REVIEW ARTICLE

Forest microbiome: diversity, complexity and dynamics

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ABSTRACT

Globally, forests represent highly productive ecosystems that act as carbon sinks where soil organic matter is formed from residuals after biomass decomposition as well as from rhizodeposited carbon. Forests exhibit a high level of spatial heterogeneity and the importance of trees, the dominant primary producers, for their structure and functioning. Fungi, bacteria and archaea inhabit various forest habitats: foliage, the wood of living trees, the bark surface, ground vegetation, roots and the rhizosphere, litter, soil, deadwood, rock surfaces, invertebrates, wetlands or the atmosphere, each of which has its own specific features, such as nutrient availability or temporal dynamicy and specific drivers that affect microbial abundance, the level of dominance of bacteria or fungi as well as the composition of their communities. However, several microorganisms, and in particular fungi, inhabit or even connect multiple habitats, and most ecosystem processes affect multiple habitats. Forests are dynamic on a broad temporal scale with processes ranging from short-term events over seasonal ecosystem dynamics to long-term stand development after disturbances such as fires or insect outbreaks. The understanding of these processes can be only achieved by the exploration of the complex 'ecosystem microbiome' and its functioning using focused, integrative microbiological and ecological research performed across multiple habitats.

Keywords: forests; microbiome; habitat; ecosystem dynamics; tree physiology; decomposition; microbial interactions; fungi; bacteria

INTRODUCTION

With an estimated size of 38 million square kilometres and a total of more than 3 trillions of trees on Earth (Perry, Oren and Hart 2009; Crowther *et al.* 2015; Peh, Corlett and Begeron 2015), forest biomes cover much of the terrestrial surface and this makes them globally important. For example, forests act as important carbon sinks, where carbon (C) fixed by primary producers exceeds C loss by respiration by 7%–25% (Malhi, Baldocchi and Jarvis 1999) but also affect the geochemical cycles of other elements and the climate (Perry, Oren and Hart 2009). Soil organic matter is accumulated as the residual components from the decomposition of litter, deadwood and microbial biomass and the rhizodeposited carbon supplied by photosynthesis are immobilised in fungal mycelia growing in soils (Clemmensen *et al.* 2013). Organic matter transformation as well as many other processes depend on the activity of microorganisms, mainly fungi and bacteria. The understanding of these microbe-catalysed processes is critical in maintaining the role of forests in the future. Forests are subject to multiple modes of disturbance, such
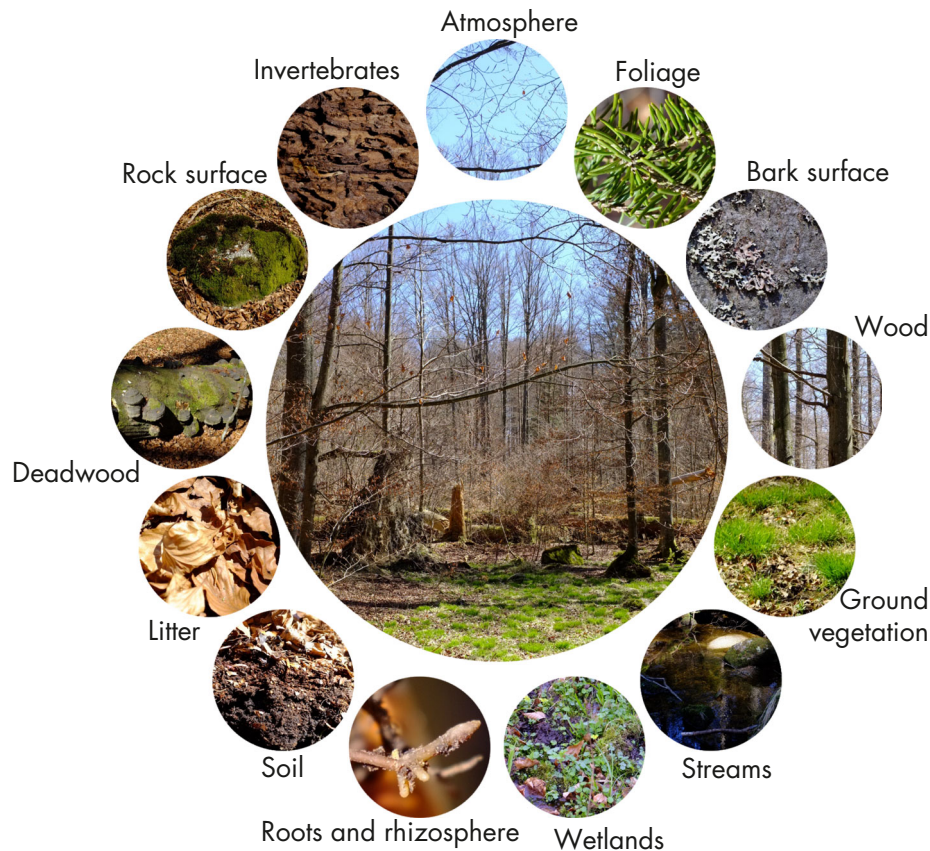
Figure 1. Habitats within the forest ecosystem. The mixed natural forest in the Žofín Nature Reserve, Central Europe, with no intervention since 1838, demonstrates the diversity of forest habitats. The pictures were captured in the area visible on the photograph.

as insect outbreaks, fires or windthrows. They are also significantly threatened by a combination of anthropogenic factors ranging from climate change to environmental pollution and inappropriate management practices (Gauthier *et al*. 2015), which together may easily shift the balance of carbon cycling processes.

Thanks to our recent ability to explore microbial communities and their functioning at an unprecedented resolution, there is an increasing appreciation for the need for integrative studies. Not surprisingly, the concept of the human microbiome was among the first to emerge with the aim to address the whole microbiota associated with habitats of the human body (Huttenhower *et al*. 2012). In a similar way, other microbiomes have been recently outlined and proposed to be the focus of future research, such as the plant microbiome (Lebeis 2015) or host hologenomes of any type (Theis *et al*. 2016). From a different viewpoint related to the exploration of the microbiota of individual environmental samples, the Earth Microbiome Project aims to collect and catalogue information on microbial diversity in the environment (Gilbert, Jansson and Knight 2014). These approaches are important, but are either too narrow to make predictions at the ecosystem level or too broad and overdependent on community description to be able to define and integrate information relevant to microbial roles in ecosystem functioning. Since ecological processes are ecosystem specific and usually affect multiple habitats at the same time, they cannot be properly understood without considering their functioning as a whole. The involvement of microorganisms in the ecosystem processes should thus integrate the microbiology of all habitats, and the

term 'ecosystem microbiome' should be introduced that encompasses the structure and function of microorganisms present in all components of certain ecosystem.

The aim of this review is to summarise the current understanding of the microbiology of forests to show that the ecosystem microbiome view can substantially increase our understanding of the role of microbes in individual habitats that often have unique properties (Fig. 1) and to define and describe the 'forest microbiome'. Because the bulk of studies in forest microbial ecology has focused on temperate and boreal forests, this paper is limited to these biomes. Despite the fact that many ecosystem processes are highly complex and affect multiple habitats, it is at the level of individual habitats that research has so far most progressed. In the future, holistic approaches to the microbiology of ecosystems seem to be inevitable to overcome the present limitations of understanding.

