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Review

Forest structure and fungal endophytes

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ABSTRACT

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Sufficient biodiversity is required for ecosystem functions. The question is how we can assess required biodiversity if we are able to recognize only a fraction of diversity, and/or unable to place a known species into a trophic level or into their niche dimensions. The species diversity of higher plants and animals usually can be assessed in most terrestrial environments. In contrast, microbial diversity is often ignored although the number and genetic diversity of microbes is enormous, and are profoundly important as plant and animal mutualists, pathogens, parasites and saprobes. Thus, one of the biggest challenges when disentangling relevant diversity to ecosystem functions is to reveal composition of focal microbial assemblage and the place of the key groups of them in the food web. In this review I focus on ubiquitous but poorly understood group of foliar fungi, asymptomatic endophytic fungi, of woody plants emphasizing how geographic, age and genetic structure of forest might affect endophyte-plant interactions.

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1. Introduction

Over the past three decades, endophytic fungi have attracted increasing attention among taxonomists, agronomists, ecologists and evolutionary biologists (see e.g. Bills 1996; Carroll 1986, 1988; Clay & Schardl 2002; Müller & Krauss 2005; Petrini 1986, 1991; Saikkonen *et al.* 1998, 2004a,b, 2006; Schardl *et al.* 2004). Endophytic fungi live asymptotically and internally within host plant tissues. They are ubiquitous and diverse. Virtually every plant studied to date harbors at least one species of endophytic fungi and many plants, especially woody plants, may contain literally scores of species (Carroll 1986; Petrini 1991; Helander *et al.* 1994; Preszler *et al.* 1996; Faeth & Hammon 1997a). Ecology of endophytes is usually studied emphasizing fungal mediated plant-herbivore interactions (Breen 1994; Clay 1990; Faeth & Bultman 2002; Faeth & Wilson 1996; Saikkonen *et al.* 1998, 2004a,b, 2006). Seeking evidence for indication of causal relationships between fungi and

herbivores sharing the host plant has been the primary motivation in the endophyte literature since the findings that some endophytes, particularly seed-borne grass-endophytes in nutrient-rich agronomic arena, negatively affect herbivores (Saikkonen *et al.* 2006). Although many studies with natural grass systems, and especially with horizontally by spores transmitted tree-endophytes, have shown more variable effects (Müller & Krauss 2005; Saikkonen *et al.* 1998, 2004a,b, 2006), alternative approaches have seldom been addressed.

Accumulating studies suggest that the role of endophytic fungi associated with woody perennials can be complex and labile both in ecological and evolutionary time. By definition, endophytic fungi live for all, or at least significant part of their life cycle asymptotically within plant tissues (Wilson 1995). Thus, they include a wide range of fungi, including latent pathogens and dormant saprophytes (Osono 2006), which may occupy different habitats and places in the food chain during different phases in their life cycles (Saikkonen *et al.*

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2004a). A position of an endophytic fungus in an ecosystem, and how it responds to resources and enemies, i.e. a niche (see e.g. Elton 1927; Root 1967), may change because a fungus continuously affect, and is affected by both abiotic and biotic environment within the limits of its genotype and phenotypic plasticity. Consequently, the length of extended latency period of the fungus may vary in ecological time. For example, an endophytic fungus may shift toward parasitic, pathogenic or saprophytic lifestyle following a mutation in a single locus of fungal genome, changes in species composition of foliar mycoflora and changes in host plant as a consequence of altered nutrient availability in soils, damage or senescence (Faeth & Hammon 1997a; Freeman & Rodriguez 1993; Minter 1981). Describing the niche and ecological role of foliar micro-fungi are further complicated because identical fungal species or lineages have been labelled as endophytic or pathogenic depending on the basis of the study and whether the study examines asexual or sexual stage of the fungal species (Ahlholm et al. 2002a,b; Kehr 1992; Kehr & Wulf 1993; Paavolainen et al. 2000; Stone 1987; Stone et al. 1996). In evolutionary time, endophytic fungi are thought to have evolved from parasites or pathogens via an extension of latency periods and reduction of virulence (e.g. Carroll 1988). The evolution of endophytes is likely to be more complex, however, involving multiple parallel and reverse trajectories driven differently by prevailing selection pressures in different environments (see e.g. Cheplick and Faeth in press; Saikkonen et al. 2004a,b; Thompson 2005). Because of the complexity and instability, “endophyte” can be a misleading conceptual framework in ecology, particularly in the case of horizontally by spores transmitted tree-endophytes.

