

Review

Forest Tree Microbiomes and Associated Fungal Endophytes: Functional Roles and Impact on Forest Health

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Abstract: Terrestrial plants including forest trees are generally known to live in close association with microbial organisms. The inherent features of this close association can be commensalism, parasitism or mutualism. The term “microbiota” has been used to describe this ecological community of plant-associated pathogenic, mutualistic, endophytic and commensal microorganisms. Many of these microbiota inhabiting forest trees could have a potential impact on the health of, and disease progression in, forest biomes. Comparatively, studies on forest tree microbiomes and their roles in mutualism and disease lag far behind parallel work on crop and human microbiome projects. Very recently, our understanding of plant and tree microbiomes has been enriched due to novel technological advances using metabarcoding, metagenomics, metatranscriptomics and metaproteomics approaches. In addition, the availability of massive DNA databases (e.g., NCBI (USA), EMBL (Europe), DDBJ (Japan), UNITE (Estonia)) as well as powerful computational and bioinformatics tools has helped to facilitate data mining by researchers across diverse disciplines. Available data demonstrate that plant phyllosphere bacterial communities are dominated by members of only a few phyla (Proteobacteria, Actinobacteria, Bacteroidetes). In bulk forest soil, the dominant fungal group is Basidiomycota, whereas Ascomycota is the most prevalent group within plant tissues. The current challenge, however, is how to harness and link the acquired knowledge on microbiomes for translational forest management. Among tree-associated microorganisms, endophytic fungal biota are attracting a lot of attention for their beneficial health- and growth-promoting effects, and were preferentially discussed in this review.

Keywords: microbiota; microbiome; endophytes; fungi; forest trees

1. What are Microbiomes

Land plants are ubiquitously associated with various microorganisms. The communities of fungi, bacteria, archaea, and protists colonizing plant tissues and inhabiting outer plant surfaces, collectively comprise plant microbiota [1]. Different plant tissues host distinct plant communities, which are commonly divided into the rhizosphere (microbial communities associated with root surface and adjacent soil layer), phyllosphere (microbial communities of outer surfaces of aerial plant parts) and endosphere (microbial communities residing within plant tissues) [1]. The plant microbiome (phytobiome), in turn, is defined as a full set of microbial genomes associated with a host plant [2].

The importance of plant-associated microbes for host plant fitness, health and nutrition is universally accepted [3]. In particular, certain fungi and bacteria promote plant growth and increase

their stress resistance [4]. However, not all symbiotic organisms provide benefits to the host, as plant-microbial interactions can also be neutral (commonly referred to as commensalism) or even deleterious for the host (parasitism or pathogenicity) [4,5]. The overall impact of plant-associated microbes on host health and fitness is determined by a number of factors, which include host and microbial genotypes, interactions within microbiota and various abiotic factors [4].

The collective efforts of research groups working in the field resulted in the accumulation of a considerable amount of knowledge about the diversity of microorganisms (mainly bacteria and fungi) associated with the model plants and the important agricultural crops. At the same time, our knowledge of microbiota associated with other plant species is still limited and often fragmentary, even in the case of the most common species of temperate and boreal forests [6]. When comparing the numbers of publications associated with “microbiome”, “microbiota” or “metagenomics”, and also combining one of these terms with either “human”, “agricultural crops” or “agricultural crops or plants” or “forest trees” between the decades of 1998–2008 and 2009–2018, the immense increase indicates the increasing level of interest (Figure 1).

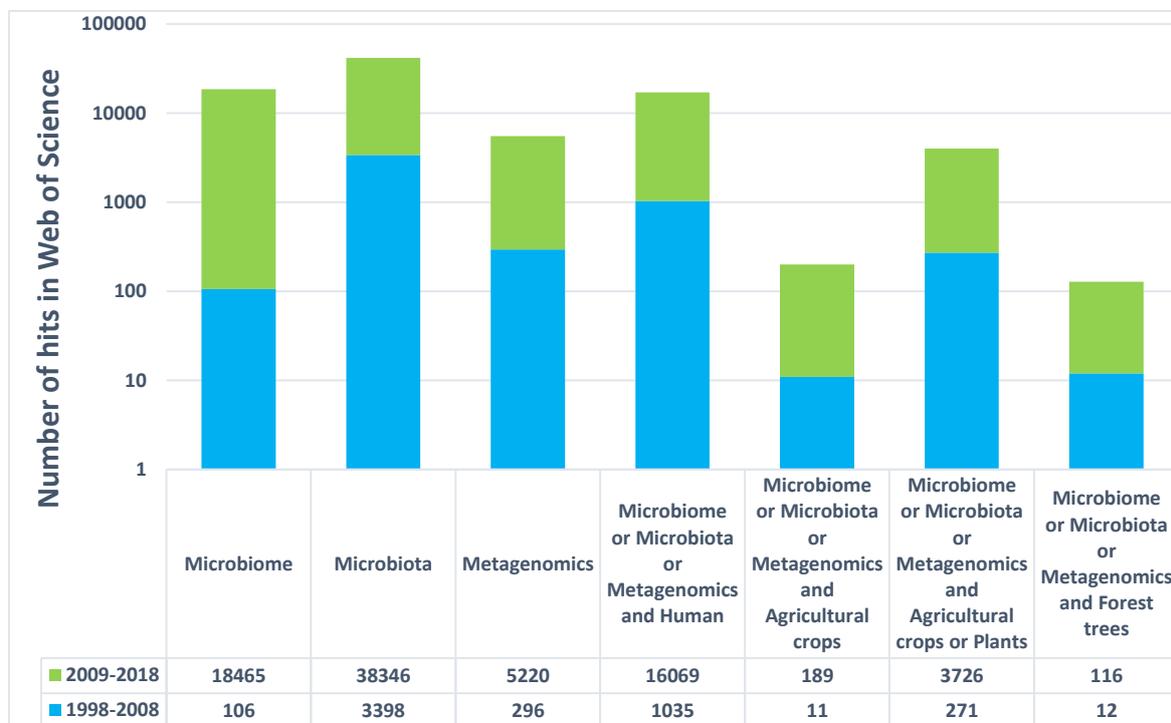


Figure 1. Total number of microbiome, microbiota or metagenomics associated peer-reviewed articles for human, agricultural crops, plants or forest trees from 1998–2008 and 2009–2018.

2. Insights from Agricultural Crops and Human Microbiome Projects

It has been acknowledged that human microbiota play key roles in human health and disease progression [7]. The increasing interest in the exploration of human microbiome has boosted the development of corresponding techniques, methodological approaches, experimental procedures and computational tools applicable to forest biomes. In turn, the studies of plant microbiomes could greatly benefit from the progress achieved in the understanding of the human microbiome and from the technical advances in the field. Currently, the focus in studies of plant microbial communities is shifted from the initial descriptive phase towards mechanisms controlling the assembly and functioning of microbiota, the functional role of individual components and the possible applications in the integrated plant management plans.

Metagenome-wide association studies (MWAS) constitute one of the important approaches towards better understanding of the functional role of individual components of microbiomes.

In MWAS, a possible association between a relative abundance of a given gene in the metagenome and an occurrence of a disease of interest is analyzed [8]. MWAS is widely used to study associations between microbiome and human diseases, such as type-2 diabetes, rheumatoid arthritis, and obesity [8]. The success achieved in the applications of MWAS in human and animal studies supports the extension of this approach to analyze associations between plant microbiomes and diseases.

Another promising approach to address the functional role of individual microorganisms and to get insights into the principles of assembly and functioning of plant microbiota is based on the concept of synthetic microbial communities [9–11]. These communities are produced by inoculations of germ-free plants with a mixture of known culturable microorganisms in defined proportions [12]. In this way, researches can control the composition of plant-associated microbial communities. Due to their lower complexity, synthetic communities provide better tractable alternatives to natural systems. The progress in the genomics of forest trees and their associated microorganisms opens the way for use of synthetic microbial communities in the study of forest tree microbiomes.

3. Phytomicrobiome

3.1. Agricultural Plants Versus Forest Trees Tissues Microbiome

Numerous studies on plant microbial communities in the last two decades have contributed to our current insights into the diversity of microorganisms (in particular, bacteria and fungi) living in association with plants. Microbial communities of several plant species, including model plants and their wild relatives, important agricultural crops and a number of tree species, have been surveyed. Available data demonstrate that plant phyllosphere bacterial communities are dominated by members of only a few phyla (Figure 2), namely Actinobacteria, Bacteroidetes, Proteobacteria and, to a lesser extent, Firmicutes [13–15]. Interestingly, our survey of bacterial communities of Norway spruce (*Picea abies* (L.) H. Karst.) revealed a relatively high abundance of members of the phylum Acidobacteria [16]. This phylum was underrepresented in other plant species analyzed so far. In total, representatives of over 50 bacterial families were found in association with various plant species [14]. The most abundant taxa in rhizosphere belong to the orders Actinobacteriales, Burkholderiales and Flavobacteriales. At the same time, *Methylobacterium*, *Pseudomonas* and *Sphingomonas* are among the most abundant genera inhabiting the aboveground parts [13,14].