THE FOREST ENVIRONMENT

Forest biomes have specific features that differentiate them. The most important defining features are the large effects of trees as the dominant primary producers and the spatial heterogeneity that also partially results from tree dominance (Fig. 2). Although forest vegetation typically grows in multiple layers that all contribute to ecosystem processes, the activity of the tree layer largely prevails (Peh, Corlett and Begeron 2015). An estimated 300–1000 trees ha^{-1} with a breast height diameter >10 cm are present in various forested biomes (Crowther *et al*. 2015) and are typically responsible for >90% of the forest primary

Figure 2. The forest in the Bohemian Forest National Park, Central Europe, regenerating after a bark beetle outbreak that killed all large trees, represents a highly spatially heterogeneous environment showing specific features of forest ecosystems. As dominant primary producers and suppliers of recalcitrant deadwood and litter material undergoing fungi-dominated decomposition, trees largely determine ecosystem processes. Spatial heterogeneity results from the combination of disturbance and succession/regeneration events leading to the patchy distribution of ground vegetation, and windthrows highly increase the heterogeneity of soil profile patterns. The presence of shaded and open spaces underlies the high diversity of microclimatic conditions.

production (Perry, Oren and Hart 2009; Peh, Corlett and Begeron 2015). As much as 33%–50% of the C fixed by trees is allocated into soil through their roots (Högberg *et al.* 2001), while tree litter and deadwood are important sources of recalcitrant organic matter. In general, vegetation, and particularly trees, regulates aboveground-belowground ecosystem interactions (Wardle *et al.* 2004).

The identity of tree species largely determines the forest microbiome. The symbiotic mycorrhizal roots harbour fungal symbionts belonging to the ectomycorrhizal (ECM) fungi, ericoid mycorrhizal (ERM) fungi or arbuscular mycorrhizal (AM) fungi, and several ECM taxa show specificity to a single tree species (Lang, Seven and Polle 2011). Tree identity also significantly affects the total microbial activity in soil and litter (Šnajdr *et al.* 2013; Augusto *et al.* 2015) as well as the composition of the fungal, bacterial and protist communities in the phyllosphere, litter and bulk soil (Redford *et al.* 2010; Prescott and Grayston 2013; Urbanová, Šnajdr and Baldrian 2015; Tedersoo *et al.* 2016). The effect of trees on the composition of fungal communities is great, and many fungal taxa are specifically associated with certain tree taxa, while the effect on bacteria seems to be weaker and partly moderated through soil and litter chemistry (Urbanová, Šnajdr and Baldrian 2015). In addition to mycorrhizal symbionts, trees also have species-specific fungal and bacterial endophytes, and saprotrophic taxa are often associated with certain types of litter (Prescott and Grayston 2013; Urbanová, Šnajdr and Baldrian 2015). In soil, the trees most strongly affect their rhizospheres, which is a consequence of direct interactions of microbial taxa with the roots, as well as the production of tree species-specific root exudates (Augusto *et al.* 2015). In bulk soil, microbial communities are affected by both tree diversity and tree identity, but the effects seem to be context dependent and at least partly mediated by tree effects on soil chemistry (Tedersoo *et al.* 2016). The tree effects on the microbiota limit our ability to generalise observations from studies obtained in stands of certain composition.

Trees are largely dependent on microbial symbionts providing growth-limiting nutrients such as nitrogen through its mobilisation from organic matter and provision in the mineral forms that can be used by plants. Mycorrhizal fungi and nitrogen-fixing bacteria are responsible for the delivery of up to 80% of all nitrogen and 75% of phosphorus acquired by plants in temperate and boreal forests (van der Heijden, Bardgett and van Straalen 2008).

Due to the multi-layered vegetation of forests, these ecosystems are characterised by their high level of spatial heterogeneity both aboveground and belowground, which is due to the presence of various cohorts of roots and/or wood debris of various sizes, compared with that of most grassland or agricultural ecosystems, in which spatial heterogeneity is often reduced through management (Saetre 1999; Štursová and Baldrian 2011). Spatial heterogeneity within forests allows for the coexistence of species and the processes that these species conduct and exists at various scales, ranging from landscapes to micrometre-sized soil pores (Ettema and Wardle 2002; Baldrian and Větrovský 2012; Baldrian 2014).

The stand-level spatial heterogeneity of soil chemistry and microbial biomass in temperate forests is high, even in even-aged forest monocultures with reduced or absent ground vegetation (Saetre and Bååth 2000; Gömöryová 2004; Šnajdr *et al.* 2008; Baldrian *et al.* 2010). Natural, unmanaged forests with multi-layered vegetation, an abundance of deadwood and a long history of disturbance show even greater variability in spatial structure (Fig. 3). In soil, this variability is a record of historical disturbances of various degrees of severity and frequency, such as tree-throws, uprooting, deadwood decomposition and bark-beetle outbreaks (Šamonil *et al.* 2011; Valtera *et al.* 2015), and results in microhabitat heterogeneity with distinct microclimates and the uneven distribution of nutrients within pits and mounds on the forest floor (Schaetzl *et al.* 1989; Šamonil, Král and Hort 2010). Recent processes, including the production of roots of various sizes, their activity and dieback, also largely contribute to soil heterogeneity.

Spatial heterogeneity of forest topsoils determines the composition of microbial communities mainly through two sets of drivers. First, soil and litter chemistry, including, most importantly, organic matter content, the pH value, and the contents of N and other nutrients, affect both bacteria and fungi, although to variable degrees (Fierer and Jackson 2006; Lauber *et al.* 2008; Rousk *et al.* 2010). Vegetation composition and activity is the second major driver and is more important for fungal than for bacterial communities (Prescott and Grayston 2013; Urbanová, Šnajdr and Baldrian 2015; Tedersoo *et al.* 2016). The relative effects of these drivers are accompanied by stochastic effects on microbial community assembly (Bahram *et al.* 2016), and these all together contribute to the variability of microbiomes within and among forest habitats (Štursová *et al.* 2016).