In this review, I suggest that the mutualistic nature of endophyte-plant interactions via enhanced herbivore resistance should be reconsidered especially when focusing on woody plants. I found 102 original publications on ecology or evolution of foliar tree-endophytes (see [Online Supplementary Material](#)). Nearly all of these are descriptive, focusing on occurrence, distribution and/or diversity of endophytic fungi in forests. Geographically studies are extensive: ~60 %, ~30 % and ~10 % of the studies were conducted in temperate, tropical and subarctic regions, respectively. Over 70 % of the studies examined plant families *Betulaceae*, *Pinaceae* or *Fagaceae*, more specifically pines (18 %), oaks (16 %), spruces (12 %), birches (12 %), and firs (10 %). In the future, focus should be turned on the questions, what are the forces driving endophyte-plant interactions, and how temporal and spatial (e.g. geographic, age and genetic) structure of potential host trees in different phases of forest succession affect the species distribution, frequency and the role of endophytes in forest ecosystems.

2. Endophyte life history adaptations to woody plants

Recently Saikkonen et al. (2004a) suggested that the size, complex architecture, and long age of sexual maturity of the woody plant probably constrain the window for (1) systemic growth, (2) vertical transmission and (3) the length of the latency period of foliar fungi. These are the life history traits

which largely determine the spatial and temporal distribution of endophytic fungi in plant populations, as well as the nature of fungus-plant interaction along the antagonism-mutualism continuum (Saikkonen et al. 1998, 2004a,b). Their reasoning was that endophytic fungi are unable to grow systemically through highly differentiated and hierarchically organized woody tissues to all above-ground parts of the tree, and that long age of maturity decreases opportunities for vertical transmission of the fungus via host seeds (Saikkonen et al. 2004a). Empirical evidence of temporal and spatial patterns of abundance and diversity of horizontally transmitted endophytes support this idea (Arnold & Herre 2003; Arnold et al. 2001; Faeth & Hammon 1997a; Helander et al. 1993; Suryanarayanan et al. 2002, 2003; Wilson & Carroll 1994).

Collectively, past studies have shown that systemic and vertically transmitted endophytes are commonly but virtually exclusively detected from grasses (but see Petrini 1991; Bloomberg 1966). Instead, nonsystemic endophytes, horizontally transmitted from plant to plant by spores, are by far most common type of infections in all types of plants including woody gymnosperms and angiosperms (see e.g. Saikkonen et al. 1998). In woody plants, newly flushed leaves are generally endophyte-free but soon become inhabited with fungal spores (Faeth & Hammon 1997a; Helander et al. 1993; Wilson & Carroll 1994) which are dispersed via air, rain splashes, and animal vectors, from senescent and abscised previous season's leaves. Germinating spores invade the plant by cuticular penetration, entry through stomates or wounds (Juniper 1991). Leaves and twigs appear to host different endophyte assemblage (Barengo et al. 2000; Sieber et al. 1991) suggesting that foliar endophytes are unable to lurk in and disperse from twigs to leaves. Thus, the lifespan of the foliage limits the lifespan and generation time of foliar fungi.

3. Endophytes in structured forests

Distribution patterns of fungal endophytes

Theory of the island-biogeography (MacArthur & Wilson 1967) provides a feasible and predictive framework to identify and interpret the relative importance of forces driving diversity and distribution of endophytic fungi. According to the theory, two predictors, island size and its distance from the mainland, relate to the immigration and extinction rates of species, thus determining the number of species inhabiting islands. A forest is hierarchically structured “archipelago” for fungi. Individual leaves serve as “islands” for single spore-origin fungal infections. A tree (genet) may be monocormic, polycormic or clonally growing cluster of trees. Individual tree genets may grow solitarily or in clusters of trees in open areas, in homogenous forests, or in mixed forests. This allows us to examine endophyte distribution and diversity at a variety of scales ranging from those within a single leaf and tree to those at landscape level.