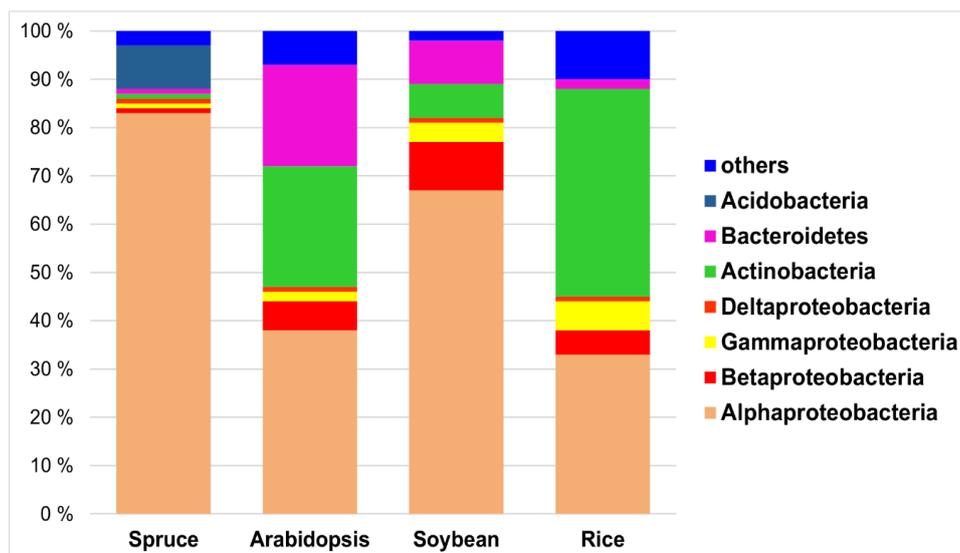


Figure 2. The relative abundance of the dominant bacterial phyla in the phyllosphere of a forest tree (Norway spruce) and herbaceous plants (Arabidopsis (*Arabidopsis thaliana* (L.) Heynh.), soybean (*Glycine max* (L.) Merr.) and rice (*Oryza sativa* L.)) [15,16].

The majority of fungi-inhabiting tissues of terrestrial plants belong to the phyla of Ascomycota, Basidiomycota and Glomeromycota. Representatives of the last group are also known as arbuscular mycorrhiza (AM) fungi, and they are an important component of the rhizosphere, forming a symbiosis with 70%–90% of land plant species [17]. Various members of Ascomycota and Basidiomycota inhabit both below- and above-ground parts of plants. Most of the plant-associated ascomycetes belong to the classes of Dothideomycetes, Sordariomycetes and Leotiomycetes, whereas Agaricomycetes is by far the most abundant group among Basidiomycota [5]. Molecular data indicate that hundreds of fungal species can be found even within a single plant [18], forming a complex spatial pattern [19]. However, species-level identification of many fungal taxa is not always possible, and numerous fungal species inhabiting plant tissues have not yet been formally described [20]. Many of the fungi associated with plants show a certain level of host specificity. For example, certain endophytes belonging to Heliales have preferences for conifer trees [20], whereas a number of ectomycorrhizal (ECM) fungi show specificity for a single host species [21]. In addition, woody tissues of trees often host fungal species, which are absent from herbaceous species, such as members of orders Polyporales and Russulales [5].

3.2. Soil Microbiome Versus Plant Tissue Microbiome

As demonstrated by numerous reports, microbial communities associated with plant roots (rhizosphere and endosphere) show pronounced differences compared with the communities of the surrounding bulk soils, and are characterized by lower microbial species richness. It is assumed that plants can actively influence, in a two-step mediated selection process, the diversity and composition of microbiota associated with their roots. Initial selection is often achieved via rhizodeposition, which mediates substrate-driven shifts in community structure. Further selection of root endophytes occurs via host genotype-mediated mechanisms, restricting number of microorganisms colonizing inner tissues [13,22,23].

The composition of fungal communities of the rhizosphere and surrounding soils also show pronounced differences. In comparison with bulk soil, rhizosphere communities are enriched in mycorrhiza-forming fungi, whereas saprotrophs are much less abundant [6]. Mycorrhizal fungi often show a certain degree of host specificity. Roots of grasses are predominantly colonized by AM fungi, whereas many important forest trees are engaged in mutualistic relationships with ECM fungi. In bulk soil, Basidiomycota is the dominant fungal group [24], whereas in needle tissues, trunk and suberized roots, Ascomycota is the most prevalent group [18] (Figure 3).

3.3. Processes Driving Tree Microbiome Dynamics and Diversity: Impact of Host Genotype and Phenotype

The applications of metagenomics and metatranscriptomics have greatly facilitated studies on the composition of plant microbiome and its role in plant health [25]. Nevertheless, many questions concerning the factors driving the composition of the plant microbiota remain open. There are indications that soil types are the main driving forces affecting the microbial communities of the rhizosphere [22,23,26]. In contrast, the host genotype is the main factor influencing microbial communities residing within plant tissues (the phyllosphere and the endosphere) [13,27].

Currently, the focus in the study of phytobiomes is gradually shifting from the initial, predominantly descriptive phase towards better understanding of the principles of plant microbiome assembly, the factors influencing the structure and composition of plant microbial communities and the development of tools for the rational manipulation of plant microbiomes towards increased plant productivity and disease protection. The integration of beneficial plant microbiomes into crop production is considered as an essential prerequisite of sustainable agriculture [28]. At the same time, the rationale engineering of microbial communities of forest trees is expected to be of great significance for the sustainable wood and timber production, for the improved tolerance of forest ecosystems against environmental stressors and for the management of forest tree diseases and pests.

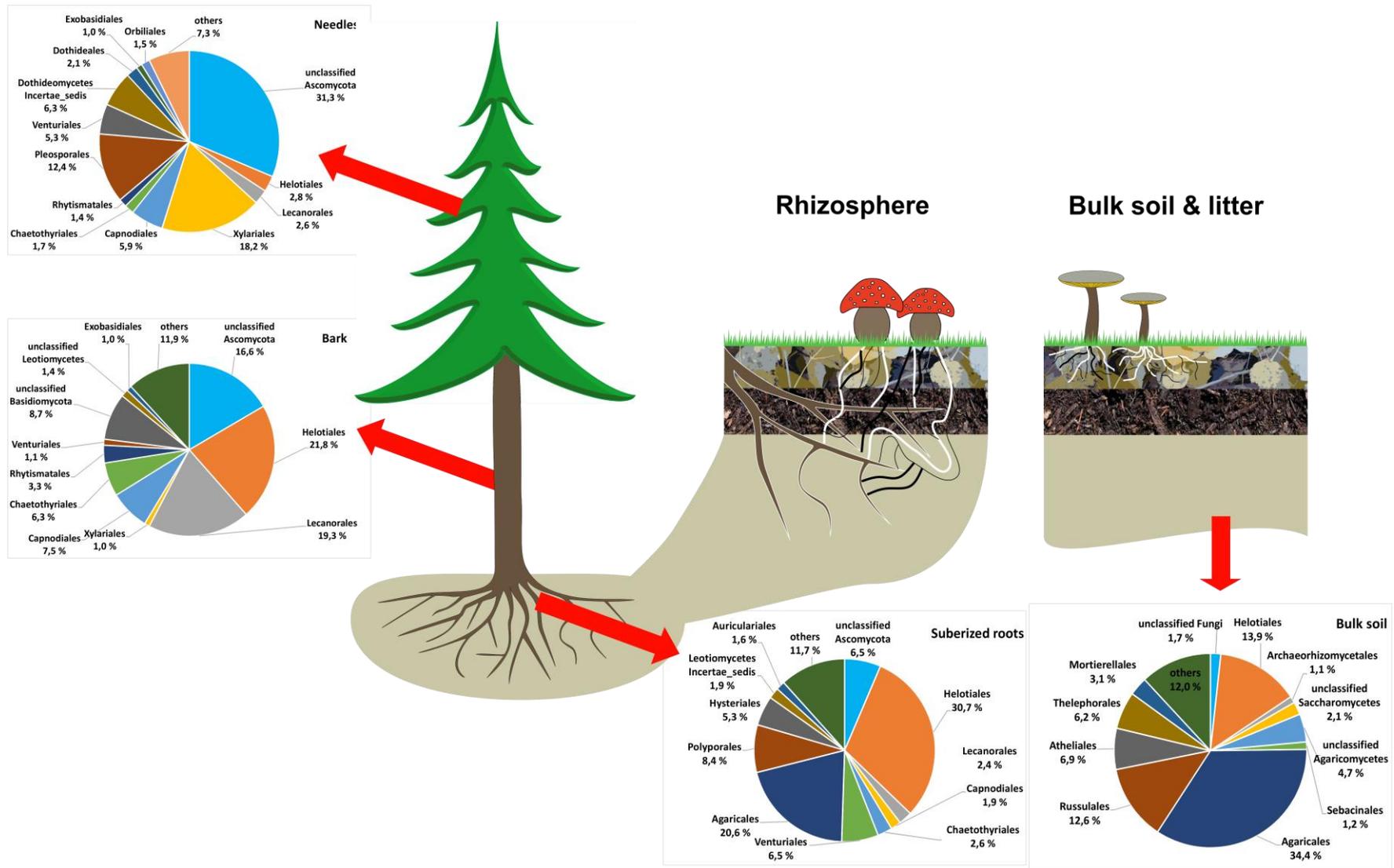


Figure 3. The relative abundance of the dominant fungal orders in bulk soil and different tissues of Norway spruce [18,24].