The spatial heterogeneity of forest soils results in high spatial variation in microbial activity (e.g. enzyme activity or respiration) and microbial biomass content. A sharp vertical gradient of decreasing microbial abundance and activity has been demonstrated (Šnajdr *et al.* 2008). The activity of extracellular enzymes and the abundance of microbial biomass also vary horizontally at the centimetre to metre scales and is often elevated in 'activity hotspots' (Baldrian *et al.* 2010; Anderson, Genney and Alexander 2014). In hotspots such as the rhizosphere, the fraction of active microorganisms may be 2–20 times higher than in bulk soil, and their specific activities (i.e. respiration, microbial growth, mineralisation potential, enzyme activities, RNA/DNA ratio) are also much higher (Baldrian *et al.* 2010; Kuzyakov and
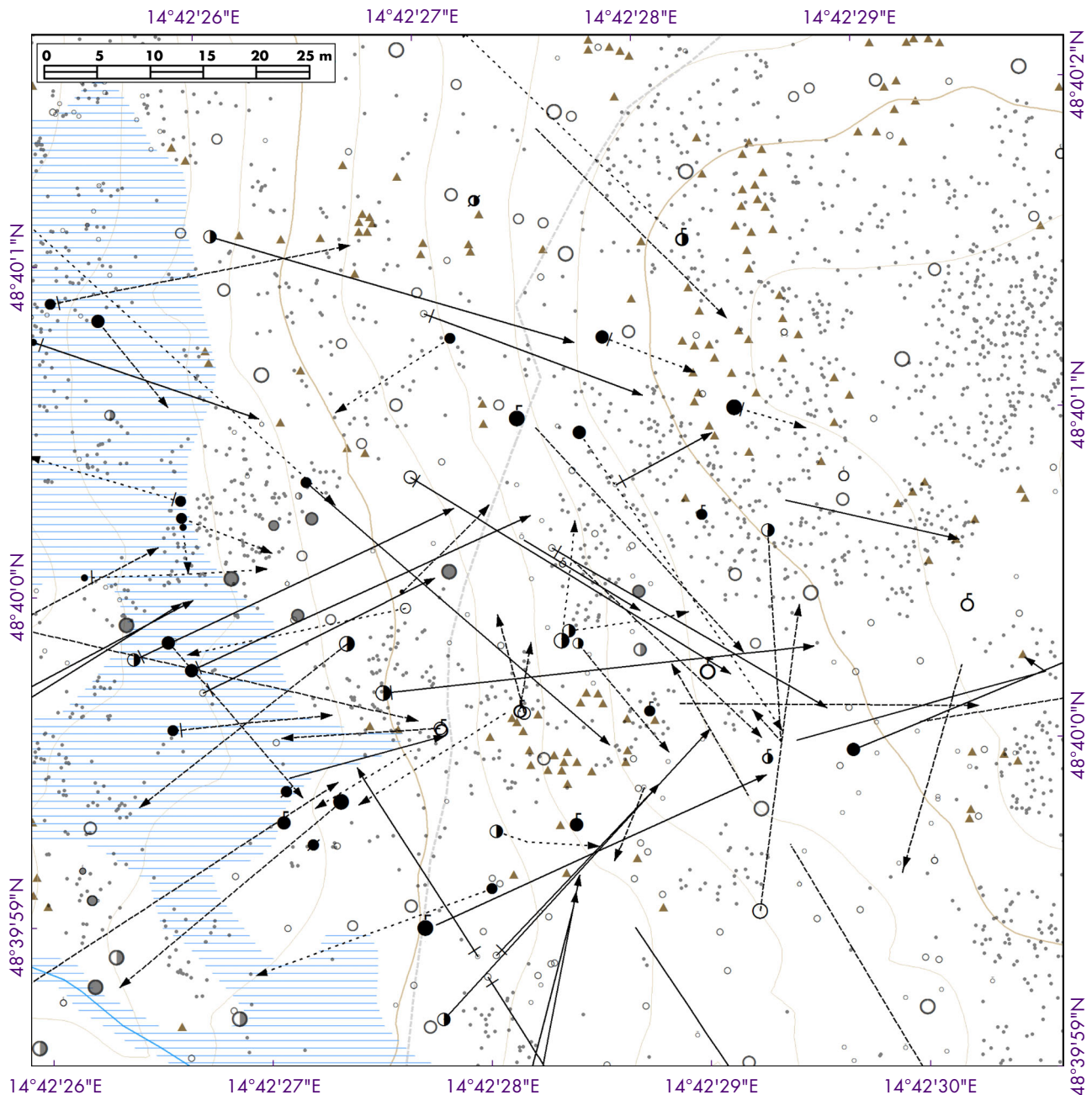
Figure 3. The locations of living and dead trees in a mixed natural forest in the Žofín Nature Reserve, Central Europe, show high spatial heterogeneity in the distribution of live trees and deadwood. The map contains the area depicted in Fig. 1. The circles indicate standing trees with all their associated habitats, foliage, bark, living wood and roots, while symbols indicate tree species (e.g. empty—*Fagus sylvatica*, full—*Picea abies*, split—*Abies alba*). The arrows indicate the deadwood habitat (decomposing tree trunks) at different stages of decay. The rocks are represented by triangles, and the wetlands and streams are indicated in blue (Šamonil *et al.* 2013a).

Blagodatskaya 2015). Spatial heterogeneity has important implications for ecosystem functioning and complicates stand-level predictions because it is difficult to address experimentally. Indeed, activity hotspots may be responsible for a large proportion of the total ecosystem activity, but the extent of their contribution remains unknown.

FOREST HABITATS

Forest ecosystems offer a wide range of habitats: the ubiquitous soil, litter and atmosphere, habitats associated with forest trees—foliage, wood, bark, roots and rhizospheres, and several others, such as the ground vegetation, deadwood, invertebrates, wetlands, streams or rocks, which are present in varying proportions (Table 1). Very often, most or all of the habitats can be found in close proximity within the forest ecosystem (Fig. 1). The habitats differ dramatically in size; while the mass of soil is enormous and the surface area of the foliage exceeds the land area of the ecosystem, other habitats may be absent or limited in size. More importantly, habitats differ in properties such as nutrient availability, major environmental conditions, processes and dynamics, which altogether affect microbial abundance and

Table 1. Properties of habitats within forest ecosystems. The values are representative of the temperate and boreal forests of the northern hemisphere, which are the most explored.

Habitat	Typical size[a]	Carbon sources	Drivers, processes and dynamics	Microbial biomass	Fungi/bacteria ratio	Characteristic (dominant) taxa, groups, ecology	Level of exploration	Selected references
Atmosphere	1 ha ha^{-1}	CO_2	Air movement, dispersal, radiation, precipitation, deposition, circadian changes in temperature and moisture content, climatic events, windstorms	10^5–10^6 bacterial cells m^{-3} and 10^4–10^5 fungal spores m^{-3}	Low	Bacteria, fungal spores	●	Bowers et al. (2011)
Foliage	1–11 ha ha^{-1}; 0.5–6.0 t ha^{-1}	Plant biomass; high C/N ratio	Interaction with host, co-metabolism, methylotrophy, N_2 fixation, high fluctuation of moisture and temperature, foliage development and activity, circadian changes in leaf ecophysiology	Low biomass, low diversity, high level of temporal fluctuation	Very high	Proteobacteria, Firmicutes, Actinobacteria, Acidobacteria, several fungi, e.g. Dothideomycetes and Leotiomycetes	●●	Vorholt (2012); Carrell and Frank (2015); Hardoim et al. (2015); Persöh (2015)
Wood	10–140 t C ha^{-1} (production 0.1–0.6 t ha^{-1} y^{-1})	Host photosynthates, plant biomass	Interaction with host, photosynthate flow, entry through injuries, seasonal changes in photosynthate flow	Low	High	Ascomycota (Dothideomycetes, Leotiomycetes), Basidiomycota, Zygomycota; endophytes and latent pathogens	●	Rayner and Boddy (1988); Giordano et al. (2009)
Bark surface	0. 9 ha ha^{-1} (14 t ha^{-1} bark)	Plant biomass (suberin), CO_2	Exposure to light and the atmosphere, fluctuation of moisture and temperature, N_2 fixation by lichen cyanobacteria	High if lichens are present	Uncertain	Lichens, yeasts, bacteria as symbionts of lichens, free-living cyanobacteria	●	Bhadra et al. (2008); Beck, Persöh and Rambold (2014); Grube et al. (2015)
Ground vegetation	0–3 t ha^{-1}	Plant biomass (cellulose, hemicelluloses, lignin, proteins)	Vegetation diversity, interaction with host, seasonality of host activity	Low aboveground, high in and on roots	Very high	AM and ERM fungi, endophytic fungi and bacteria; saprotrophic Ascomycota on mosses	●●	Öpik et al. (2008); Davey et al. (2012)
Wetlands	0–1 ha ha^{-1}	Organic matter decomposition	Temporary or permanent O_2 limitation due to changes in water level; slow decomposition; habitat-specific stratification; vegetation (bryophytes); seasonal changes in vegetation activity, fluctuation of the water table, bacterial methanogenesis, methanotrophy, N_2 fixation	10^8–10^9 bacterial cells ml^{-1} in peat extract	Very low	Acidobacteria, Proteobacteria, Actinobacteria, Verrucomicrobia, Planctomycetes; Metazoa; high share of Archaea	●●	Serkebaeva et al. (2013); Bragina, Berg and Berg (2015); Schmidt et al. (2015); Kostka et al. (2016)

Table 1. (Continued).