At the finest scale, frequencies of highly restricted local endophyte infections, often confined between few plant cells, appear to increase towards the basal part of the midrib within the leaves of broad-leaved trees (Cannon & Simmons 2002; Bertoni & Cabral 1988; Helander et al. 1993), and the needle

bases of conifers (Bernstein & Carroll 1977); presumably because of leaf and needle topography, higher moisture compared to the blade and the lamina favouring the germination of spores. Importance of tissue specificity to fungal distribution should not be ruled out either. Leaves and twigs host usually different endophyte assemblages (Barengo *et al.* 2000; Collado *et al.* 1996; Sieber *et al.* 1991), and in the case of Douglas fir, needle endophytes *Rhabdocline parkeri* and *Phyllosticta* sp. are found to colonize even different parts of the needle (Petrini 1991). Frequency of individual single spore-origin infections gradually increase during the growing season (Faeth & Hammon 1997a; Helander *et al.* 1993; Wilson & Carroll 1994) and in evergreen trees, the frequency of infections may continue to increase during the subsequent years until leaves reach a saturation point (Helander *et al.* 1994). Because of sexual reproduction, genetic diversity of fungal infections is high even within single leaves.

At the level of branches and a tree, tree architecture determining height of crown, age structure of foliage, light availability and microclimate within the crown, appear to become important. A tree is a complex genetic succession mosaic of hierarchically organised modular construction which promotes heterogeneity in foliage to cope with organisms subsisting on it (see e.g., Gill *et al.* 1995; Whitham 1981). Thus, fungal responses may vary (e.g., between non-clonal and clonal trees, mono- and polycormic trees or deciduous and evergreen trees). Some general trends can be, however, detected in abundances and distribution patterns of fungal endophytes in woody plants. One of the major determinants for endophytic fungi seems to be the leaf age, or in fact the duration of exposure. Because infection frequencies accumulate over time, the age of leaves and needles is strongly positively correlated with the fungal colonization (Arnold & Herre 2003; Bernstein & Carroll 1977; Carroll 1995; Faeth & Hammon 1997a; Gaylord *et al.* 1996; Hata *et al.* 1998; Helander *et al.* 1993, 1994; Lehtijärvi & Barklund 2000; Magan & Smith 1996; Petrini & Carroll 1981; Poteri *et al.* 2001; Stone 1987). Studies examining other within-branch and –tree patterns show more variable results. For example, some studies have failed to find correlation between height in the crown and endophyte infection frequencies (Bernstein & Carroll 1977). In contrast, others demonstrate that endophyte abundances may increase towards the trunk and the lower parts of the tree (Helander *et al.* 1993; Johnson & Whitney 1989; Petrini & Carroll 1981). Usually no correlation between compass direction and infections has been detected (Bernstein & Carroll 1977; Fisher & Petrini 1990; Helander *et al.* 1993; Johnson & Whitney 1989). The detected trends in endophyte distribution patterns do not, however, correlate with the age structure of leaves in crown because of modular and functional organization of woody perennials. Thus, rather than the age of leaves, liquid precipitation such as rain, dew and fog (see e.g. Carroll 1995), as well as growth form of a tree affecting the microclimate within the crown (Bahnweg *et al.* 2005; Bernstein & Carroll 1977; Gaylord *et al.* 1996; Helander *et al.* 1993; Johnson & Whitney 1989; Stone 1987) may better explain the endophyte distribution within the crown. For example, rain splashes bring propagules from the fallen previous year leaves in soil and vegetation to the lower part of the tree, and colonization success is higher in shade and humid closed canopy

compared to sun leaves of the outermost branches (Bahnweg *et al.* 2005; Helander *et al.* 1993; Johnson & Whitney 1989).