Available data indicate that the composition of plant microbiota is synergistically determined by plant genotype and environmental factors. The dissection of effects of various factors simultaneously affecting plant microbial communities is considered as one of the main challenges currently faced by this research area. It is recognized that the understanding of abiotic and biotic factors influencing plant microbial community assembly and stability will be crucial for any effort to manage plant microbiomes [28]. At the same time, this understanding is crucial for our ability to predict the possible effects of climate changes on the functioning of plant microbial communities.

The studies of the effect of individual abiotic factors are often performed under controlled conditions, as a simultaneous action of multiple factors exhibiting fluctuations greatly complicates this type of studies of natural ecosystems. The data available so far indicate that the key abiotic factors affecting plant microbiome include temperature, light, nutrient and water availability and soil pH [29]. Arguably, most of the available experimental data are related to the structure of microbial communities of plant rhizosphere. Soil properties (type, structure and chemistry (pH and nutrient availability)) affect the microbial communities associated with plant roots both directly and indirectly, via their effect on the vegetation cover. Several studies have shown that for a given plant species, soil properties have a stronger effect on the composition of root microbial communities than a host genotype [22,23,26]. Temperature, humidity and light intensity might be important factors shaping the structure and composition of microbial communities of the phyllosphere, whereas endosphere communities residing within plant tissues might be affected by environmental factors to a somewhat lesser extent, as they can benefit from the relatively stable conditions of their growth niche [29]. However, the effects of the individual abiotic factors on the functioning of microbial communities of phyllosphere and endosphere have not yet been sufficiently experimentally addressed. Interestingly, the control of plant microbiomes by abiotic factors and host genotype features could be achieved via a small number of microbial taxa, so-called microbial “hubs”, as was recently demonstrated [30]. It is predicted that “hub” microbes are directly affected by both biotic and abiotic factors, and in turn, transmit the effects to the microbial community via microbe–microbe interactions.

Another important topic that receives a lot of attention is the role of plant microbiome in the disease resistance and the impact of pathogens on the composition of plant microbial communities. A number of available studies indicate a possible correlation between host plant resistance to pathogens and the structure of their microbial communities [31,32]. At the same time, colonization of plants by pathogens was shown to cause changes in the diversity and/or structure of plant microbiota [18,33–36]. However, the effects of pathogens might differ depending on the chosen experimental model [4].

3.4. Lifestyle and Phenotypic Plasticity among Phytomycobiontes

Fungi display a wide spectrum of lifestyles ranging from beneficial mutualistic symbionts [37], latent endophytes [20,38,39], and benign saprotrophs [40] to devastating necrotrophic pathogens [41]. Both necrotrophic and saprotrophic lifestyles and the ability to form mutualistic symbiosis (e.g., mycorrhiza) or endophytic relationships can be found among diverse groupings of fungi at all taxonomic levels. Cairney [42] reported that the evolution of mycorrhiza symbiosis occurred simultaneously with the first establishment of plant on land 450–500 million years ago, and that it still exists in most plant species. Also, based on phylogenetic evidence, Hibbett et al. [43] suggested that ectomycorrhizal symbionts with diverse plant hosts might have evolved repeatedly from saprotrophic progenitors. Furthermore, many of these fungi are often characterized by phenotypic and lifestyle plasticity. Under diverse interaction conditions or circumstances, many fungi have been reported to be capable of multi-trophic life strategies such as biotrophy and saprotrophy, or necrotrophy and saprotrophy, or endophytism and saprotrophy, as these are not necessarily “mutually exclusive” [44–47]. *Armillaria mellea* (Vahl) P.Kumm. is a typical example of a necrotrophic basidiomycete known to be pathogenic to living trees but forming transient mycorrhizal association with orchids [48,49]. The saprotrophic wood decayer *Phlebiopsis gigantea* (Fr.) Jülich has also been demonstrated to colonize fine roots of living trees similar to functional mycorrhizal associations [45].

Jaber et al. [46] showed that the saprotrophic basidiomycete *Stereum sanguinolentum* (Alb. & Schwein.) Fr. promoted lateral root formation in Scots pine (*Pinus sylvestris* L.) seedlings but caused mortality on Arabidopsis plants. Using *Neurospora crassa* Shear & B.O. Dodge as a model, Kuo et al. [44] demonstrated that the fungus is capable of so-called endophytic–pathogenic–saprotrophic (EPS ring) lifestyles. Cairney [42] considered that all these complex symbiosis interactions may likely involve mutual genetic exchanges in free-living fungi and their descendants, which may suggest an ongoing reciprocal and parallel evolutionary changes between fungi and diverse plant taxa.

4. Endophytes as Part of Tree Microbiomes

As stated above, trees have relationships with microbiomes that play important roles in the health of an individual tree. All parts of trees have their own specific features that influence the microbial abundance, as well as the composition of their communities [6]. Forest tree microbiome studies have traditionally concentrated on mutualistic associations (mycorrhizas) [50] or pathogenic (e.g., root rot) relationships [41]. The ubiquitous diversity of endophytes within individual hosts suggests that they may have a significant impact on their host trees.

The term “endophyte” was first coined by Anton de Bary already in the mid-19th century, and it was freely translated by Stergiopoulos and Gordon [51] as “any fungus or bacterium found inside plant tissues” and by Rodriguez et al. [52] as “the living together of dissimilar organisms” [51–53]. Later, endophytes were characterized as microorganisms that invade tissues of living plants without causing any apparent effect [54,55]. The most used definition includes also the life cycle: endophytes are microorganisms that colonize plant tissues for a considerable part of their life cycle (Figure 4) without causing disease to their host [56,57]. This definition excludes beneficial microorganisms such as mycorrhizal fungi, as well as microorganisms with negative effects. The exceptions are the latent pathogens that have an endophytic stage in their disease cycle (so called cryptic life cycle) [5,55]. However, endophytes that establish symptomless associations with their hosts are not automatically obligate endophytes. Rather, they may switch between pathogenic and commensal or mutualistic lifestyles, depending on external factors, such as environmental conditions and the host [39,58–60].

Fungal endophytes are considered ubiquitous, because there have been no reports of any natural plant or tree species devoid of endophytes [20,61]. Although fungal endophytes and their interaction with a diverse range of tree hosts have been studied for decades, many concepts of these complex interactions are still not well understood [59,62]. Nevertheless, the benefits conferred by endophyte colonization were demonstrated by numerous studies, but at the same time, the negative effects are also constantly documented. Hence, understanding the functioning of this possible symbiosis is significant in its own right. The increasing interest in endophyte communities of plants is derived from their apparent potential to positively influence the stress tolerance in trees [63–67]. Endophytes of forest trees have, in recent years, received noticeable attention for their potential as a major source of bioactive compounds with novel chemical features [52,68,69], further providing new sources to be exploited in tree health protection [70].