Habitat	Typical size[a]	Carbon sources	Drivers, processes and dynamics	Microbial biomass	Fungi/bacteria ratio	Characteristic (dominant) taxa, groups, ecology	Level of exploration	Selected references
Streams and lakes	0–0.5 ha ha^{-1}	CO_2; organic matter decomposition (mainly allochthonous plant litter)	Gas exchange limitation; movement (zoosporic taxa), sedimentation, biofilm formation; fluctuation of allochthonous C input	10^6–10^8 bacterial cells ml^{-1}, 40–60 mg g^{-1} detrital mass fungi; annual production 0.2–2 t ha^{-1}	Very high on decomposing litter	Aquatic hyphomycetes (Ascomycota), zoosporic Chytridiomycetes, Actinobacteria, Bacteroidetes, Proteobacteria, protist predators	•	Hieber and Gessner (2002); Newton et al. (2011); Bärlocher and Boddy (2016)
Roots and rhizosphere	Tens of t ha^{-1} of roots (root production 1.0–5.0 t ha^{-1} y^{-1}); 0.2 t ha^{-1} first-and second-order roots (production 0.2 t ha^{-1} y^{-1})	Host photosynthates, exudates	Interaction with host, rhizodeposition, commensalism, gradients of nutrient availability and chemistry, interaction of/with root-symbiotic organisms, priority effect in mycorrhizal colonisation, root development, seasonality of root production and activity	Higher than in soil, very high in mycorrhizal roots, 10^8–10^{10} bacterial cells g^{-1}	Intermediate in rhizosphere, high fungal dominance in mycorrhizal roots	ECM fungi, AM fungi, endophytes, occurrence of wood decomposers, rhizosphere-specific bacteria, mycorrhizal helper bacteria	••••	Prescott and Grayston (2013); Hardoim et al. (2015); Kohler et al. (2015); Lukešová et al. (2015); Marupakula, Mahmood and Finlay (2016)
Soil	50–300 t ha^{-1} organic matter	Humic compounds, dissolved and particulate OM, dead microbial biomass, dead roots	Microbial interactions; limited niche size (pores); interaction with fungal hyphae of ECM fungi; vertical stratification; spatial heterogeneity; seasonality of ECM mycelia and rhizodeposition, moisture variation	10^7–10^9 bacterial cells g^{-1}, 0.1–0.6 t ha^{-1} of ECM biomass; 0.2–0.7 mg g^{-1} fungal mycelia; production of 2 t ha^{-1} y^{-1} ECM mycelium, 0.2^{-1} t ha^{-1} y^{-1} fungal fruiting bodies	Intermediate to low, decreases with soil depth	Mycorrhizal fungi, saprotrophic fungi and bacteria of multiple phyla	••••	Lindahl et al. (2007); Baldrian et al. (2012); Clemmensen et al. (2013); Žifčáková et al. (2016)
Litter	2–50 C ha^{-1} (production 1–5 t ha^{-1})	Plant biomass (cellulose, hemicelluloses, lignin, proteins); high C/N ratio	Successive decomposition; fluctuations of moisture and temperature	10^8–10^9 bacterial cells g^{-1}, 0.7–7 mg g^{-1} fungal biomass	High to intermediate, varies during decomposition	Dominance of fungi, bacteria of multiple phyla, diverse ecology, high abundance of saprotrophs, mycophagous bacteria and fungi	•••	Lindahl et al. (2007); Voříšková and Baldrian (2013); López-Mondéjar et al. (2015); Žifčáková et al. (2016)
Deadwood	1.5–300 t ha^{-1} (5–1000 m^3 ha^{-1}), woody litter production 0.5–1 t ha^{-1} y^{-1}	Wood components (cellulose, hemicelluloses, lignin), fungal biomass; very high C/N ratio	Stochastic community assembly, priority effect, non-random development; high effect of microfauna; slow, successive fungi-dominated decomposition, moisture variation; commensalism, mycophagy, N$_2$ fixation and translocation	Typically very high, up to 0.15 g g^{-1} fungal biomass; several t ha^{-1} of fungal fruiting bodies	Very high	Saprotrophic Basidiomycota and Ascomycota; lichens; Myxomycota; abundant Proteobacteria, Acidobacteria and Actinobacteria; saproparasites	••••	Rayner and Boddy (1988), Stokland, Siitonen and Jonsson (2012); Clissmann et al. (2015); Hoppe et al. (2015); Johnston, Boddy and Weightman (2016); Svensson et al. (2016)

Table 1. (Continued).

Habitat	Typical size[a]	Carbon sources	Drivers, processes and dynamics	Microbial biomass	Fungi/bacteria ratio	Characteristic (dominant) taxa, groups, ecology	Level of exploration	Selected references
Rock surface	Typically a small fraction	CO_2, external C sources	Physical support, temperature and moisture fluctuation; interactions with associated vegetation (mosses); weathering by organic acid production, leaching of cations	High if lichens are present	High in case of ECM weathering	ECM fungi, lichens, bacteria	•	Banfield et al. (1999); Hoffland et al. (2004); Uroz et al. (2009); Schmalenberger et al. (2015)
Invertebrates	<1 t ha^{-1}	Plant biomass in invertebrate gut, external C sources when invertebrates serve as vectors	Wood and litter decomposition using symbiotic gut microbes; grazing on fungal mycelia or bacterial colonies; soil mixing, symbiosis, commensalism, vectors; dispersal, outbreaks, seasonal reproduction	High in specific organs (guts, bacteriosomes)	High or low, depending on niche (gut, bacteriosome, surface)	Bacteroidetes, Actinobacteria, Proteobacteria, wood-decomposing fungi	•••	Schloss et al. (2006); Adams et al. (2011); Štursová et al. (2014)

[a]Source of values: Swank and Schreude (1974); Rayner and Boddy (1988); Boddy and Watkinson (1995); Ostonen, Lohmus and Pajuste (2005); Waring and Running (2007); Perry, Oren and Hart (2009); Bowers et al. (2011); EUROPE et al. (2011); Pankratov et al. (2011); Sesartic and Dallafior (2011); Ekblad et al. (2013); Baldrian et al. (2013b); Leppälammi-Kujansuu et al. (2014); Delhomme et al. (2015); Peh, Corlett and Begeron (2015); Bärlocher and Boddy (2016); Domke et al. (2016); Hendricks et al. (2016).

community composition. Until recently, research on the forest microbiome has been highly focused on soil habitats, emphasising tree roots, their symbionts and on deadwood and litter to some extent, while other habitats have been greatly underexplored. Yet, there are already the first clues that help us to understand their specific properties shaping their microbiomes, at least in the temperate and boreal forests that are described best (Table 1).