Wider scale spatial patterns of endophyte species distribution relates to climate, history and biogeography of the area determining characteristics of forest stands and continuity of favourable habitats for endophytes. Within a forest stand, seasonal and spatial variation in the infection frequencies is largely dependent on the host density, surrounding vegetation, ground topography and abiotic environmental factors such as weather condition, moisture regime within the microclimate of the plant crown and plant damage (Ahlholm *et al.* 2002a; Faeth & Hammon 1997a; Helander *et al.* 1994; Saikkonen *et al.* 1996). Although mycelial biomass remains relatively low compared to plant biomass (Stone 1987), the diversity of fungi can be high; the species assemblage comprising of few dominant and several sporadically isolated and identified species, morphospecies or genera (Arnold & Herre 2003; Arnold *et al.* 2001; Faeth & Hammon 1997a; Helander *et al.* 1993; Suryanarayanan *et al.* 2002, 2003; Wilson & Carroll 1994). Globally and at a regional scales, fungal abundances and diversity appear to be (1) highly abundant and hyperdiverse in tropics (Arnold *et al.* 2000, 2001; Arnold & Herre 2003; Fröhlich *et al.* 2000; Gamboa & Bayman 2001), (2) higher during the wet seasons compared to dry seasons in semi-arid regions and tropics (Faeth & Hammon 1997a; Rodrigues 1994), (3) high in rainy slopes of mountains (Carroll & Carroll 1978), and (4) to increase with increasing annual precipitation (Ahlholm *et al.* 2002a,b; Helander *et al.* 1993, 1998).

Habitat fragmentation

Firstly, successful infection in foliage depends on exposure to endophyte infections. Thus, infection frequencies tend to be higher in dense and closed host stands ensuring exposure to infections compared to open ones (Helander *et al.* 1993, *in press*; Legault *et al.* 1989; Petrini & Carroll 1981). Habitat fragmentation likely affects abundances and diversity of endophytes similarly to other organisms (see e.g. Fahrig 2003). The fungal species assemblage of the host plant species clearly varies among geographically isolated populations especially outside the native range of the plant species (Carroll *et al.* 1977; Fisher *et al.* 1993, 1994). For example, Fisher *et al.* (1993) showed that the endophyte assemblages of *Eucalyptus nitens* in Australia were different from those found in England. Similarly foliar mycofloras of holly oak (*Quercus ilex*) in England, Majorca, and Switzerland were distinct (Fisher *et al.* 1994). At the regional scale, endophyte community tends to be similar throughout the distribution range of the host (Rodrigues 1994; Rollinger & Langenheim 1993). However, recent evidence indicates disparity between species composition of endophytes in different stands of discontinuous forests. In an archipelago in southwestern Finland, Helander *et al.* (*in press*) found that although foliar endophytes of two native birch species (*Betula pubescens* and *B. pendula*) were able to disperse across the 14 examined islands, the birch trees on the largest islands near the mainland had the highest endophyte frequencies, and the frequencies and the proportions of most common endophyte species (*Fusicladium betulae*, *Gnomonia setacea* and *Melanconium betulinum*) depend on the

density of the host trees in a stand, distance to mainland and size of the island.

