

Editorial special issue: soil, plants and endophytes

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Introduction

Despite the inception of the endophyte research dates back to the nineteenth century, studies on this topic have only recently bloomed, producing a fast-growing body of literature (Compant et al. 2012; Hardoim et al. 2015; Saikkonen et al. 2016). Several definitions of endophyte have been furthermore proposed; while some have been criticized, others have been suggested to better define this particular lifestyle. We currently describe endophytes as any microbe that can be isolated from asymptomatic plant tissue (Chanway 1995; Wilson 1995; Hardoim et al. 2015). This definition includes neutral,

commensal and/or beneficial microorganisms as well as dormant saprobes and pathogens during their latent phase of their life cycle. These microorganisms engage an intimate association within their host plants, establishing a microbial community in the plant endosphere and could be found in various plant parts (Hardoim et al. 2015).

Although endophytes have been previously extensively studied, the interplay between different endophytes and their hosts is however yet poorly understood. The mechanisms underlying these interactions, the driving forces determining specific microbial community assemblages found in different plant organs, the influence that a range of factors (e.g. environmental, genetic, phenological, etc.) have on shaping the endophytic microbiomes, or how to exploit/harness the benefits these inner microbial consortia provide to their hosts are just a few exciting matters currently under study. Nevertheless, novel and powerful methodological approaches already available must be implemented to obtain a better picture of this complex and fascinating ecological niche (i.e. the host plant and its inner microbiome).

Despite descriptive and comprehensive research is done, important gaps in our knowledge are evident, and thorough insights are still needed to fully understand these particular plant-microbe interactions. We need, for instance, to move beyond cataloguing microorganism identities in different plant organs/tissues, or from plants growing in different soils and/or under diverse environmental conditions. Indeed, providing more hypothesis-driven studies will help answering

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questions related to microbial functions and how these intimate associations between plants and endophytic microbes do not result in disease.

The plant interacts and intimately associates with an array of taxa that is organ-specific to roots, stems, leaves, flowers, fruits, and seeds (Compant et al. 2010; Mitter et al. 2013) with some of them having beneficial effects on plants (Fig. 1). Endophyte origins from the rhizosphere, laimosphere, caulosphere, phyllosphere, anthosphere, carposphere, and spermosphere to the plant endosphere compartment, how the endophyte microbiota is able to penetrate plant tissues and establish an intimate asymptomatic partnership with their hosts in the appropriate plant organs, how some might switch to a virulent form while others could be beneficial for their hosts, are however some lingering questions requiring in-depth insight to obtain satisfactory answers. The still enduring important gaps in our comprehension are also on some other details of symbioses (when they occur) between plant and microorganisms, e.g. what are the mechanisms deployed by endophytes to protect the host against a range of different a/biotic stresses, what are the microbial machineries allowing endophytic establishment and endurance, why some taxa are better colonizers than others, where they go, and what they do at cellular and tissue levels?

More understanding is currently provided through mechanism-based studies, and using ecological, genetic and ‘-omics’ approaches. Despite this effort currently carried out by an increasing number of research teams, several questions and hypothesis should still be put on the table and contrasted. Several studies related to endophytes are, moreover, mostly biased by experimental models evaluated under gnotobiotic conditions, that is, far away from natural conditions. We need to move beyond and to analyze how the whole plant and its associated microbiota are working together under multitrophic scenarios.

We must have lost important information regarding endophytes by testing in very simplified systems. Indeed, several environmental factors, either working coordinately or acting separately in time and/or space, are dynamically influencing plant-endophyte association. Moreover, in this research scenario we must not forget the soil compartment, as most of the endophytes, especially bacteria, derive from the soil environment.