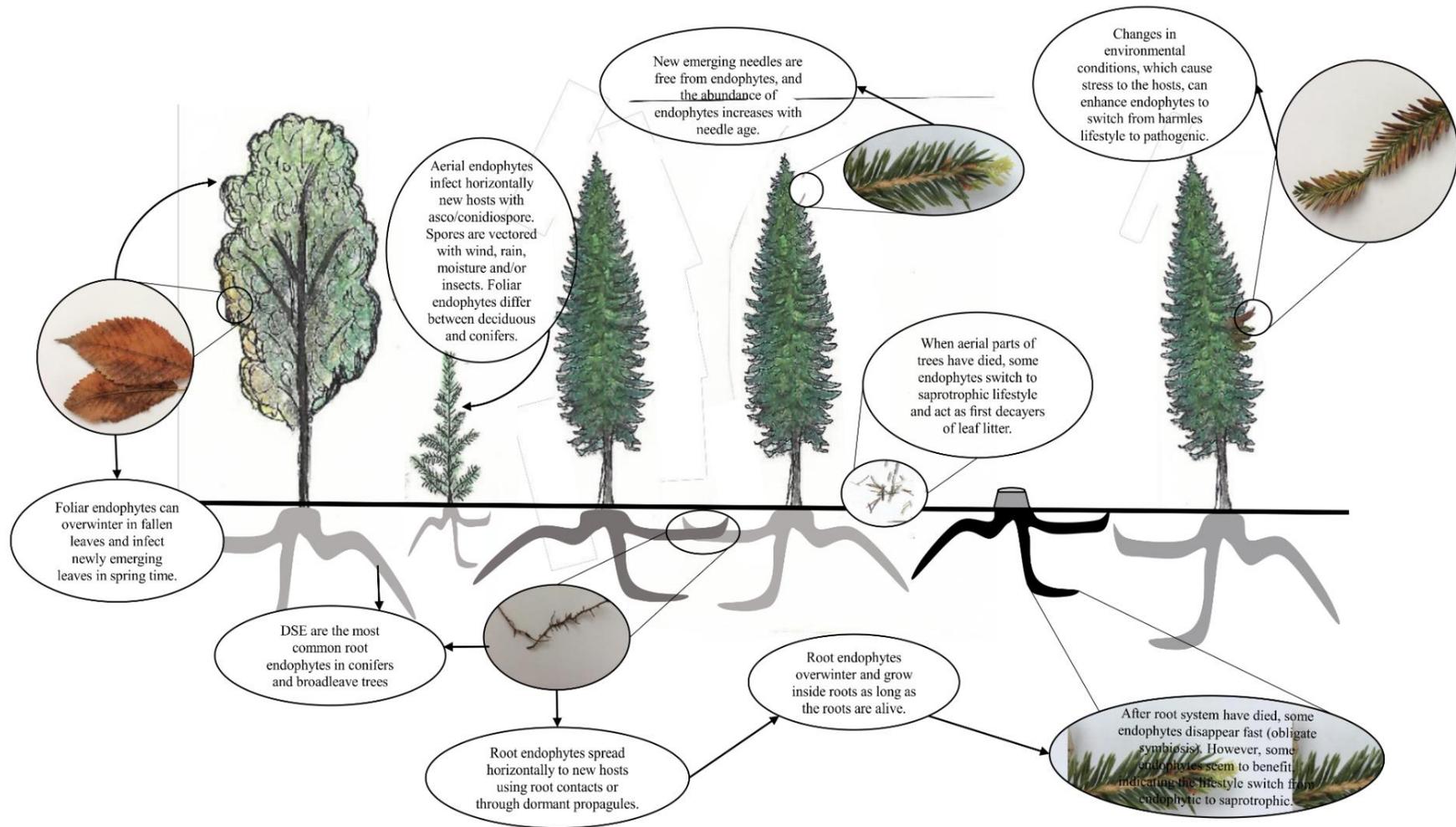


Figure 4. Scheme illustrating life cycles of fungal endophytes.

5. Nature of Fungal Endophytes

When endophytes infect and grow inside the host tissues, they face host defense reactions. The asymptomatic development of endophytes within their host depends on their ability to maintain balanced antagonisms with the host and with the competing microorganisms [71]. Often in pathogenic interactions, host defenses are breached, leading to disease; on the other hand, endophytes only tolerate and accommodate host defense primarily to infect and colonize the plant tissues [72].

Two main groups of endophytic fungi are widely known: non-clavicipitaceous endophytes (NC-endophytes) and clavicipitaceous endophytes (C-endophytes) (Table 1) (see review by Rodriguez et al. [52]). Furthermore, clavicipitaceous endophytic fungi are grouped into Class 1, and they infect mainly grasses [52,73]. The non-clavicipitaceous endophytic fungi are grouped into Classes 2, 3 and 4 according to host range, colonized plant tissue, biodiversity, transmission, fitness benefits and in planta colonization (Table 1 in Rodriguez et al. [52]). C-endophytes within Class 1 (phylum Ascomycota) have developed specialized interactions with grasses and their transmission to a new host is primarily vertical; the fungi are passed on from maternal plants to offspring via seed infections [52,74]. These C-endophytes which are not discussed in detail in this review have been reported to enhance drought tolerance and increase plant biomass as well as to produce chemicals that are toxic to animals, leading to decreased herbivory [39,75–78]. However, the benefits to the hosts are not always mutualistic, as they are often dependent on environmental factors, host species and genotype [39,79–81].

All forest tree endophytes belong to NC-endophytes (Classes 2, 3 and 4) that infect the host plants mainly horizontally (infections between one individual to other) [52], but some fungal endophytes in Class 2 are known to transmit vertically [82]. Class 2 endophytes comprise a diversity of species, all of which are members of the subdivision Dikarya (Ascomycota or Basidiomycota) [52]. Class 2 endophytes can be found in both above- and below- ground tissues (shoot, root and rhizome) [52]. Their host range is broad, but a notable fact is that even the colonization is extensive inside plant tissues. It has been reported that the biodiversity of Class 2 endophytes within individual host plants is limited [52,83]. Rodriguez et al. [52] defined endophyte-conferred fitness to the hosts as habitat-adapted, which are mostly derived from environment-specific selective pressures such as salinity, pH, and temperature [52]. Only Class 2 endophytes are shown to have this ability to confer stress tolerance to host plants [83].

Class 3 endophytes are distinguished from other classes based on the restricted occurrence to aboveground tissues. The class 3 endophytes often form localized infections and the benefits they confer on their hosts are usually not habitat-specific. High diversity of Class 3 endophytes within a host plant tissue has also been reported (Table 1 in Rodriguez et al. [52]). Members of Class 3 endophytes belong to the fungal group Dikaryomycota (Ascomycota or Basidiomycota), with specialization to Ascomycetes [52]. Virtually all plant leaves are colonized by fungal endophytes [52,57] and foliar endophytes of trees are relatively well studied [84–87]. The composition of Class 3 endophyte species within the same host and different forests stands can be quite distinct [86,87]. Equally, the same endophytic species have been reported to occupy several and diverse plant hosts [86,88–92].

The niche of Class 4 endophytes is restricted to host roots and they are capable of extensive colonization of these tissues [52]. Endophytic fungi in Class 4 belong to different taxonomic groups mainly in the phylum Ascomycota, and some belong to Basidiomycota [52]. Dark Septate Endophytes (DSE) are the largest group in the Class 4. DSEs most likely can be found from all terrestrial plants, as they have been discovered from all over the world, from the tropics to the arctic, and in nearly 600 plant species (see review by Jumpponen and Trappe [61]). To classify an endophyte as DSE, it should be able to form specialized structures (microsclerotia) in the host roots, and also present in plant roots as asexual, both septate and melanized hyphae [61,93]. Other non-DSE species of Class 4 include *Gibberella*, *Ilyonectria*, *Fusarium*, *Cylindrocarpon*, and *Neonectria* and the *Sebacinales*, while the genera *Microdochium* and *Cryptosporiopsis* comprise both DSE and non-DSE species [62]. In tropical trees, the dominating DSEs belong to genera *Alternaria*, *Ascochyta*, *Cladosporium*, *Microdiplodia*, *Nigrospora* and *Phoma* [94]. The dominant group of DSEs in conifers consist mostly of *Phialocephala fortinii* C.J.K.

Wang & H.E. Wilcox s.l.-*Acephala applanata* Grünig & T.N. Sieber species complex (PAC), and they are among the best-characterized DSEs [95–102]. The PAC members are very widespread and abundant in the roots of ericaceous plants and conifer trees [18,96,98,103–106]. Members of PAC species complex cannot be differentiated based on morphology. Rather, multilocus molecular markers have usually been used for the identification of members of the PAC to species level [96,99–103]. Generally, DSEs do not have host specificity; however, there are some species that seem to prefer certain host taxa e.g., *Cadophora*, *Cryptosporiopsis*, and some of the PAC species (*Acephala applanata* Grünig & T.N. Sieber) preferentially occur on family Pinaceae [18,20,92,96,105–107]. Despite the apparent abundance of Class 4 endophytes, their functions and ecological roles have not yet been determined [62].