Continuous forests can also be fragmented for the endophytic fungi in several ways. First, discontinuous distribution of suitable host species may constrain distribution of specialist endophyte in a continuous mixed forest. Second, fungal assemblage may vary along the forest succession, and the same fungal species may occupy different micro-habitats or host species even within the lifespan of the fungus (Osono 2006; Saikkonen *et al.* 2004a,b). For example, Helander *et al.* (2006) revealed that abundance and species composition of endophytic fungi significantly differed among silver birch (*B. pendula*) leaves from seedling stands, managed mature forests and natural old forests. The sapling stands had the highest and the managed forest the lowest total endophyte infection frequency. The old natural forests tended to have the most diverse identified fungal species community. The most frequently isolated endophytic fungi were *Fusicladium betulae*, consisting 70 % of the isolates from the sapling stands and 31 % and 21 % of the isolates from the managed and natural forest, respectively. In the natural old forests *Gnomonia setacea* was the most frequently isolated endophyte genera (30 %), while in the sapling stands only 4 % of the isolates belonged to the species. In natural forest *G. setacea* infections were positively correlated with stand age indicating that the species is favouring the old forest habitats. Third, endophyte diversity may be fine-tuned by genetic structure of otherwise seemingly continuous and homogenous forests (Ahlholm *et al.* 2002b) or hybrid zones of the host species (Saikkonen *et al.* 2003). Ahlholm *et al.* (2002b) revealed that mountain birch (*B. pubescens* ssp. *czerepanovii*) genotypes (half-sibs), along with environmental conditions, affected the probability of infection by particular genotypes of endophytic fungus, *Venturia ditricha* (anamorph *Fusicladium betulae*). Genetic variation correlated negatively with infection frequencies of the fungus; i.e. the most susceptible birch genotypes were infected with genetically similar endophytes, whereas the most resistant trees were poorly infected by genetically highly variable group of endophytes. The results also showed environment-host genotype interaction, suggesting that the susceptibility of the host to a particular endophyte genotype may change when environmental conditions are changed. In short, these results demonstrate, for the first time, that genetic differences of the host trees can affect genetic diversity and the evolutionary potential of host associated organisms interactively with environmental conditions. Indeed, importance of phenotypic plasticity of birch is evident in host endophyte-interactions.

The situation is further complicated if we acknowledge that species are not stationary and discrete entities. At least 25 % of plant species are involved in hybridization and potential introgression with other species (Mallet 2005), and hybridization appears to be associated with perennial habit, outcrossing breeding systems, and asexual reproductive modes of the species (Rieseberg 1997). For example, birch, pine, poplar and willow species are known to hybridize frequently with their close relatives (Elkinton 1968; Fritz 2001; Wang & Szmidt 1994). Resistance of hybrids to herbivores and pathogens is studied intensively (Fritz 2001). Studies of endophytes, however, lag far behind (but see Gaylord *et al.* 1996; Saikkonen *et al.* 2003). Similarly to many plant-pathogen

studies (Fritz 2001), for example the study on foliar endophyte frequencies in two native (*Betula pendula* and *B. pubescens*) and three exotic (*B. ermanii*, *B. platyphylla* and *B. resinifera*) birch species and their hybrids demonstrate that the resistance of hybrids was generally very close to the more resistant parent (Saikkonen *et al.* 2003). The result supports the hypothesis that plant resistance to endophytic fungi is caused by dominant inheritance of resistance traits.

Spatial and genetic structure of forest is likely to structure endophyte, herbivore and pathogen communities, and their interactions. Increased complexity in forest vegetation creating opportunities for organisms subsisting on them, and thus promoting diversity and windows for specialized interactions between only a few species or even genotypes seems to be norm in general. However, I propose that complex geographic mosaic in the structure of these interactions may also constrain host specificity.

Are tree endophytes host specialist or generalists?

The species composition of endophytes typically comprises of a few dominant species and numerous only sporadically detected species. The dominant fungal species are usually presumed to be specific to the host tree species or closely related species (see e.g. Gennaro *et al.* 2003) because each host species usually harbours a characteristic assemblage of endophytic fungi (Barklund 1987; Danti *et al.* 2002; Stone 1987; Toti *et al.* 1992; Viret *et al.* 1994; but see e.g. Suryanarayanan *et al.* 2003). Furthermore, aforementioned genotype-genotype interactions between endophytes and their host plants lend support to the proposed host specialism. The apparent great importance of geographical and regional disjunction to the fungal distribution raises, however, the question how then specialist endophytes are able to cope with the immense diversity of tropical forests. Lower densities of host species or genotypes in high-diversity communities should reduce the odds to find a host of specialized endophyte. For example, Gentry (1988) found 300 tree species, from which over 60 % were represented only once and 15 % by more than two individuals, in single hectares in upper Amazonian forests. I propose, as indicated by recent empirical studies (Cannon & Simmons 2002; Suryanarayanan *et al.* 2003), that host specificity of endophytes is more common in less diverse forests world-wide, and should decrease when going from higher to lower latitudes in tropics where forests are most species-rich in the world. If so, the question is whether endophyte-plant interactions accordingly vary and range from antagonistic to mutualistic.