Issues such as the ecology of the endophytes, the composition of the core and satellite microbiomes within host plants, the endophyte colonization process, as

well as niche establishment and mechanisms behind need to be better understood. A better knowledge on the interplay of soil, plants and endophytes is currently needed and still requires in-depth studies on the role that endophytes play in ecosystems. Furthermore, endophytes pose promising alternatives to synthetic chemistry in crop production and protection against abiotic and biotic stresses, fitting sustainable agriculture criteria and being useful tools in phytoremediation strategies (Gundel et al. 2013; Mercado-Blanco and Lugtenberg 2014; Mercado-Blanco 2015; Kauppinen et al. 2016; Saikkonen et al. 2016). However, successful applications in agricultural practice require efficient plant colonization by endophytes. This can only be achieved by a thorough understanding of the basic biology of the microbe including type of growth (systemic vs. non-systemic), transmission mode (horizontal vs. vertical) as well as genetic interplay and molecular basis of their association with the plants (Saikkonen et al. 2010b, 2013; Hamilton et al. 2012; Lòpez-Fernández et al. 2015; van Overbeek and Saikkonen 2016).

In this Special Issue, contributors from around the world improve our understanding of the mechanisms of endophytic colonization, soil-plant-endophyte interactions, how endophytes exploit niches inside the plant, how plants respond to endophyte establishment, and how we can decipher mechanisms of plant-endophyte interactions, both for bacteria and fungi. Additional studies were also done on plant-associated endophytic communities when subjected to various stresses.

New understanding of beneficial bacterial endophytes and plant-soil interactions

Inoculated bacteria-nodulating bacteria interactions and endophytes for plant growth promotion

New bacterial strains that could be used for plant growth promotion and more understanding on how these strains make association within their hosts is relevant for agriculture. There is indeed a current need of new strains for crop improvement as well as bacterial combination. The application of single strains does not always lead to positive results when used under gnotobiotic conditions, a scenario highly dependent of the chosen model. Moreover, they may have an effect on other beneficial microorganisms, thereby conferring better results. This could be the case, for instance, of the improved effects