6. Fungal Endophyte Diversity in Forests

6.1. Aerial Endophytes

Foliar endophytes are well studied in the tropics, where the Class 3 endophyte composition has been noted to harbor extremely high biodiversity [84,85,108]. For example, more than 20 fungal endophyte species have been recorded from a single tropical leaf [109]; similarly, around 242 and 259 fungal endophyte morphospecies were recovered from the neotropical trees *Heisteria concinna* Standl. and *Ouratea lucens* (Kunth) Engl. respectively [110]. Class 3 endophytes have notably high biodiversity also in the temperate forest trees [54,87,111–119], as well as in boreal conifer communities [86,120–123]. Higgins et al. [118] found that the cultivable endophyte community diversity in healthy foliage of *Picea mariana* (Mill.) Britton, Sterns & Poggenburg in Mingan Archipelago was consistent with that observed with several hosts in tropical and temperate sites [84]. The diversity of endophytes in conifers tends to increase with needle age, as the colonization rate is higher in older needles [114,122,124–126], but culture-free studies showed that current-year needles harbor an enormous diversity of fungal endophyte species [86]. The biodiversity of fungal endophytes in the needles of Pinaceae (*Pinus* sp. and *Picea* sp.) have been studied since the 1970's [54,127]. In Pinaceae, the dominant endophytic fungal species documented belong to the classes Leotiomyces, Dothideomyces and Sordariomyces [20,86,128–131]. The frequency is extremely high in aerial parts of trees, but the studies have shown that for foliar endophytes, a relatively small number of endophyte species dominate the fungal communities [20,91,108,110,132–134].

U'Ren et al. [135] showed that plants harbor diverse and abundant cultivable fungal endophyte communities. They also reported that the composition and diversity of these endophytes are affected by the interaction of the host genotype, abiotic factors and geographical distance. Nguyen et al. [86] using next generation high-throughput sequencing (NGS) observed significant differences in the fungal endophyte communities of *P. abies* needles in several geographically-separated forests (Finland, Romania, Germany and Poland), which further underlines the impact of geographic distance on endophytic communities. The abundance and diversity of tree-associated fungi have further been shown to be affected by increases in latitude [122,123]. Differences were documented in the endophyte community of *Fraxinus excelsior* L collected from the north and south side of the Alps [87,136]. The presence of diverse tree species in a mixed forest that consisted of *Alnus glutinosa* (L.) Gaertn, *Larix sibirica* Ledeb., *P. abies*, *Pinus sylvestris* L.) was shown to have an effect on a foliar fungal community of *Betula pendula* Roth. [137]. In tropical tree species, the host associations have also been noted to have an influence in the composition of the fungal endophyte community [138]. Outside the native range of trees (*Fraxinus ornus* L., *Fagus sylvatica* L.), they harbor distinct species diversities compared to native range where more host-specific fungi can be observed [139,140]. Some dominant fungal endophytes show a strong host specificity (e.g., *Venturia fraxini* Aderh., *V. orni* M. Ibrahim, M. Schlegel & T.N. Sieber) [136,141,142]. These results suggest that diverse forest ecosystems, due to site-specific factors (climate, host species and latitude), have an effect on the species distribution and frequency of fungal endophytes [86,135].

The species composition and relative abundance of endophytic fungi in the leaves of broadleaf plants can vary widely between developmental stages of the diverse hosts (natural old forests, managed mature forests and seedling stands) [143]. Taudière et al. [144] found that young (two-year old) and mature trees (10–15 years) host similar numbers of foliar endophytes with some differences in community compositions and species richness. Similarly, Koukol et al. [145] documented differences in fungal endophyte species composition of *P. abies* needles obtained from diverse host sources (seedlings, mature trees, clonal cuttings, wind-fallen). Rajala et al. [60] demonstrated variations in the communities of endophytes between Norway spruce clones, which suggests a potential influence of the host tree genotype. Albrechtsen et al. [146] further confirmed that the foliar endophyte composition of *Populus tremula* L. is influenced by the host genotype. These observations indicate that foliar endophytes communities vary not only among diverse host species [86,135,138], but also among genotypes of the same species [60,146].

Nowadays, it is acknowledged that several factors (environmental variables, geographic location, host genotype and host lineage) influence the composition of foliar fungal endophyte communities in different forest sites. Further empirical studies are still needed to ascertain the variables that determine the fungal communities of tree foliage at the individual tree and forest biome levels [60,86,123].

6.2. Root Endophytes

Root endophytes are dominated primarily by the assemblage of ascomycetes fungi with poorly-defined ecological roles, and are strictly horizontally transmitted. Although first reported over one hundred years ago as ‘mycelium radicus astrovirens’ (MRA) [147,148], their global diversity and functional roles are still largely unknown [62,92,107]. Studies have shown that the composition of root endophytes in the same host plants in different forest sites are restricted to a few fungal lineages [105,106,149,150]. As previously mentioned, the main observed root endophytes belong to the group dark septate endophytes (DSE). Root-inhabiting fungi other than DSEs are even less studied, and their ecology is poorly understood [62]. Root endophytes have more restrictive living environments compared to other tissue regions. In boreal forests, they often co-habit with ectomycorrhizal (ECM) fungi in the root tips of trees [106,151,152]. It has been estimated that in forest ecosystems, endophytic DSE fungi root colonization could be more abundant than mycorrhizas [62,153]. Sietiö et al. [106] reported that ericoid plants and *P. sylvestris* shared many species with each other. Some root-associated fungi also display certain host or ecological niche preferences [106,154–157]. By contrast, no evidence for host specificity among Ericaceae plants was found by other authors [158]. This indicates that the mechanisms determining high diversity in root-symbiotic communities merit further study.

Beside the host effects, the change in environment can also influence the composition of root fungal endophytes. Considerable differences have been reported between members of PAC communities (*Phialocephala fortinii* C.J.K. Wang & H.E. Wilcox and *A. applanata*) in managed and undisturbed forests [150,159]. Other authors have shown that clear cutting can significantly alter the resident PAC community of *P. abies* roots [160]. Terhonen et al. [105] found no significant difference between root endophytes of trees inhabiting drained and pristine peatlands. Generally, the communities of undisturbed PAC are often not very dynamic and can take several years to become measurable [101, 161]. In nature, the transfer of PAC is assumed to occur via root contacts [160], as is known in the cases of root pathogens such as *Heterobasidion* or *Armillaria* species [162,163] or by means of dormant propagules within root debris [160,161].

Several factors can affect root endophytes. For example, natural infection by root rot pathogens could have an indirect effect on the composition of endophytic community of the host tree [18]. Site-specific factors (e.g., pH) can also have effect on composition of endophytes. The root endophyte *Phialocephala sphaeroides* B.J. Wilson was isolated from plants growing in highly acidic sites by Wilson et al. [164]. Other authors also observed *P. sphaeroides* from *P. abies* and *P. sylvestris* roots growing on highly acidic sites (pH 4) [105,106]. *Phialocephala sphaeroides* has so far not been isolated

from alkaline sites (pH 6) [161,164–167], which suggests that pH might be the main factor restricting its distribution.

7. Functional Relevance of Fungal Endophytes of Forest Trees

The so-called “insurance hypothesis” in evolutionary ecology suggests that high diversity maintains the overall integrity of an ecosystem [168–172]. In this sense, the hidden diversity of endophytes in forest ecosystems can have an extremely important function. The diverse composition of the unseen endophytes might enhance the fitness of not only individual trees, but also of the whole forest ecosystem.

7.1. Aerial Endophytes and Tree Health

Class 2 endophytes have been reported to increase host root and/or shoot biomass [52]. This could possibly be due to the induction of plant hormones by the host or mediation of phytohormone biosynthesis by the fungi [173]. Sometimes, Class 2 endophytes provide some protection to the host against pathogens [174–176]. This protection might be partly due to the production of bioactive compounds (Table 1) [72,173,177], fungal parasitism [178], or the induction of systemic resistance [179]. As mentioned above, Class 2 endophytes have been demonstrated to confer habitat-specific stress tolerance to host plants [83]. The mechanisms behind this has not been fully resolved, but it is clear that they have significant effects on the adaptation of host plants to their environment. This may help plants to establish, tolerate and survive in high-stress habitats [52].

Another important function of aerial endophytes (Class 3) is to act as pioneer decomposers [180,181]. After foliage or conifer needle dies, facultative endophytes are known to switch to a saprotrophic habit and initiate the decay process [180,181]. Other significant roles, apart from being opportunistic saprotrophs, include the ability to protect their host against herbivores/pathogens by the production of inhibitory bioactive chemicals [78,182], niche competition [66] or the induction of systemic resistance [183].