4. Tree endophyte – plant mutualist or just another plant consumer?

Endophytic fungi and other plant consumers, such as plant pathogens and herbivores, are likely to meet and interact with each other because of their great abundance and diversity. Although the species rarely occupy exactly the same niche (Chesson 1994; Crawley 1986; den Boer 1986; Diehl 2003; Elton 1927; Hutchinson 1961; Lenas & Pavlou 1995; Richards *et al.* 2000; Silvertown 2004), ecological needs of

coexisting fungal and herbivore species sharing the host plant are likely to overlap to some extent. Thus, it is generally thought that the species compete and reciprocally negatively affect each other, thereby determining the species distribution and abundance in the community inhabiting plant foliage according to “the competitive exclusion principle” (Gause 1934; Hardin 1960; Levin 1970; MacArthur 1972; Volterra 1926). In this power struggle, endophytic fungi can be armed with direct chemical antagonism or subsidized by endophyte mediated host defence against other players (Arnold *et al.* 2003).

However, accumulating evidence has revealed the fundamental differences between tree and grass endophytes in terms of benefits from increased defence against pathogens and herbivores to endophytes (Müller & Krauss 2005; Saikkonen *et al.* 1998, 2004a,b, 2006). Antiherbivore properties of systemic and vertically transmitted grass endophytes are advantageous because the fungus has lost entirely contagious spreading by spores, and thus, the fitness of the fungus is highly dependent on the fitness of the host (Saikkonen *et al.* 2004a,b). In contrast, the interests of horizontally transmitted tree endophytes, pathogens and herbivores can be aligned toward tolerance, or even encouragement, to each other. That's because herbivory can increase the fitness of horizontally transmitted endophytes by facilitating penetration of endophytes into the leaves either by damaging the leaf surface or distributing spores and hyphae into the leaf (Faeth & Hammon 1996, 1997a,b; Hatcher 1995; Saikkonen *et al.* 2004a,b). Although some tree endophytes can increase plant resistance to pathogens and herbivores (see e.g. Arnold *et al.* 2003; Clay 2004), deterrence to herbivores is clearly more commonly detected in grass endophytes (Saikkonen *et al.* 1998), and in general, endophyte interactions in woody plants are found to be more variable and range from antagonistic to mutualistic (Ahlholm *et al.* 2002a; Carroll 1988; Faeth & Hammon 1996, 1997a,b; Faeth & Wilson 1996; Gange 1996; Petrini *et al.* 1992; Preszler *et al.* 1996; Saikkonen *et al.* 1996, 1998, 2001; Valkama *et al.* 2005; Wilson 1995; Wilson & Carroll 1994; Wilson & Faeth 2001). This variability is suggested to be related to fungal life history adaptations to woody plants, i.e. horizontal transmission, sexual reproduction, localized nature of infections and the length of latency period of fungi (Saikkonen *et al.* 2004a,b) promoting high species and genetic diversity of endophytic fungi, and endophyte-plant interactions.

Despite the demonstrated diversity in endophytic fungitree interactions, tree endophytes are suggested to hold potential as biological control agents (Arnold *et al.* 2003; Clay 2004). I believe, however, that great potential of endophytes as biological control agents in natural settings should be reconsidered for several reasons. First, the majority of the studies supporting the idea have been either correlative field observations or experimental studies carried out with endophyte infected and endophyte-free saplings in greenhouse location. Although the difference in plant defence between manipulatively endophyte infected and endophyte-free saplings in greenhouse experiments can be statistically significant, the difference is likely to be biologically negligible in nature where trees can not escape endophyte infections, and consequently endophytes are usually abundant and hyperdiverse in all older leaves. Second, abundance and diversity of endophyte infections even within a single leaf indicate