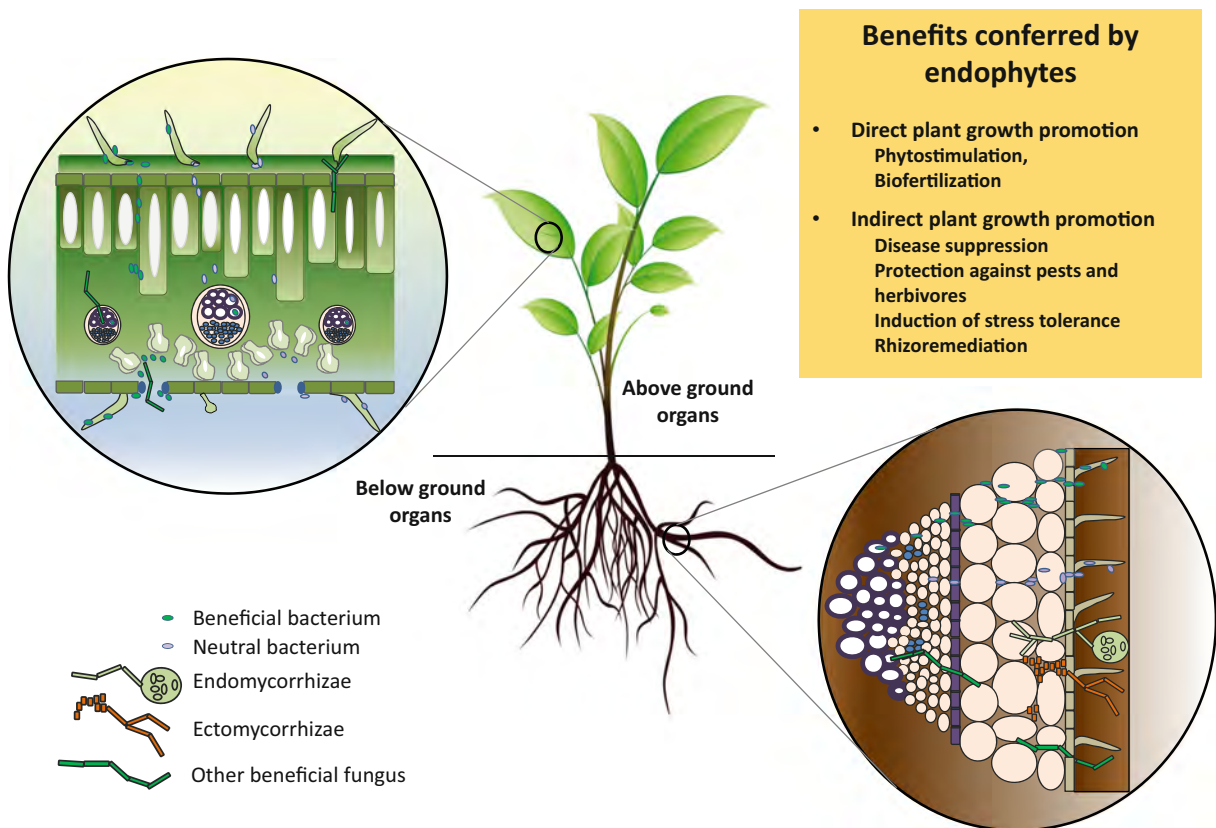


Fig. 1 Drawing showing the niches inside plants and ways of colonization of endophytes

of rhizobia on nodulation and N_2 fixation. Le et al. (2016a, b) described the use of combination of actinomycetes on N_2 fixation and nodulation by *Sinorhizobium meliloti* on Lucerne plants. Egamberdieva et al. (2016) also showed synergistic interactions between *Bradyrhizobium japonicum* and the endophyte *Stenotrophomonas rhizophila* resulting in improved plant growth, nutrition, and fitness of soybean subject to salt stress. Providing plants with a multitude of plant beneficial activities can be achieved by combining several microorganisms, but also by combining different activities within one strain. Such a strain engineering approach was shown by Lowman et al. (2016). In this study the well-known plant growth-promoting endophyte *Burkholderia phytofirmans* strain PsJN was transformed with DNA containing the *nif* operon from *Burkholderia phymatum* STM 815, and was able to promote in vitro growth of switchgrass under low nitrogen conditions. Bacterial engineering could be a successful strategy enabling better effects, albeit for commercial purpose this approach will have limitations.

The identification of microbial strains that do not only promote plant growth but are also able to alleviate a/biotic stresses, and to understand the underlying mechanisms, is highly relevant for agriculture and to comprehend the functioning of plant-microbe-soil interfaces. Comparative analyses of strains could lead to a better implementation of plant growth promotion-related traits, also model used could be relevant. However, the assessment of these beneficial effects under laboratory conditions does not necessarily correlate with outcomes observed under field and/or glasshouse conditions. Indeed, contrasting or contradictory results can be obtained. Rybakova et al. (2016a) compared in this way both antagonistic properties against fungal pathogens and plant growth abilities of five *Serratia* and five *Paenibacillus* endophytic isolates under different growth conditions. They demonstrated that treatment of surface-sterilized oilseed rape and cauliflower seeds with *Serratia* isolates could promote plant growth depending on the strain applied. In contrast, *Paenibacillus* strains damaged roots when applied under

gnotobiotic conditions. However, *P. polymyxa* Sb3–1 did not have a significant effect on plant growth in non-sterile soil, suggesting that gnotobiosis does not represent an ideal system to be used in plant growth promoting studies. Thus, specific soil components may lead to an effect different to that observed under sterile conditions. However, in order to mechanistically determine components targeted by beneficial microbes, a reductionist approach where genes and microbial symbionts can be individually added or removed have proved to be useful. To investigate the growth promotion activity of an endophytic bacterium, analyses of derivative mutants and the effects on the host plant should be compared, as they can provide key information about pathways and/or genes involved in the beneficial effect under study. *Arabidopsis* mutants are widely used for studying plant-microbe interactions enabling the identification of pathways involved in root system development. Mechanisms involved can be auxin dependent, as showed for *Martelella endophytica* YC6887 (Khan et al. 2016). As mentioned above, however, reductionist approaches (i.e. only using a model system without testing/challenging other species/crops under diverse conditions) are not always enough to understand mechanisms involved since a range of different factors may interfere, for instance, with signalling processes.