For example, in the tropical rubber tree *Hevea brasiliensis* Muell. Arg., its high diversity of beneficial natural and indigenous fungal endophytes (e.g., *Trichoderma* and *Tolyposcladium*) have been reported to protect the host against pathogens (protective mutualism) [184]. Similarly, in other tropical trees *Theobroma cacao* L. and *T. grandiflorum* (Willd. ex Spreng.) K. Schum., inoculation with the most dominant endophytes (isolated from *T. cacao*) effectively prevented the damages caused by the pathogen *Phytophthora palmivora* Butler. Several other studies have also confirmed these findings on the protective effects of endophytes in tropical trees [109,185–189]. In conifer trees, it has been shown that prior inoculation of young needles with fungal endophytes protects the host from natural infection by *Dothistroma septosporum* (Dorog.) M. Morelet., as well as modifying the subsequent disease severity [190]. Higher infection rates of endophytes in oak trees have been reported to reduce parasitism of a leaf-mining moth [191]. The production of toxigenic metabolites (rugulosin) by foliar endophytes (*Phialocephala scopiformis* T. Kowalski & Kehr) was shown to diminish herbivory of eastern spruce budworm *Choristoneura fumiferana* Clemens [192]. Besides rugulosin (the major insect toxin), *P. scopiformis* also produces skyrin and emodin [193,194]. Rugulosin has been shown to inhibit the growth of *C. fumiferana* at very low concentrations (10–25 μ M) [195]. Needles infected with this endophyte have significantly reduced the growth rate of *C. fumiferana* [192,194,196]. When inoculated on the seedlings, foliar endophyte *P. scopiformis* has been shown to persist for at least a decade, producing its respective metabolite rugulosin in the needles [197]. Most importantly, it was shown that growth of *C. fumiferana* and damage to the foliage of *Picea glauca* (Moench) Voss were either reduced or mitigated using low concentrations of the anti-insect compounds vermiculine (from endophyte *Phialocephala* sp.) and rugulosin (*P. scopiformis*) [198].

Other foliar endophytes have been noted to have antipathogenic potential. Several metabolites with antifungal properties have recently been isolated from endophytes of *Picea rubens* Sarg. and *P. mariana* [199]. Similarly, Tanney et al. [200] isolated bioactive metabolites from *P. rubens* and *P. mariana* endophyte *Diaporthe maritima* J.B. Tanney. The crude liquid culture extracts from this

endophyte showed growth inhibitory effects towards the biotrophic pathogen *Microbotryum violaceum* (Pers.) G. Deml & Oberw., as well as antibacterial properties towards *Bacillus subtilis* (Ehrenberg) Cohn. Sumarah et al. [201] extracted bioactive compounds secreted by foliar endophytes of white pine, *Pinus strobus* L. Only the extracts from *Lophodermium nitens* Darker were found to have antifungal activity. Further analysis revealed that homodimeric macrolide pyrenophorol present in the extracts was responsible for the growth inhibition of the pine pathogen *Cronartium ribicola* J.C.Fisch. Other authors [198] have shown that the antifungal compounds griseofulvin (from endophyte *Xylaria* sp.) and pyrenophorol (from *L. nitens*) were present in sufficient amounts to affect conifer needle diseases including white pine blister rust *C. ribicola* [198]. These results support the hypothesis that several metabolites with antifungal properties secreted by fungal endophytes may enhance the tolerance of the host tree to fungal pathogens and herbivory [198–203]. The mechanism for the endophytes' ability to restrict the pathogens and herbivory in these studies, however, are not fully known. These findings are nevertheless extremely important, as in future, there might be a possibility to favor the use of beneficial foliar endophytes that can act as biocontrol agents against pathogens.

Ganley et al. [204] showed that fungal endophytes could mediate resistance in *Pinus monticola* Douglas ex D. Don, and thereby increase host fitness against *C. ribicola*. Mejía et al. [183] inoculated *T. cacao* leaves with the fungal endophyte *Colletotrichum tropicale* Rojas, Rehner & Samuels and compared the gene expression of the host to un-inoculated host. They found that priming with endophytes enhances the expression of large suites of host genes that are important for defense against herbivore and pathogen [183]. These included upregulation of genes involved in plant defense (e.g., ethylene pathway, receptor kinases), cell wall development, chloroplast, and nitrogen metabolism [183]. This experiment indicates that fungal foliar endophytes might have an influence on host gene expression, particularly with genes that are related to disease resistance [183]. Raghavendra and Newcombe [205] inoculated several *Populus* genotypes with different foliar endophytes, followed with pathogen (*Melampsora*) inoculation. They observed differences among endophytes and concluded that endophytes might contribute significantly to quantitative resistance against the rust fungus *Melampsora* in leaves of *Populus* [205]. These studies are a starting point for the evidence that some foliar endophytes can enhance resistance in their host, but the overall specific contribution of aerial endophytes to the quantitative resistance of the host has not been determined. Besides the metabolic production and induction of systemic resistance, endophytes compete for space and substrates with harmful pathogens. This can be referred to as niche competition. Blumenstein et al. [66] tested the hypothesis that endophytes inhabiting the same host with aggressive pathogens are able to utilize carbon substrates more efficiently. They found that carbon utilization profiles of the highly virulent Dutch elm disease (DED) pathogen *Ophiostoma novo-ulmi* Brasier and four asymptomatic elm (*Ulmus* spp.) endophyte isolates exhibited extensive niche overlap. The results further underline the potential for exploratory research on the use of endophyte strains to protect elms against DED-pathogen through their unique ability to compete for niches, substrates and nutrients. Furthermore, other authors found that the exposure of young cacao tree plants to microbiomes derived from the litter of healthy adult trees protected the seedlings against pathogen damage [206].

The potential for aerial endophytes to enhance tree growth and health fitness through competition, induced resistance, or by production of bioactive compounds deserves further exploration.

7.2. Root Endophytes and Tree Health

To reveal the functions of root endophytes in forest trees, several studies have been performed through inoculation experiments on the hosts. The observed effects of these inoculations have been noted to vary from beneficial [207,208] to neutral [209], and sometimes even to pathogenic [208,210] interactions. The meta-analyses of root-inhabiting endophytic fungi (DSE) revealed that the responses of host plants to DSE fungi colonization tended to be either negative [211] or positive [212]. The observed negative effects of the endophytic colonization to the host seem to be affected by the strain of endophyte and experimental environment [210,213–215]. These observed differences to the

host's fitness could indeed be explained by the experimental conditions, as they usually do not reflect the natural biodiversity of the root microbiota, and differ between most of the studies (pH, nutrient level, strains). For example, Wilcox and Wang [216], inoculated DSE fungi (*Chloridium paucisporum* C.J.K. Wang & H.E. Wilcox, *P. fortinii*, and *Cadophora finlandia* (C.J.K. Wang & H.E. Wilcox) T.C. Harr. & McNew) on seedlings of *Betula alleghaniensis* Britt., *P. rubens* and *Pinus resinosa* Sol. ex Aiton. Their results showed that some DSE fungi were either weak or serious pathogens, whereas others appeared to improve host growth. Similarly, Terhonen et al. [208] showed that the inoculation of *P. sphaeroides* to *P. abies* seedlings increased shoot/root growth. By contrast, inoculation with *Cryptosporiopsis* sp. was detrimental to the host [208]. Tellenbach et al. [210] noted that interactions between different strains of *Phialocephala subalpina* Grünig & T.N. Sieber and Norway spruce ranged from neutral to highly virulent, and no mutualistic interaction was observed. The negative effects on the host have been noted to increase with increasing the number of endophytic strains [59]. It seems that the mutualistic interaction in roots depends on the endophyte species or strain of the endophyte. However, under natural environments, the lifestyles of these endophytes are in balance, and no harmful effects on their hosts have been detected to date.

The host-DSE association differs from mycorrhizal symbioses, as the cellular interface where specialized structures (e.g., Hartig net, mantle, arbuscules) occur is lacking [217]. DSEs instead colonize intracellular spaces of ectomycorrhizal hosts and form microsclerotial structures [218]. The morphology of some DSE-colonized roots of ectomycorrhizal host has been described to be ectendomycorrhizal [216,219]. Because some DSE endophytes are able to colonize a great variety of hosts, which are not ecto- or ectendomycorrhizal, they have been considered as ectendomycorrhizal symbionts, [61,220]. Indeed, Lukešová et al. [221] showed that DSE *Acephala macrosclerotiorum* Münzenberger & Bubner could form ectomycorrhizae with conifers. The mycorrhizal colonization is mutualistic and has benefits to both partners. Sietiö et al. [106] found the first proof that root endophytes in their natural environments are able to utilize photosynthates from the host plants. This indicates that host plants and root endophytes could have somewhat mutualistic interactions. Phosphates are commonly a major limiting factor for plant growth, which has evolved to depend on mycorrhizas to increase the host foliar P concentration [222]. There is evidence that fungal endophytes in roots can improve P uptake by the host under some experimental conditions. First, Haselwandter and Read [223] inoculated unknown DSE strains in *Carex* species and observed increased shoot P concentrations in the hosts. Similarly, Jumpponen et al. [215] recorded that the inoculation of PAC member *P. fortinii* in *Pinus contorta* Douglas seedlings increased foliar P concentration. *Piriformospora indica* Sav.Verma, Aj.Varma, Rexer, G.Kost & P.Franken an endophytic root colonizing fungi has been reported to mediate the uptake of radiolabeled P from the culture medium to its host [224]. Hiruma et al. [225] reported that the root endophyte *Colletotrichum tofieldiae* (Pat.) Damm, P.F. Cannon & Crous under phosphorus-deficient conditions was able to transfer the macronutrient P to shoots of *Arabidopsis thaliana* (L.) Heynh., thereby promoting plant growth and increasing fertility. Surono and Narisawa [226] noted that the inoculation of *P. fortinii* isolates to *Asparagus officinalis* L. enhanced growth by using phytic acid sodium salt as the sole source of organic phosphorus (P). *Phialocephala glacialis* Grünig & T.N. Sieber and *Phialocephala turiciensis* Grünig & T.N. Sieber are able to mineralize organic P in vitro [227], indicating that DSE fungi can release P from organic sources to be utilized by plants [227]. These results suggest that some of the root endophytic fungi could contribute to the host nutrient levels, similarly to mycorrhizas. The mechanism behind the beneficial role of endophytes in plant health promotion may be somewhat different compared with ectomycorrhizal fungi [228]. However, it is clear that some root endophytes can induce positive responses of their tree hosts through the modulation of the host physiology and growth via nutrient acquisition [92,152,212,220].