Atmosphere

Atmosphere is largely an environment where microbes are present transiently and represents a medium for dispersal. Microbial biomass content is relatively low (Table 1), but transport seems to be very efficient; environmental filtering has been demonstrated to be a much more important barrier for fungal establishment than dispersal (Kivlin et al. 2014). Nevertheless, dispersal and survival of spores decreases rapidly with distance from the source, and their transport is thus most efficient at short ranges (Edman et al. 2004). This has been shown to be the case in the wood-decomposing fungus *Phlebia radiata* and several ECM fungi in which dispersal was largely confined to tens to hundreds of metres (Norros et al. 2012). The dispersal ability of fungal taxa varies considerably depending on the properties of their spores (Peay et al. 2012). Although the mass of spores produced seems to be low (2.1 kg ha^{-1} y^{-1}), the number of propagules produced is extremely high, ranging from 1–14×10^{13} ha^{-1} y^{-1}, with a mean of 6×10^{13} ha^{-1} y^{-1} (Sesartic and Dallafior 2011). Bacteria recovered from the atmosphere seem to reflect land use type but typically differ from potential source communities in the immediate proximity. This may indicate that long-distance transport occurs. Their abundances ranged from 10^5 to 10^6 m^{-3} in the forests of western USA (Bowers et al. 2011). Microorganisms in the atmosphere are affected by solar radiation and circadian and seasonal variation in temperature and moisture, which apparently favour resistant cells and propagules (Norros et al. 2015). The dynamics of the atmosphere microbiome is apparently governed by the combination of air movement, spore production and climatic events such as precipitation or windstorms, but remains very little understood.

Foliage

With the leaf area index above 1, the habitat provided by tree leaves is large in size (Table 1): the global estimate of the total area is 10^8 km^2 (Morris and Kinkel 2002). Foliage (and especially leaf surfaces) represents an environment exposed to multiple stressors, with dynamic changes in solar irradiation, temperature and moisture. Microbes typically exhibit low abundance and low diversity, particularly compared to the soil or litter (Šnajdr et al. 2011; Bringel and Couée 2015). Although the habitat provided by foliage is rich in organic compounds, these nutrients are largely inaccessible to foliar microorganisms. Plant defence mechanisms prevent microbial endophytes from entering cells, and many endophytes and epiphytes survive by scavenging on quantitatively minor substrates, including volatile organic compounds, or methylated compounds, which are frequently utilised in cometabolism (Redford et al. 2010; Vorholt 2012; Hardoim et al. 2015; Lebeis 2015). Leaf-associated fungi are more abundant than bacteria, but their sources of nutrition are unclear, although several of them are likely able to decompose plant cell wall biopolymers (Žifčáková et al. 2011; Voříšková and Baldrian 2013; Peršoh 2015) and methylotrophic yeasts were also recorded (Peter, Tornai-Lehoczki and Dlauchy 2008). In *Picea*

abies, more diverse fungal communities were found in needles with symptoms of disease than in the healthy ones, indicating the enrichment in plant pathogens or decomposers (Millberg, Boberg and Stenlid 2015).

The community assembly of the foliar microbiome is affected through a range of factors, including the effects of random deposition following atmospheric dispersal, stochastic events and the location within the canopy (Lebeis 2015). Temporary stress events, such as high temperatures or desiccation, likely induce bottlenecks during community development, resulting in dynamic changes in communities over time (Penuelas *et al.* 2012). Likely as a consequence of differences in stress intensity (such as irradiation), fungal communities in leaves differ within the canopy of a single tree, although they include a high proportion of generalists. At the stand level, they respond to phylogenetic relationships among tree species and also to genetic distance between trees of the same species (Redford *et al.* 2010; Cordier *et al.* 2012). Non-fungal eukaryotes are likely of minor importance in tree leaves; in the eukaryotic transcript pool from spruce leaves, fungi showed high level of dominance, especially the members of Dothideomycetes and Leotiomycetes (Delhomme *et al.* 2015). Bacteria on *Sequoia* spp. leaves showed low biomass and low diversity, with the dominance of a few taxa, which are often generalists that are shared across multiple biomes (Carrell and Frank 2015). Recent reports indicate that N_2 fixation may be important in this N-limited habitat. This was shown for acetic acid-utilising bacteria that are stable symbionts of *Pinus flexilis* and may provide 7–14 g N m^{-2} d^{-1}. (Moyes *et al.* 2016).

Foliage represents a dynamic substrate, with an annual production ranging within tons of biomass per hectare (Hendricks *et al.* 2016). Importantly, while evergreen foliage remains active at all times, deciduous trees produce their leaves after winter and shed them in late autumn. This makes the microbiomes of deciduous trees much more dynamic (Peršoh 2015). Indeed, development follows plant phenology; community structure clearly depends on leaf age and shows rapid turnover (Redford and Fierer 2009; Penuelas *et al.* 2012; Lebeis 2015).

The bark surface

As a protective tissue, tree bark is composed of compounds recalcitrant to microbial decomposition, such as suberin, and is impregnated with resins that inhibit microbial growth. Instead of these recalcitrant compounds, CO_2 is an important C source for algae and cyanobacteria, both free-living and lichen symbionts. Fungi form relatively rich communities on bark, primarily comprising lichens, but yeasts have also been reported (Bhadra *et al.* 2008; Beck, Persoh and Rambold 2014). Temporal variation in the fungal community composition on tree bark has been observed in a temperate forest (Beck, Persoh and Rambold 2014), but it remains unclear whether community development has a seasonal pattern or is rather stochastic.

Lichens were recently demonstrated to be complex symbiotic associations of fungi, CO_2- and N_2-fixing bacteria but they also other bacterial associates. Bacterial communities in lichens have been identified to be stable, specific and structurally integrated partners of the symbiosis, including taxa that are endosymbiotic to fungi. More than 800 bacterial species are able to contribute multiple aspects to the symbiotic system, including essential functions such as the supply of nutrients, especially nitrogen, phosphorous and sulphur, the support of fungal and algal growth by the provision of hormones, and the degradation of older lichen thalli (Grube *et al.* 2015). Importantly, N_2

fixation by lichen-associated cyanobacteria may be important at the ecosystem level in the boreal zone (Rousk *et al.* 2015). Bacteria have also been documented to colonise symbiotic propagules of lichens developed for transmission so that fungal, cyanobacterial and bacterial partners are cotransported during dispersal. Due to the large size of such propagules, transmission occurs at rather short distances (Aschenbrenner *et al.* 2014).

Wood of living trees

The woody biomass of living trees represents a large resource in forest ecosystems that is rich in potential nutrients (Table 1). However, because stem infections might be fatal, trees efficiently protect themselves against the entry of microbes, and the microbial biomass in healthy trees is therefore low. Because of their filamentous growth, fungi are better adapted to wood penetration and seem to dominate this niche (Rayner and Boddy 1988; de Boer *et al.* 2005). Diverse fungal communities in *P. sylvestris* wood included potential endophyte and parasite species (Giordano *et al.* 2009), as well as potential saprotrophs that typically grow on deadwood (Parfitt *et al.* 2010). Fungi also dominate the eukaryotic transcript pool in spruce shoots (Delhomme *et al.* 2015). Knowledge regarding bacterial wood endophytes is generally lacking, and the wood of healthy trees remains one of the least explored forest habitats.