Bacterial endophytes, colonization and biocontrol: It's up to the endophytes

Some bacterial endophytes do not only stimulate plant growth by making an intimate association with their hosts, but can also reduce severity of pathogenic infection, either directly or indirectly. It is well known that production of antibiotics by bacteria could be a factor contributing to reduce pathogen effects. While some strains have been widely described and used, others which also yield positive effects have not been studied in so much detail. An example is an endophytic *Pseudomonas synxantha* strain, isolated from kiwi plant (*Actinidia chinensis* Planch.), effective against *Pseudomonas syringae* pv. *actinidiae* causing kiwi canker (Tontou et al. 2016). Endophytic bacteria can also exert biocontrol activities against pathogens of invasive plants thereby contributing to their growth and survival. However, scant data are currently available on this specific topic. Soares et al. (2016) identified *B. amyloliquefaciens* strain C6c, from the invasive

English ivy (*Hedera helix* L.), and showed that this bacterium systemically colonized leaves, petioles, and seeds of this invasive plant species, synthesized hormones and secreted different antifungal lipopeptides, eventually resulting in the inhibition of fungal pathogens such as *Alternaria tenuissima* and contributing to plant growth and survival.

Regarding biocontrol, it is also worth mentioning that previous data on some genera can lead to new insights after using metadata analysis. Rybakova et al. (2016b) reviewed the occurrence of *Paenibacillus* spp. in microbial metagenomes, as well as their occurrence as endophytes and the function of volatile organic compounds produced by members of this taxon. These authors also discussed strain-specificity and system-dependent growth promotion effects on plants. Efforts like this are required to extend our knowledge on some bacterial genera used as biocontrol agents, including strains developing an endophytic lifestyle.

Aziz et al. (Aziz et al. 2016) investigated the capacity of endophytic bacteria to suppress diseases as well as the impact of such benefit for the host plant. Several chemical fungicides are still under used to control diseases affecting grapevine (*Vitis vinifera* L.). Searching for new strains exerting effective biocontrol, and elucidating the mechanisms underlying these beneficial effects, will help to develop novel tools for sustainable agriculture. These authors studied single bacterium treatment, or combination of bacteria, to set up an Induced Systemic Resistance response in grapevine against the necrotrophic pathogen *Botrytis cinerea*, and the ability of these bacterial strains to trigger phytoalexins accumulation without compromising grape yield. This is particularly relevant for viticulture, as new approaches excluding or decreasing the use of pesticides should be implemented. Moreover, these strategies must be based on a comprehensive understanding of the underlying mechanisms of protection, particularly when operating under field conditions.

Yet, our understanding of the evolution and mechanisms of beneficial plant-microbe interactions is poor. It is known that some endophytes trigger stress responses, both at local and systemic level, when establishing inside their hosts (e.g. Schiliro' et al. 2012; Gómez-Lama Cabanás et al. 2014). These endophyte-mediated changes in the host may have an effect on its capacity to overcome further pathogen attacks, although it might be strain dependant. Using grapevine as a model, López-Fernández et al. (2016) studied the effects of endophytic

bacterial colonization of strains belonging to families *Sphingomonadaceae* and *Enterobacteriaceae*, which were previously isolated from wild grapevine plants. They described that colonization pattern of these bacteria diverged and was strain dependent. These authors identified metabolic signatures involved in plant colonization and defence and described the modulation of secondary metabolites which seem to be key factors for successful endophytic colonization by different bacterial strains.