The other beneficial aspect of root endophytes is the production of unique bioactive compounds such as plant growth-promoting phytohormones [68,229,230] or by limiting pathogen growth [92,208,231]. Schulz et al. [72] found that fungal endophytes constitute the highest proportion of herbicidally-active isolates compared to phytopathogenic isolates. Increases in phenolic defense metabolites in *Larix*

decidua Mill (proanthocyanidins) were found to be accompanied by prior endophyte infection [72]. Tellenbach et al. [232] isolated sclerin and sclerotinin A from PAC member *Phialocephala europaea* Grünig & T.N. Sieber, which was shown to significantly reduce the growth of *Phytophthora citricola* Sawada sensu lato. Similarly, metabolites extracted from liquid cultures of root endophytes *P. sphaeroides* and *Cryptosporiopsis* sp. inhibited the growth of several plant pathogens [208].

Studies to test if root endophytes can protect host tree roots against pathogens are somewhat limited, and most studies have concentrated on agricultural crops. Tellenbach and Sieber [231] demonstrated that in *P. abies* seedlings, the disease intensity caused by the two oomycete root rot pathogens, *Elongisporangium undulatum* (H.E. Petersen) Uzuhasi, Tojo & Kakish. and *Phytophthora plurivora* T. Jung and T.I. Burgess, was reduced by some strains of the endophyte *P. subalpina*. Similarly, Terhonen et al. [208] showed that the major root endophyte *P. sphaeroides* isolated from *P. abies* [105] was, under in vitro conditions, able to prevent the infections of seedling roots by the pathogen *Heterobasidion parviporum* Niemelä and Korhonen. In roots, endophytes have the potential to protect host plants also against herbivores. One example is from agricultural crop, where non-pathogenic endophytic *Fusarium oxysporum* Schlecht. emend. Snyder & Hansen strain Fo162 produces bioactive compounds which has adverse effects on the nematodes [233]. These results further indicate that endophytes can serve as a valuable reservoir for finding effective biologically-active compounds towards nematodes. These outcomes could form a basis for exploring alternative control methods to manage the threat of underground root pathogens on forest trees.

Our knowledge of the functional roles of root endophytes in plant defences is primarily based on studies of agricultural crops, as relatively few experimental studies have been conducted on forest trees. Many endophytes of crop plants have been shown to be able to trigger host plant resistance. Martinuz et al. [234] reported induced systemic resistance following the application of endophytic fungi (*F. oxysporum* and bacteria *Rhizobium*) to root system of squash plants, which led to a significant reduction of aphid (*Aphis gossypii* Glover) population. Similarly, Singh et al. [235] reported that root endophyte inoculation to tomato plant roots induced systemic resistance, decreasing the nematode feeding. *Trichoderma* has also been shown to induce systemic resistance against nematode, which adapts its priming of salicylic acid (SA)- and jasmonic acid (JA)-related defense responses according to the stage of the nematode infection cycle [236]. Roylawar et al. [237] found that the pre-colonization of roots with *P. indica* resulted in decreased disease severity in tomato caused by early blight. They concluded that *P. indica* treatments led to priming of defense-related gene expression in tomato.

Recent studies have shown that root fungal endophytes of agricultural crops can help host plants to live in harsh environments, thereby increasing their stress tolerance against abiotic factors. Redman et al. [238] demonstrated that *Dichanthelium lanuginosum* (Ell.) Gould inoculated with endophyte *Curvularia* sp. were more tolerant to heat compared to non-inoculated ones. Waller et al. [239] observed that the root endophytic fungus *P. indica* had increased *Horleum vulgare* L. tolerance to salt stress. Similarly, Baltruschat et al. [240] showed that *P. indica* protects *H. vulgare* from high salt stress (300 mM NaCl). Yamaji et al. [241] recorded that *Clethra barbinervis* Siebold & Zucc. can tolerate high concentrations of heavy metals due to the support of root fungal endophytes including *P. fortinii*, *Rhizodermea veluwensis* Verkley & Zijlstra, and *Rhizoscyphus* sp. reflecting growth enhancement, K uptake promotion and decrease of heavy metal toxicity. Wang et al. [242] found that DSE fungi significantly alleviated the deleterious effects of excessive cadmium amendments and promoted the growth of *Zea mays* L. As DSE fungi are the most dominant endophytes in the roots of trees [62,153], theoretically, they could have similar health benefits to their hosts as in agricultural plants. Likar & Regvar [243] found that DSEs reduced the metal uptake by the *Salix caprea* L. cuttings, thus suggesting a beneficial role for *S. caprea* in metal-enriched soils. Similarly, four fungal root endophytes were found to be highly tolerant to metals (Cd, Zn, Pb, and Cu), further highlighting the potential use of these endophytic strains for tree-based phytoremediation of metal-contaminated sites [244]. It is possible that under stressful environments, the interactions between plants and root fungal endophytes could switch from neutral to beneficial, and in that sense, could be counted as constituting a mutualistic relationship [245].

Table 1. Categories of fungal endophytes and their main characteristics.

Main Group	Class	Transmission Type	Endophyte Classification	Host Range	Tissue Type	Functional Roles/Characteristics of Endophytes	Bioactive Compounds/Function	Literature Reference Number ¹
C ²	1	vertical	Ascomycota	Grasses		Enhance drought tolerance, increase plant biomass, decrease herbivory	Yes ²	[39,52,73–78]
	2	most horizontal, few vertical	Dikarya (Ascomycota, Basidiomycota)		Shoot, root and rhizome	Enhance stress tolerance of host plants (salinity, pH, temperature), increase host root and shoot biomass	E.g., phytohormones, seimatoric acid, colletonic acid	[52,72,82,83,173,177]
NC	3	horizontal	Dikarya (Ascomycota, Basidiomycota)	Forest trees ³	Aboveground tissues, especially leaves	Localized infections, pioneer decomposers, protection against herbivores or pathogens, niche competition, induction of systemic resistance, inhibition of insect and pathogen growth	Rugulosin, skyrin, emodin, vermiculin; homodimeric macrolide pyrenophorol, griseofulvin	[52,57,66,78,84–87, 180–183,192–198]
	4	horizontal	Ascomycota and Basidiomycota; mainly DSEs		Roots	Growth inhibition of pathogens, host plant growth promotion	Sclerin, sclerotinin, phytohormones	[52,61,68,229,230,232]

¹ Reference number refers to literature cited in the text regarding the functional roles and the production of bioactive compounds. ² As Clavicipitaceous endophytes are not further described in this review, no further characteristics are listed here. ³ Here, we refer to forest trees, but naturally endophytic fungi occur ubiquitously in all plants.

8. New Perceptions of Phytomicrobiomes

8.1. Novel Technological Advances for the Study of Tree Microbiomes and Associated Endophytes

Significant progress in the investigation of plant microbiomes was achieved with the advent of ‘omics’ technologies and the application of next generation sequencing (NGS), which enabled cost-efficient high-throughput analysis of microbial communities associated with plants. Importantly, the introduction of metagenomics and metatranscriptomics promoted the functional studies of plant microbiome and its role in plant health and stress tolerance. Metagenome-wide association studies (MWAS) are considered as a promising approach in the identification of the key components of plant microbiomes. Using this approach, it is possible to establish an association between a relative abundance of a certain gene in the metagenome and the occurrence of a disease [8]. Alternatively, network models can be applied to functional analysis of plant microbiome. They can be used to identify keystone species crucial for plant health and functioning [246–248].

Plant microbiota in natural environments are highly complex systems. Several hundred species of bacteria and fungi can be associated with a single plant. Due to this complexity, these systems are less tractable for experimental studies. For this reason, synthetic communities provide an attractive alternative to natural communities in experimental setups [9–11]. Synthetic microbial communities are composed of well-defined culturable microorganisms, and their composition and structure can be adjusted to meet the needs of particular experimental setup [12]. The complexity of synthetic communities can vary from just a few to several dozens of species. Lower numbers of species increase reproducibility and simplify the interpretation of the obtained results, but there is a relatively high risk of missing important keystone components of the microbiota [9]. The emerging publications demonstrate the viability of this approach, which is rapidly developing from early proof-of-principle works to complex experiments designed to address key questions about functioning of plant microbiota [249–251].