Ground vegetation

Forests (or forest patches) with sufficient light penetration typically support the growth of ground vegetation of variable compositions and biomass, which is dependent on the combination of factors that include dominant trees in the canopy, fertility, light penetration and moisture (Perry, Oren and Hart 2009; Sterkenburg *et al.* 2015; Urbanová, Šnajdr and Baldrian 2015). Although the biomass of ground vegetation varies considerably, its mass and net primary production contribute typically <20% of the total net primary production in the ecosystem (Malhi, Baldocchi and Jarvis 1999; Sabo *et al.* 2008; Peh, Corlett and Begeron 2015). The niches associated with ground vegetation are diverse, as is typical for the plant holobiont and similar to the corresponding habitats associated with trees (Vorholt 2012; Hardoim *et al.* 2015; Lebeis 2015). The roots of ground vegetation mostly form symbioses with AM or ERM fungi (Öpik *et al.* 2008; Clemmensen *et al.* 2015), which frequently coexist in soils with the ECM tree symbionts. Mosses harbour other fungal communities dominated by saprotrophic Ascomycota (Davey *et al.* 2012). In contrast to those of trees, the composition of microbiomes of forest plants on the ground remain largely unexplored.

As in trees, the activity of ground vegetation is typically seasonally variable and depends on the temperature and precipitation regime. In addition, the ground vegetation composition of deciduous forests changes during the year with the change of light penetration and different cohorts of plants are present before tree leaf emergence and during the shady summer. Vegetation development is also highly dependent on the successional age of forests, with very young and very old stands harbouring more plants (Wallander *et al.* 2010; Clemmensen *et al.* 2015). The seasonality of ground vegetation activity obviously contributes to the seasonality of associated microbial communities (Davey *et al.* 2012). In annual plants, symbiotic and endophytic taxa are expected to be replaced by saprotrophs after the senescence and dieback of their plant hosts. It should be noted that due to the limited contribution of the ground vegetation to total photosynthetic production in comparison to trees, the size of its effect on

forest microbiota is likely limited. For example, AM and ERM taxa contributed only marginally to the transcription of ribosomal RNA in a *Pi. abies* forest (Baldrian *et al.* 2012). Still, within monocultures of *P. contorta*, specific microbial community and chemical similarities were detected in soils covered by similar underground vegetation (McIntosh, Macdonald and Quideau 2016).

Streams and lakes

Streams and lakes represent largely specific habitats (Table 1), that are, however, due to high inputs of allochthonous biomass, such as plant litter and soil organic matter, largely connected to other forest habitats as well as wetlands with stagnant water. In addition to allochthonous material, primary production represents another source of C in these aquatic ecosystems to a varying extent. Decomposition of litter in streams is rapid and decomposing litter is mainly colonised by specific aquatic hyphomycetes. In litter, fungal biomass exceeds that of bacteria more than 20-fold (Hieber and Gessner 2002). In the water, bacterial abundance is typically low, with 10^6–10^8 cells ml^{-1}, and characterised by high relative abundances of Actinobacteria, Bacteroidetes and Proteobacteria (Newton *et al.* 2011). Fungal communities in aquatic ecosystems are dominated by Ascomycetous hyphomycetes and zoosporic fungi such as Chytridiomycetes (Bärlocher and Boddy 2016). Specific bacterial communities rich in oligotrophic taxa were reported from submerged decomposing wood (Zaichikova, Berestovskaya and Vasil'eva 2016) and immersed litter; the latter substrate harbours mostly Proteobacteria, Bacteroidetes and Verrucomicrobia, and the bacterial community changes profoundly as decay progresses (Newman, Liles and Feminella 2015; Wymore *et al.* 2016). The environment is typified by spatial gradients in oxygen availability, the process of sedimentation and the formation of biofilms on litter or other surfaces, and is largely different from terrestrial conditions (Bärlocher and Boddy 2016). Hypoxic conditions and droughts lower diversity and activity (Bärlocher and Boddy 2016). The dynamics of productivity is driven by variation in primary production (affected by temperature and light conditions) and the largely variable inputs of allochthonous material, such as during the litterfall period in autumn or the spring snowmelts that bring soil organic matter.

Wetlands

Forested wetlands represent a specific habitat for multiple reasons. The organic matter content of such ecosystems is typically high and has a specific composition, such as the bodies of the *Sphagnum* mosses. Due to limited oxygen solubility in water, decomposition is slowed and stratified vertical profiles develop (Table 1). The deep, anoxic parts of the profile may be the source of methane production by methanogens, while the upper layers harbour methanotrophs and aerobic decomposers (Schmidt *et al.* 2015).

With 10^8–10^9 bacterial cells per ml of peat extract, wetlands harbour fewer bacteria than soils, but more than lakes or streams. Dominant bacterial taxa are typically Acidobacteria, Proteobacteria and Actinobacteria, but Verrucomicrobia and Planctomycetes are also common (Serkebaeva *et al.* 2013). The abundance of fungi is typically very low due to the absence of root symbionts (Pankratov *et al.* 2011) and is largely unexplored. Euryarcheota may represent >7% of the total microbial abundance in wetlands compared to a typical representation of <2% in soils (Bragina, Berg and Berg 2015). A low level of plant-host specificity among bog bacteria has been reported, and most

of the core taxa were associated with the dominant *Sphagnum* mosses (Bragina, Berg and Berg 2015). Although the majority of the *Sphagnum* microbiome remains uncultured and its metabolic capabilities uncharacterised, prokaryotes and fungi have the potential to act as mutualists, symbionts or antagonists of *Sphagnum*. For example, methanotrophic and N$_2$-fixing bacteria, most frequently Alphaproteobacteria and Cyanobacteria, may benefit their plant hosts (*Sphagnum* spp. or other mosses) by providing up to 20%–30% of their carbon and nitrogen. Nitrogen fixation appears to be quantitatively important in forest wetlands (Leppänen *et al.* 2013; Leppänen, Rissanen and Tiirola 2015; Kostka *et al.* 2016).

Changes in the water table level that change oxygen availability along the vertical profile represent one of the most important factors in microbial C cycling (Laiho 2006). In terms of immediate short-term changes, such as during the summer drought, decomposition is boosted by a decrease in the water table. If the effect is long term, complex processes follow that involve changes in vegetation cover, litter amount and quality, and decomposition (Straková *et al.* 2012), all of which obviously largely affect microbial communities.

Roots and the rhizosphere

Plant nutrient exchange with the soil environment is mediated through plant root tissues, ECM or AM roots, rhizospheres and fungal mycelia extending from the roots and rhizospheres into the bulk soil. At the level of fine roots, ECM tips represent symbiotic organs combining the structures of tree hosts and their fungal associates. Roots and rhizospheres clearly represent a large and unique habitat (Table 1), highly specific and rich in microbial abundance and activity (Lebeis 2015).

Microbial communities in this habitat clearly differ from those in the bulk soil, most obviously due to the presence of root-symbiotic mycorrhizal fungi (Prescott and Grayston 2013). This is thought to be the result of the release of a diverse array of exudates originating both from the roots and from mycorrhizal fungi. The exudates are comprised of carbohydrates, amino acids, low molecular mass aliphatic and aromatic acids, fatty acids, enzymes and hormones (Prescott and Grayston 2013). The current understanding of the rhizosphere microbiota in forests is unfortunately largely limited to ECM fungi. ECM root tips support specific and diverse populations of bacteria and microfungi, including bacteria that help to establish mycorrhizal symbioses (Garbaye 1994; Frey-Klett, Garbaye and Tarkka 2007; Toljander *et al.* 2007). In addition, tree roots also harbour a phenotypically defined group of dark septate endophytes with an unclear ecology (Ahlich and Sieber 1996; Lukešová *et al.* 2015) and wood-decomposing fungi (Vasiliauskas *et al.* 2007). Rhizosphere communities of bacteria show higher cell counts than those of bulk soils, a specific enrichment of certain bacterial phyla and a lower abundance of archaea (Uroz *et al.* 2010; Karlsson, Johansson and Bengtson 2012). Experiments with *P. contorta* suggest that in addition to ECM, trees can also derive their N from bacterial N-fixers living in their rhizosphere (Bal and Chanway 2012). Symbiotic ECM tree roots represent an important niche where ECM fungi and bacteria interact. This is due to the large surface area of root-associated fungal mycelia and the direct access to photosynthetically derived carbon. Bacterial communities are highly dynamic in time, and individual ECM fungi tend to select for specific bacteria (Marupakula, Mahmood and Finlay 2016).