Bacterial endophytes and phytoremediation: engineering the colonizers

Endophytic bacteria can not only be useful for plant nutrition and biocontrol but also for phytoremediation purposes. Phytoremediation using endophytes has been studied since the 90's. However, more research is still needed to understand and improve increase phytoremediation processes. Related to this, Ijaz et al. (2016) covered recent developments either on engineering catabolic/metabolic genes from a wide range of sources into plants or endophytic bacteria for the development of modified plant-endophyte interactions aiming to increase the effectiveness of phytoremediation strategies.

Endophytic fungi and plant associations: opening new doors

To fully understand beneficial fungal endophytes and plant-soil interactions of root endophytes requires a thorough understanding of the diversity and complexity of microbes associated with all plant parts, how these microbes subsisting in the same plants interact with each other, and how these microbes modulate above- and below-ground communities and processes.

Foliar endophytes and above-ground processes

Foliar fungal endophytes can profoundly affect above-ground ecosystem processes from the growth-promotion of the host plant to community structure of plants and associated species in food webs. However, interactions between fungal endophytes and plants are variable and range from antagonistic to mutualistic depending on morphological and chemotypic adaptations, and life history traits of the fungus and the host plant

(Saikkonen et al. 1998, 2004). For example, systemic and vertically, via host seeds, transmitted *Epichloë* species and their grass hosts appears to have a higher probability of mutualistic interactions than nonsystemic, horizontally transmitted endophytes in herbs, woody plants and grasses (Saikkonen 2007; Saikkonen et al. 1998). Ecological observations demonstrate that *Epichloë* species can promote plant growth, reproduction and resistance to various a/biotic stresses, and defensive mutualisms against herbivores and pathogens. The defensive mutualism appears to provide the best framework for the understanding of the ecological role of endophytes. However, the defensive mutualism appears to be most commonly detected in systemic and vertically transmitted grass endophytes compared to horizontally-transmitted fungal endophytes (Saikkonen et al. 2010a).

The conceptual framework for endophyte–grass interactions can be, however, biased by limited model systems impeding the understanding (Saikkonen et al. 2016). Here, studies by Lledó et al. (2016) and Casas et al. (2016) focused on foliar fungal endophytes and how they may modulate plant-animal interactions using less studied species and ecosystem functions. Lledó et al. (2016) evaluated the association of six leaf fungal endophytes on *Trifolium subterraneum* forage. They described that beneficial endophytic fungi affected biomass yield, nutritive value and mineral status of this legume species, although effects varied between experiments and depended on fungal species. *Chaetosphaeronema* sp. E202 increased forage productivity by around 80 % in the field, while *Fusarium lateritium* and the Pleosporales member strain E244 reduced AI concentration. A strain of *Epicoccum nigrum* can also reduce Pb content in the host plant under greenhouse experimental conditions. An increase in essential nutrients was mainly due to the presence of *Stemphylium globuliferum*. Overall, this study demonstrated that inoculation with beneficial endophytes can increase forage productivity and also help in reducing potential nutrient deficiencies and/or potential mineral toxicity in *T. subterraneum*.

Casas et al. (2016) determined the extent to which aboveground *Epichloë* endophytes and grazing consumers induce legacy effects on subsequent plants and their interactions with floral visitors. The presence of one or both interactions reduced total visits in subsequent *Carduus acanthoides* L. plants by 45 %. In particular, honeybees and other bees were reduced by 42

and 51 %, respectively. Interestingly, the flower head number or biomass of thistle plants may only partially mediate these effects, demonstrating that symbiosis or grazing affect multiple interactions, including that in the above-ground organs.