absence or minor endophyte mediated plant defence against micro fungi by leaf chemistry. And third, although some of the fungal strains are able to produce mycotoxins, or locally induce defence responses in host plant, many herbivores are known to be selective about the foliage they ingest (Waldbauer & Friedman 1991), thus avoiding hazardous fungal patches (Faeth & Hammon 1997b; Wilson & Carroll 1997), or they are able to compensate suboptimal diets (see e.g. Simpson & Simpson 1990; Slansky 1993). Thus, strong conclusions of feasibility of endophytes as biocontrol agents tackling pathogens and pests are premature, and can distort views of interactions among organisms feeding on woody plants.

I agree that endophytes, pathogens and herbivores interact and can mediate plant quality to each other. However, I propose, as proposed in a recent paper by Ahlholm *et al.* (2002a), that the seemingly endophyte mediated plant defence against pathogens and herbivores may actually better indicate plant quality to fungi and herbivores without a causal relationship between them. In a series of bioassays and field observations in two environments over a 3 y period, comparing phenotypic and genetic correlations of fungal frequencies and performance of invertebrate herbivores on mature half-sib progenies of mountain birches (*Betula pubescens ssp. czerepanovii*), Ahlholm *et al.* (2002a) found very little evidence for direct interactions between herbivore performance and fungal abundance. A weak negative correlation between the late season herbivore, *Dineura pullior*, and the seasonally accumulating rust fungus indicate that pathogen-driven premature senescence and abscission of leaves may turn out to be detrimental to late season herbivores. Instead, genetic correlations suggested that fungal frequencies and herbivore performance relate separately to genetically determined plant qualities, or genetic differences in plant responses to environmental conditions. Furthermore, the results suggest that the birch resistance is (1) potentially adjusted to herbivory risk in the environment (see e.g. Karban *et al.* 1999), but (2) genetically constrained from reaching optimal species-specific resistance because birch resistance to the one species will change if resistance to other is under selection. Thus, birch quality to the pathogenic rust fungus *Melapsorium betulinum* (Fries) and the autumnal moth *Epirrita autumnata* (Borkhausen) can vary among and within birch populations over time depending on past selection pressures imposed on populations by the species.

All aforementioned suggests that similarly to fungal pathogens and herbivores, endophytic fungi should be considered as primary consumers that may induce plant responses. Although it is impossible to disentangle all the processes and their consequences involved with plant based food webs, endophyte research should be better embedded in more advanced understanding of mechanism, and ecological and evolutionary consequences, of multispecies interactions in plant-herbivore and plant-pathogen interactions (Berryman 2002; Holdenrieder *et al.* 2004; Ohgushi 2005; Parker & Gilbert 2004; Strauss & Irwin 2004; Thompson 1994, 2005).

5. Conclusions

I propose that balancing future research on endophyte-tree interactions with strengthened and pooled understanding of

diversity, basic biology and ecology of the endophytic fungi combined with trophic interactions and multispecies coevolution, will lead to novel ways to understand the role of endophytes in ecosystem functions. A vast majority of ecological studies have focused either on diversity and distribution of endophytes or on endophyte mediated plant-pathogen and plant-herbivore interactions. Here I propose that forces driving these interactions include structure of individual trees as well as forest structure, comprising of species diversity and geographic, age and genetic structure of potential host trees for endophytic fungi. All this primarily determines the distribution, diversity and dynamic niche dimensions of endophytes, pathogens and herbivores. While more comprehensive understanding of microbial communities has theoretical interest, it also provides valuable knowledge of causes and consequences of microbial mediated interactions in terrestrial ecosystems which may have economical value when developing sustainable management strategies for forestry, and restoring damaged terrestrial ecosystems.

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Supplementary material

Supplementary data associated with this article can be found, in the online version, at [10.1016/j.fbr.2007.05.001](https://doi.org/10.1016/j.fbr.2007.05.001)

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