8.2. Technical Limitations

The identification of endophytic microorganisms with potential beneficial properties is greatly facilitated by recent technical advances in the field. However, even if the beneficial properties of the organisms in question were confirmed in *in vitro* experiments, there are numerous issues that should be addressed prior to the potential field applications [252]. Abiotic factors, such as climatic conditions (temperature, humidity, precipitations), might affect the reproducibility of field trials. Additionally, host genotype and interactions with members of resident microbial communities are crucial factors determining the success of any potential practical application of endophytic microorganisms. The effect of host tree genotype on the structure of endophytic microbial communities was confirmed in several studies [253–255]. These observations emphasize the importance of host genotype and, at the same time, suggest that the interactions of beneficial microorganisms with a particular plant (tree) genotype must be taken into consideration in potential applications of endophytes as biocontrol or growth-promoting agents [249,256,257]. The interactions of trees with beneficial microbiota should also be taken into account in future tree breeding programs to develop tree varieties suitable as hosts for microbial inoculants. The identification of genetic determinants controlling host-microbial interactions would be an important factor for the success of these efforts [258].

9. Prospects for Translational Applications of the Knowledge for Improvement of Forest Health and Productivity

Forest management practices consist mainly of the expensive eradication of infected or dead trees after a disease outbreak has been identified and damages in the forest have occurred. In some cases, chemical pesticides which do not differentiate between beneficial and harmful organisms are applied [259], which may negatively affect the forest area long-term. The silvicultural approach of changing the tree species or genotypes in the diseased forest area is also commonly practiced [260].

Witzell and Martín [259] indicated that an ecosystem-based approach to enhance forest health requires the principles of integrated pest management strategies that take into consideration the ecological elements of forest systems. This approach includes intra- and intercellular endophytic fungi, which are known to function as biological control agents [67,261] through various mechanisms. A few known examples on how to apply endophytic fungi or their products to improve forest health are summarized below.

Endophytes can influence pathogens or herbivores through mycoparasitism or direct interaction by mutualistic antagonism [20,67,71,262–265]. The study by Arnold et al. [109] demonstrates that an antipathogenic defense by a certain assemblage of endophytes from naturally infected but asymptomatic tissues reduced leaf necrosis caused by *Phytophthora* sp. and mortality in leaves of *T. cacao*. As young leaves are free of endophyte infections, the authors proposed that endophytes might have entered the foliage after surface wetting by dew, fog or rainfall. However, they suggested that the host-specific leaf chemistry mediates interactions in planta, and that the endophyte compositions are influenced by the growth medium. Translating these results to forest management practises, it might be possible to spray the leaves of tree seedlings with a spore-inoculum of a set of chosen endophytes to establish a beneficial endophyte community in the young trees before pathogen infections occur, thus enabling the endophyte assemblage to remain in the tree by fertilizing to guarantee the needed soil conditions.

In Martínez-Arias et al. [266], the successful pretreatment of *Populus alba* L. seedlings with a spore suspension from endophytes isolated from healthy *P. alba* trees was shown to significantly strengthen the health status and vitality of the trees towards *Venturia tremulae* Aderh., i.e., the cause of shoot dieback in *Populus*. The *P. alba* endophyte community showed in vitro antagonistic activity towards the pathogen and increased the host's tolerance. The study by Ridout and Newcombe [190] provides insights on the antagonistic effect of *Penicillium goetzii* J. Rogers, Frisvad, Houbraeken & Samson against the pathogens causing *Dothistroma* needle blight in *Pinus ponderosa* Douglas ex C. Lawson. *P. goetzii*, an endophyte occurring naturally in pine, was applied as an inoculum to the newly-emerging needles in fresh shoots at the same time when infection by either of the pathogens, *D. septosporum* or *Dothistroma pini* Hulbary., was documented. The reduction in disease severity indicates the successful antagonistic effect of the endophyte towards the pathogen [190]. The mechanism behind the antagonism could be the endophytes' production of inhibitory secondary metabolites [66,68,252,266], or they may outcompete pathogens for their habitat and nutrients, as demonstrated in several studies [52,66,68,267,268]. Blumenstein et al. [66] reported that endophytes have strong potential as biocontrol agents, as their capability for outcompeting plant pathogens might be rather stable and effective.

Through the induction of plant defense response in the host's metabolism, infections of pathogens or herbivores [269] can be prevented by a persistent form of resistance [204]. Since 1992, the commercial biocontrol product Dutch Trig[®] (Apeldoorn, The Netherlands) has been used to protect elm trees from infection [270] by the blue stain fungus *O. novo-ulmi* causing Dutch elm disease (DED). The product consists of a conidiospore suspension of the endophytic fungus *Verticillium albo-atrum* strain WCS850 (Dutch Trig, Apeldoorn, The Netherlands). It is applied annually as a vaccination by direct inoculation into the vascular tissues of healthy elms. Consequently, the natural defense mechanisms of elms are enhanced when *V. albo-atrum* starts to germinate and grow [271]. Another example for the applied use of endophytes in forest practices also relies on the ability of fungi to induce resistance in their host trees as described by Ganley et al. [204]. In the white pine blister rust disease, the endophytes of the host were able to reduce disease symptoms caused by the pathogen *C. ribicola* in seedlings of *P. monticola* by the enhancement of the host defences and increased tolerance. Translationally, the pre-inoculation of *P. monticola* seedlings with fungal endophytes could be used in a standardized procedure in nurseries to enhance the fitness of young trees before they are out-planted in areas where white pine blister rust is common. A similar practical application could be adopted for the pre-inoculation of conifer species with fungal pathogens for systemic enhancement of resistance in their host trees [272,273].

The listed examples describe varieties for which the internal endophyte community is influenced by the inoculation of trees to enhance the host tree health status. Witzell and Martín [259] outlined two active manipulation application measures to engineer endophyte communities at the forest stand level: (a) at clear-cut level, where soil amendment with beneficial endophytes is possible and (b) at regeneration level, where the pre-planting inoculation of plants or seeds with beneficial endophytes could take place. Passive manipulation can be done through the promotion of natural spore sources, such as young, mature and old growth forest that provide substrates for diverse fungi.

However, in applying endophytes to forest management practices, diverse challenges still have to be overcome. Schlegel et al. [142] suggested that the mechanism for the potential impact of endophytes and epiphytes on the ash dieback pathogen *Hymenoscyphus fraxineus* (T. Kowalski) Baral, Queloz & Hosoya could be through resource competition, toxin secretion or activation of plant defenses. But the long-term effect of the endophytic fungi against *H. fraxineus* could not be observed [142]. In several studies, in vitro antagonism assays revealed antagonistic effects of endophytic fungi towards pathogens [20,66,252,267,274]. Nevertheless, the stable establishment and survival of the endophyte in planta is not necessarily guaranteed. Schlegel et al. [142] also noted that the ability of an endophyte to infect a host is influenced by several factors, including the presence of other organisms, and the physical and chemical environments [142]. In the case of applying a fungal inoculum as a spray to larger forest areas, factors promoting or likely to restrict spore dispersal are humidity, understory vegetation, wind, canopy characteristics and previous wounds of the host tree [259]. Further research is therefore required partly due to the nature of endophytic life style, such as the ability to shift from symptomless to saprotrophic or pathogenic mode when environmental conditions change. For example, Diplodia tip blight, caused by *Sphaeropsis sapinea* (Fr.: Fr.) Dyko & B. Sutton, has the ability to persist asymptotically in its host tree, but also causes disease symptoms under favorable temperature and moisture conditions [275]. In addition, the colonization of many plant taxa by endophytes are often naturally not systemic [276].

10. Conclusions

Fungi and bacteria are ubiquitous associates of plants; the integration of genetics, metagenomics and bioinformatics methods will be required to unravel the diversity of lifestyles as well as their impact on the health of forest trees. The apparent interest in the endophyte communities in the endospheres, phyllospheres and rhizospheres of trees also reflects the increasing interest in the potential of endophytes to modify, influence and affect the biotic and abiotic stress tolerance of their hosts through several mechanisms [63–67]. Endophytes have in recent years received considerable attention due to their envisaged potential as a source of novel and unique bioactive chemicals to be exploited for forestry, agricultural, pharmaceutical and industrial purposes [52,68,141]. These observations highlight the fact that there are still gaps in our knowledge on how the complex interactions that exist in different ecosystems with respect to fungal endophyte composition, nutrient availability, and host interaction could be harnessed for the benefit of forest trees. The biggest challenge is to link the acquired novel knowledge on microbiomes to translational forest management for the benefit and improvement of forest health. In the long term, this will facilitate policy and decision making in forest health management.

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