Root endophytes and nutrient uptake

The importance of root-associated fungal endophytes has increasingly recognized during the last decades (Jumpponen and Trappe 1998). Similarly to foliar endophytes, root endophytes are abundant, taxonomically diverse, often phenotypically plastic, and their ecological role appears to overlap with soil fungi, saprotrophic and pathogenic fungi, and mycorrhizal fungi. Sebaciniales are a classic example of root-associated fungi detected as mycorrhizal but also as endophytic in many angiosperms with poorly understood ecological role (Selosse et al. 2009). Ngwene et al. (2016) studied endophytic Sebaciniales member *Piriformospora indica*, which was isolated a decade ago from an Indian desert, and which is known for increasing plant resistance and tolerance to stress and for promoting plant growth. The authors hypothesized its ability to support plant nutrition and showed that *P. indica* growth was higher in the presence of inorganic P than in organic P sources. Significant amounts of P are solubilised by *P. indica* from $\text{Ca}_3(\text{PO}_4)_2$ and rock phosphate. Albeit RNA accumulation of related genes was detected, no relevant intra- or extracellular enzymatic activity was detected. Furthermore, related genes were all repressed by higher amounts of inorganic P, but mostly expressed when the fungus received phytate. Interestingly, a pH decrease was observed in the presence of *P. indica* irrespective of the P source. Ngwene et al. (2016) indicated that *P. indica* is able to solubilise phosphate from inorganic, but not from organic P sources, and that P solubilisation could not be due to enzymatic activities, but rather to the lowering of the medium pH.

Foliar endophytes and below-ground processes

Although studies demonstrating the effects of foliar and root endophytes on primary producers and food webs have accumulated during the past decades, endophytes associated with aboveground and belowground plant parts are examined separately (Omacini et al. 2012;

Saikkonen et al. 2015). Here, we propose that a more comprehensive understanding of endophyte mediated ecosystem processes requires studies expanding our knowledge how these above- and below-ground microbial communities interact in the shared host plant. The following five papers of this Special Issue emphasize the complexity of these interactions, and strongly suggest that the integrated knowledge of the role of endophytes in the aboveground food webs and nutrient cycling are very much in need to understand ecosystem functions.

Slaughter et al. (2016) examined whether novel endophyte or common toxic endophyte-infected tall fescue could affect symbiotic and non-symbiotic biological N_2 fixation, and utilization of biologically-fixed N_2 in tall fescue. Infection of tall fescue with the common toxic fungal endophyte *Epichloë coenophiala* is known as harming livestock via toxic alkaloid production, and the need of new non-toxic strains of the endophyte has been recently pointed out (Gundel et al. 2013; Kauppinen et al. 2016; Saikkonen et al. 2016). However, whether new endophytic strains have an impact on biological N_2 fixation in mixed species pastures is unknown. The results by Slaughter et al. (2016) showed that endophytic strains produce different effects on tall fescue and nitrogen utilization. In mixed pastures, the deployment of novel endophytic strains to decrease alkaloid toxicity will differentially impact the use of biologically fixed N_2 in tall fescue and nitrogen concentration in red clover.

Mikola et al. (2016) tested whether the infection of meadow fescue, *Schedonorus pratensis*, by *Epichloë uncinata* can decelerate litter decomposition, N release, increase soil C and N accumulation and lower the availability of mineral N in the soil under infected grass. They found that *E. uncinata* infection neither affected meadow fescue litter N%, litter mass loss nor litter N release. Soil C and N content and resin NH_4 and NO_3 contents did not differ either between the endophyte infected and non-infected grass plots, and litter did not decompose faster when endophyte were used. Finally, these authors did not find evidence that *E. uncinata* infection would decelerate N cycling and reduce N mineralization in meadow fescue grasslands. This suggests that the Epichloid may not decrease the benefit of the endophyte-grass symbiosis by reducing soil fertility.

Soto-Barajas et al. (2016) using several *Epichloë* endophytes and *Lolium perenne* showed also that endophyte-infected plants had significantly lower P, Ca, S, B, neutral detergent fiber and lignin contents, and higher Mn and digestibility than non-inoculated plants, independently of the plant origin. Biomass production was not affected by endophytes but by the plant origin. However, asymptomatic endophyte and choke diseased plants differed in nutrients, fibers, and digestibility, indicating that *Epichloë* may affect aboveground, and possibly underground, processes involved in nutrient absorption.