The seasonal production of roots and variation in their activity leads to seasonal differences in root and rhizosphere microbial communities (Ekblad *et al.* 2013; Lebeis 2015). Priority

effects are important in the ECM fungal colonisation of root tips (Kennedy, Peay and Bruns 2009), and the communities of ECM fungal symbionts of tree fine roots continue to change with tree age (Wallander *et al.* 2010).

Soil

Soil clearly represents the quantitatively most important habitat for soil microbes (Table 1), with their activity being fuelled by the decomposition of organic matter and photosynthetically derived C entering the soil through the mycelia of mycorrhizal fungi (Clemmensen *et al.* 2013). The most important feature of temperate and boreal forests is the presence of large quantities of ECM mycelia that may represent up to one-third of the total microbial biomass and may produce 50% of the dissolved organic carbon (Högberg and Högberg 2002; Ekblad *et al.* 2013). Mycorrhizae liberate N and P from dead organic matter and transport it to their plant symbionts (Read and Perez-Moreno 2003) but also form complex networks connecting multiple trees, including both overstorey and understorey members (Högberg *et al.* 1999). Although ECM have lost much of their enzymatic toolkit during evolution from their saprotrophic ancestors (Kohler *et al.* 2015), they likely still contribute to organic matter decomposition while mining for organic N (Bödeker *et al.* 2009; Lindahl and Tunlid 2015). ECM fungal mycelia often form dense mats that have specific properties such as low pH (Kluber *et al.* 2010), and ECM mats consequently harbour microbial communities that differ from soils without such mats (Kluber, Smith and Myrold 2011). In addition to bacteria and fungi, these also include predators such as testate amoebae, collembolans, nematodes, microarthropods and enchytraeids that substantially affect mycelial productivity (Schroter, Wolters and De Ruiter 2003; Kanters, Anderson and Johnson 2015). ECM fungi also harbour endobacteria, mainly Alphaproteobacteria (Bertaux *et al.* 2005).

In addition to ECM fungi and their associated organisms, soils also harbour saprotrophic fungi and bacteria. With the decreasing organic matter content and turnover that occur with increasing soil depth (Šnajdr *et al.* 2008), the microbial community composition also changes (O'Brien *et al.* 2005; Voříšková *et al.* 2014; López-Mondéjar *et al.* 2015). While saprotrophs are common in the upper parts of the soil profile, mycorrhizal dominance and the relative abundance of bacteria increase with depth (Lindahl *et al.* 2007; Šnajdr *et al.* 2008) and ECM communities change in composition (Dickie, Xu and Koide 2002; Rosling *et al.* 2003). Archaea often show low diversity and abundance in forest soils, increasing with depth (Pesaro and Widmer 2002; Hartmann *et al.* 2009), but some groups, such as the ammonia-oxidising Thaumarchaeota, seem to be important in nitrogen cycling in acidic forest soils with ammonia concentrations too low to support bacterial ammonia oxidisers (He, Hu and Zhang 2012; Levy-Booth, Prescott and Grayston 2014); in acidic soils with higher ammonia concentrations, archaea seem to be much less abundant and active (Žifčáková *et al.* 2016). The abundance of yeasts in the bulk soil is low compared to the rhizosphere (Yurkov, Kemler and Begerow 2011). It should be noted that soil is also highly heterogeneous horizontally, with activity concentrated into hotspots such as the rhizosphere, the detritusphere and biopores (Baldrian 2014).

Bacteria dominate the total transcription in the soil of *Pi. abies*, followed by fungi, with the contribution of archaea lower than 2% (Hesse *et al.* 2015; Žifčáková *et al.* 2016). In temperate forest soils, fungal sequences dominate in eukaryotic metatranscriptomes, with protists being the second most active eukaryotic microbial group (Bailly *et al.* 2007; Damon *et al.* 2012;

Žifčáková *et al.* 2016). Microbial activity, community composition and abundance are largely variable in time, showing seasonal responses to the activity of tree roots (Voříšková *et al.* 2014; López-Mondéjar *et al.* 2015; Žifčáková *et al.* 2016). This is largely due to the seasonality of ECM: the relative abundance of fungal transcripts in summer, when ECM are active, was found to be twice as high as in winter (Žifčáková *et al.* 2016). In addition to ECM fungi, other microbial taxa also seem to depend on seasonal C allocation belowground (Yarwood, Myrold and Hogberg 2009; Voříšková *et al.* 2014; López-Mondéjar *et al.* 2015) because root-derived carbon can be more readily utilised than recalcitrant organic matter.

In addition to general seasonal trends, soil activity is highly inconsistent on a shorter timescale, with 'hot moments' such as rainfall, snowmelt, freezing/thawing cycles, animal and root activity greatly affecting microbial activity (Kuzyakov and Blagodatskaya 2015). Under certain conditions, anoxic microsites may temporarily appear. These are characterised by the dominance of heterotrophic, fermentative bacteria, while fungi are less abundant and are represented by yeasts (Reith, Drake and Kusel 2002). Damage to roots or mycelia temporarily boosts the activity of r-strategist microorganisms (Lindahl, de Boer and Finlay 2010).

Litter

Plant litter, especially the litter of forest trees, is the major source of organic matter accumulation on the forest soil surface (Table 1), which is the driving force behind the establishment of the soil profile (Berg 2000). Being composed of plant cell wall biopolymers, litter supports mainly saprotrophic taxa (Lindahl *et al.* 2007) that are able to decompose recalcitrant plant-derived biopolymers. Litter-decomposing saprotrophic basidiomycetes that are physiologically related to white-rot wood-decomposing fungi often act as major litter decomposers together with ascomycetous microfungi (Osono 2007; Eichlerová *et al.* 2015). In the *Pi. abies* litterlayer, fungi dominate microbial transcripts, with a share of >60%, compared to 30% for bacteria and <2% for archaea (Žifčáková *et al.* 2016). The expressed decomposition-related enzymes in litter are largely of fungal origin (Kellner, Zak and Vandenbol 2010; Schneider *et al.* 2012; Žifčáková *et al.* 2016). Among bacteria, Proteobacteria and Bacteroidetes seem to be enriched in temperate forest litter compared to soil (López-Mondéjar *et al.* 2015), and multiple litter-inhabiting bacteria are able to accumulate C from decomposing plant biomass (Štursová *et al.* 2012; López-Mondéjar *et al.* 2016). Due to the high fungal biomass in litter, fungal mycelia represent another important source of nutrients in this habitat that is used by a specific functional guild of microorganisms, especially bacteria (Brabcová *et al.* 2016; Tláskal, Voříšková and Baldrian 2016). Decomposition of mycelia is typically faster than that of plant residues, but depends on their composition, such as the amount of chitin and melanin (Fernandez and Koide 2012). Fine roots represent another litter source, quantitatively comparable to the aboveground litter, but typically more recalcitrant to decay (Xia, Talhelm and Pregitzer 2015). The composition of decomposer communities in this substrate, however, remains so far largely unknown.

