 2012. Microbial life in the phyllosphere. Nat. Rev. Microbiol. 10 (12), 828–840.

Voříšková, J., Baldrian, P., 2013. Fungal community on decomposing leaf litter undergoes rapid successional changes. ISME J 7 (3), 477.

Walthert, L., Meier, E.S., 2017. Tree species distribution in temperate forests is more influenced by soil than by climate. Ecol. Evol. 7 (22), 9473–9484.

Xiao, H., Schaefer, D.A., Yang, X., 2017. pH drives ammonia oxidizing bacteria rather than archaea thereby stimulate nitrification under *Ageratina adenophora* colonization. Soil Biol. Biochem. 114, 12–19.

Yurgel, S., Douglas, G.M., Dussault, A., Percival, D., Langille, M., 2018. Dissecting community structure in wild blueberry root and soil microbiome. Front. Microbiol. 9, 1187.

Zhao, Y., Gao, Z., Tian, B., Bi, K., Chen, T., Liu, H., Xie, J., Cheng, J., Fu, Y., Jiang, D., 2017. Endosphere microbiome comparison between symptomatic and asymptomatic roots of *Brassica napus* infected with *Plasmodiophora brassicae*. PLoS One 12 (10), e0185907.

Zilber-Rosenberg, I., Rosenberg, E., 2008. Role of microorganisms in the evolution of animals and plants: the hologenome theory of evolution. FEMS Microbiol. Rev. 32, 723–735.

Zuppinger-Dingley, D., Schmid, B., Chen, Y., Brandl, H., Van der Heijden, M.G.A., Joshi, J., 2011. In their native range, invasive plants are held in check by negative soil-feedbacks. Ecosphere 2 (5), 1–12.