Vignale et al. (2016) also worked on *Epichloë* species and evaluate how two different asexual species can modulate the establishment of arbuscular mycorrhizal fungi in a wild forage grass under different soil fertilization levels. The authors showed that endophyte-inoculated plants produced more panicles than non-inoculated plants. Thus, endophytism increased arbuscular mycorrhizal fungi colonization and arbuscular frequency. However, fertilization did not affect mycorrhizal symbiosis albeit plant biomass was increased.

Finally, Perez et al. (2016) studied the interaction between *Epichloë occultans*, *Lolium multiflorum* as host plant and soil-borne pathogens. They included neighbouring plants as well to assess whether *Epichloë* endophytes have a role on protecting other plants against pathogens. Results showed that endophytes improved *Lolium multiflorum* host establishment and that of the neighbouring grass *Bromus catharticus* growing in soil infected with *Rhizoctonia solani* and *Fusarium acuminatum*. This demonstrates that endophytes protected host grasses against pathogens, a benefit going beyond to that observed on their hosts.

All the above-mentioned studies clearly showed new advances in our understanding on the benefits exerted by endophytic bacteria and fungi on plants. However, this Special Issue also aimed to investigate the effects of endophytes on the whole plant microbiome, and on the behavior of the endophyte microbiome(s) subjected to abiotic and biotic stresses.

Microbial assemblages within the plants: going to the communities

Following the hologenome theory of evolution the plant genotype is the result of the interplay between the plant

and its microbiome acting in consortia (Zilber-Rosenberg and Rosenberg 2008). Consequently, the outcome of the application of beneficial microbes in plant production is based on a complex interplay between the inoculant strain, the plant and its indigenous microbiota. A better understanding of the mechanisms and driving forces of these interactions are needed to be able to explain beneficial plant-microbe interactions and to explore the full spectrum of microbial assisted plant production. Massart et al. (2015) postulated exciting new avenues in the development of biocontrol solutions by integrating microbial community understanding. Moreover, van Overbeek and Saikkonen (2016) emphasized that the divide between bacterial and fungal endophytes and the related scientific disciplines can impede scientific progress. Here we advocate bridging the gap between the disciplines by the following papers.

Endophytes, biocontrol, disease and microbiome

In this Special Issue, Ardanov et al. (2016) investigated whether the biocontrol effects of the endophyte *Methylobacterium* sp. IMBG290 are modulated through the indigenous endophyte community present in potato (*Solanum tuberosum* L.) host. The positive effects of bacterial treatments correlated with a shift in the bacterial and fungal endophytic communities. This highlights the importance of considering inoculant-microbiome interactions when designing complex microbial inoculants for plant protection.

Steinrucken et al. (2016) opens up new avenues in the research on endophytes and disease control by analysing whether changes in archaeal, bacterial and fungal endophytic community structure are associated with dieback occurrence in the invasive leguminous tree *Parkinsonia aculeata* L. The authors showed that microbial community composition strongly differed according to the disease status and plant part. The authors also found evidence for both pathogenic and potentially protective endophytes in the onset of dieback. This study supports the hypothesis that a complex of endophytes (beneficial or pathogenic) may play a role in dieback disease development.

Microbiome and endophytes in the missing plant organs

All organs of plants have been found to host complex microbiomes, but the microbial assemblages associated with plant reproductive and disseminating organs could

be of outermost importance for plant development, establishment and evolution. However, little research has been performed on this topic so far. Seed microbiomes have not been studied until recently (Barret et al. 2015; Klaedtke et al. 2015) and many aspects in the ecology of seed endophytes remain elusive. The sources of the seed microbiome, routes of transmission, possible heritability from one seed generation to the next and the role of the seed endophytes in the development of the microbiome in the emerging plant are still hardly understood. Using the plant model *A. thaliana*, Truyens et al. (2016) investigated the effect of different growth substrates, frequently used for propagation of this species, on the assemblage of its endophytic community. Both cultivation-based and cultivation-independent approaches were used to study soil bacteria and endophytic bacteria from seeds, radicles and leaves. Interestingly, the authors showed that despite differences found in soil bacterial assemblages, seed and radicle endophytic communities were similar, and that the leaf endophytic assemblage was mainly derived from the environment and not from the seed. Truyens et al. (2016) claimed that “During plant growth, bacteria seem to be recruited from the environment to complement the endophytic population from which the seed endophytes of the next generation can again be selected”, which is of special interest to better understand how plants select microbes eventually thriving as endophytes inside different tissues. Similarly, Johnston-Monje et al. (2016) assessed the impact of soil microbes and plant genotype on the composition of *Zea mays* ssp. *Mays* L. associated bacterial communities. They found that maize rhizospheres are influenced by the genotype or treatment of the seed, and are dominated by species of *Proteobacteria*, *Actinobacteria*, *Bacteroidetes*, and *Firmicutes*, concluding that seed communities can colonize the new plant generation. Moreover, they also colonized the rich zone of the rhizosphere, suggesting that the seed can also shape the rhizosphere community.

Endophytes, microbiome and extreme conditions

The plant microbiome has been further suggested as an extension of the host phenotype (Alekklett and Hart 2013) and an intact microbiota is crucial for healthy growth of plants especially under extreme conditions. Microbial components of plants growing under extreme environmental conditions are supposed to play an important role in plant establishment and adaption.

However, the effect of harsh environmental conditions on the composition of microbial assemblages has not been studied well so far. Soussi et al. (2016) provided a comprehensive overview of the microbial diversity in arid lands and deserts versus specific microbial assemblages associated with the endosphere of plants. Discussion about the drivers shaping the endophytic diversity, on how plant-associated microbiomes are selected, and on their biotechnological potential was well provided. Selection and recruitment of the plant-associated bacterial assemblages was mediated by the combination of several factors such as the bio-pedo-agroclimatic conditions and the plant species or varieties. This study does not only enhance our understanding of the ecology of endophytes, but also identified desert-adapted strains for plant improvement.

Endophytes, microbiome and plants under other conditions

Pili et al. (2016) characterized the endophytic fungi assemblage associated with rice roots in irrigated and upland ecosystems in Kenya. The study was focused on *Fusarium oxysporum* (FOSC) and *Gibberella fujikuroi* (GFSC) species complexes, but more fungal species were found in the irrigated ecosystems than in the upland ecosystems. The authors concluded that flooding may affect the assembly of endophytic fungi in rice roots, but rice cultivars, geographical locations and soil types could also be important. In another study, Robinson et al. (2016) reported on the role of tissue type, growth stage and soil fertilizers in shaping the root and leaf bacterial endophyte communities of winter wheat (*Triticum aestivum* cv. Hereward), demonstrating that the plant microbiome is shaped by a complex interplay between biotic and abiotic factors.

Conclusions and future prospects

Overall, this Special Issue focusing on soil, plant and endophytes made advances in understanding the plant-soil-microbe network. New components of plant-soil-microbe interactions were revealed and the potential of some endophytes to serve as fertilizers and pesticides to promote plant growth, strengthen plant health and fight off pathogens in sustainable crop cultivation systems have been highlighted. Complexity of microbiome subjected to environmental stresses have been also studied.

Further research, however, is needed to understand plant-soil-endophyte interactions as a multi-dimensional network between plants, complex microbiomes consisting of fungi, bacteria and viruses and the environment, and it will in future help to crack the black boxes of endophyte ecology and to exploit better the potential of these fascinating microorganisms for a sustainable agriculture. More mechanistic studies are furthermore still required to elucidate the many open questions on endophytes. Key approaches to comprehend better the role of endophytes in above- and below-ground processes should also not only be focussed on plant effects, but also on the microbiome itself, its functionality, the artificial inoculation of endophytes and to try to think in a plant or a microbe viewpoint, which was done in this volume, but that still requires additional hypothesis-driven approaches.

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