The chemical composition of litter changes as its decomposition progresses, and litter of various ages thus offers different nutrients (Šnajdr *et al.* 2011). This is reflected by differences in enzyme activity, as well as in the composition of fungal and bacterial communities associated with litter (Šnajdr *et al.* 2011; Voříšková and Baldrian 2013; Purahong *et al.* 2015; Tláskal,

Voříšková and Baldrian 2016). The initial stages of litter decomposition show high fungal/bacterial biomass ratios, and the fungal endophytes of leaves are important primary decomposers (Voříšková and Baldrian 2013; Purahong *et al.* 2015). Later in the process, litter decomposers are recruited from the soil and the relative abundances of Basidiomycota and bacteria increase (Voříšková and Baldrian 2013).

Deadwood

Deadwood represents a specific habitat, whose amount varies largely among different forests (Table 1). While the deadwood volume in natural forests can reach up to 1200 m³ ha⁻¹ and can exceed the biomass of living trees, the stock is typically 2–65 m³ ha⁻¹ in managed forests where wood is harvested (Hahn and Christensen 2005; Stokland, Siitonen and Jonsson 2012). Most deadwood is represented by coarse wood (fallen trees and large branches), fine woody debris typically total only 2–8 t ha⁻¹ (Domke *et al.* 2016). Due to its physical and chemical properties, such as impermeability, high lignin and low N concentrations, fresh wood is resistant to colonisation by most bacteria (de Boer *et al.* 2005). Thus, fungi, particularly saprotrophic cord-forming basidiomycetes, dominate wood decomposition (Rayner and Boddy 1988), reflecting the ability of these microorganisms to efficiently colonise and decompose complex organic matter (Eichlerová *et al.* 2015). Decomposing wood is strongly influenced by fungi and fungal decomposition machinery, which requires an acidic pH. The bacterial community is composed of low pH-tolerant bacteria, combining decomposers, commensalists and likely also mycophages (Folman *et al.* 2008; Valášková *et al.* 2009; Johnston, Boddy and Weightman 2016). Deadwood surfaces represent an important niche for specialised lignicolous lichens (Svensson *et al.* 2016).

Decomposition of coarse wood such as logs or stumps typically takes tens of years to accomplish, and it is characterised by the successive development of fungal communities with an initial dominance of decomposers and an increase of ECM fungi during late decay (Rajala *et al.* 2011; Baldrian *et al.* 2016). Because several fungal taxa can colonise fresh wood, the assembly and development of fungal communities is stochastic. Due to the priority effect, the identity of primary colonisers largely determines the establishment of later-arriving species (Fukami *et al.* 2010; Lindner *et al.* 2011; Hiscox *et al.* 2015), and deadwood decomposition can therefore follow very different tracks, such as brown-rot or white-rot decay, that lead to profound differences in wood chemistry and decomposition rates (Baldrian 2008; Schilling *et al.* 2015; van der Wal, Ottosson and de Boer 2015). At certain stages of development, wood fungi produce fruiting bodies and spores to ensure dispersal to novel substrates (Ovaskainen *et al.* 2013). Climate, soil properties, sun exposure, and deadwood size and type (log, twig, or stump) have been recorded as important determinants of fungal community composition (Forrester *et al.* 2015; Seibold *et al.* 2015).

The composition of the bacterial community also develops with decay, primarily reflecting the increasing N content and changing pH (Hoppe *et al.* 2015; Kielak *et al.* 2016; Rinta-Kanto *et al.* 2016). The initial community assembly appears stochastic but becomes more deterministic in later stages, although the changes in community composition are less pronounced than in fungi (Kielak *et al.* 2016). Myxomycotan protists that are often associated with deadwood respond to wood pH rather than to the decomposition stage of beechwood (Clissmann *et al.* 2015).

Fresh deadwood is typically N limited, but N content increases during decay (Baldrian *et al.* 2016). This has been demonstrated to be the result of N₂ fixation by deadwood bacteria (Wei and Kimmins 1998; Brunner and Kimmins 2003), translocation of N by mycelial networks of cord-forming saprotrophic fungi (Bebber *et al.* 2011; Philpott *et al.* 2014) and possibly also by mycorrhizal mycelial networks (Rajala *et al.* 2012). Nitrogen fixation in deadwood can be significant at the ecosystem level, with estimates ranging up to 2.1 kg fixed N ha⁻¹ y⁻¹ (Brunner and Kimmins 2003).

Rock surfaces

Rock surfaces, both aboveground and belowground, represent specific habitats in certain forests (Table 1). Both fungi and bacteria contribute to the weathering of mineral surfaces (Hoffland *et al.* 2004; Uroz *et al.* 2009). ECM fungi produce organic acids to mobilise mineral nutrients and deliver them to their plant hosts in exchange for carbon (Landeweert *et al.* 2001; Gadd 2007), and mineral weathering by the production of acids and chelators has also been described in bacteria, including those associated with mycorrhizae (Uroz *et al.* 2009). Mineral weathering by the ECM fungus *Paxillus involutus* was found to be fuelled by photosynthate-derived carbon from its *Pinus* host and to preferentially dissolve minerals that yield important bivalent cations (Schmalenberger *et al.* 2015). Aboveground, rock surfaces are habitats for mosses and lichens with their own specific microbiomes and their important involvement in the weathering of rock in the lichen/rock contact zone mediated by organic acid production (Banfield *et al.* 1999; Grube *et al.* 2015).

Invertebrates

All invertebrates have their own microbiomes, ranging from loosely associated taxa over commensalists to symbionts, but only some of these organisms are of importance in ecosystem-level processes (Table 1). For example, bark beetles act as vectors that spread fungi. The fungi can serve as a nutrient source for larvae, assist the insects by modifying the environment in a living tree to make it more favourable for the insects or kill the trees (Stokland, Siitonen and Jonsson 2012). Blue stain fungi are typically associated with bark beetles contained within myalgia, small cavities with fungal spores containing symbiotic fungi that aid to decompose wood. Less specific fungal associates (e.g. yeasts, moulds or wood-rotting basidiomycetes) are transmitted more incidentally when attached to body surfaces (Six 2003). Other invertebrates such as wood-boring beetles or woodwasps have specialist microbial symbionts in their guts that assist them in decomposing lignocellulose. Proteobacteria, Actinobacteria and Bacteroidetes were recorded in the guts of beetles, while the guts of the woodwasps, *Sirex* sp., which feed on wood, contain Actinobacteria, Proteobacteria and the basidiomycete *Amylostereum* (Schloss *et al.* 2006; Adams *et al.* 2011). Xylophagous beetles contain hindgut microbiomes composed mainly of Bacteroidetes, Firmicutes, Proteobacteria and Actinobacteria, which help them to digest wood (Berlanga *et al.* 2016). As vectors, insects clearly facilitate the establishment of wood-decomposing fungi on living as well as dead trees (Persson, Ihrmark and Stenlid 2011). Also forest soil earthworms were demonstrated to have specific gut microbiota that includes bacterial denitrifiers (Karsten and Drake 1997).

Multiple guilds of invertebrates in soil, litter and deadwood also act as grazers of fungal mycelia. Extensive grazing leads to the alteration of fungal enzyme production and community composition and may ultimately affect decomposition (Crowther *et al.* 2011, 2013). It should be noted that also
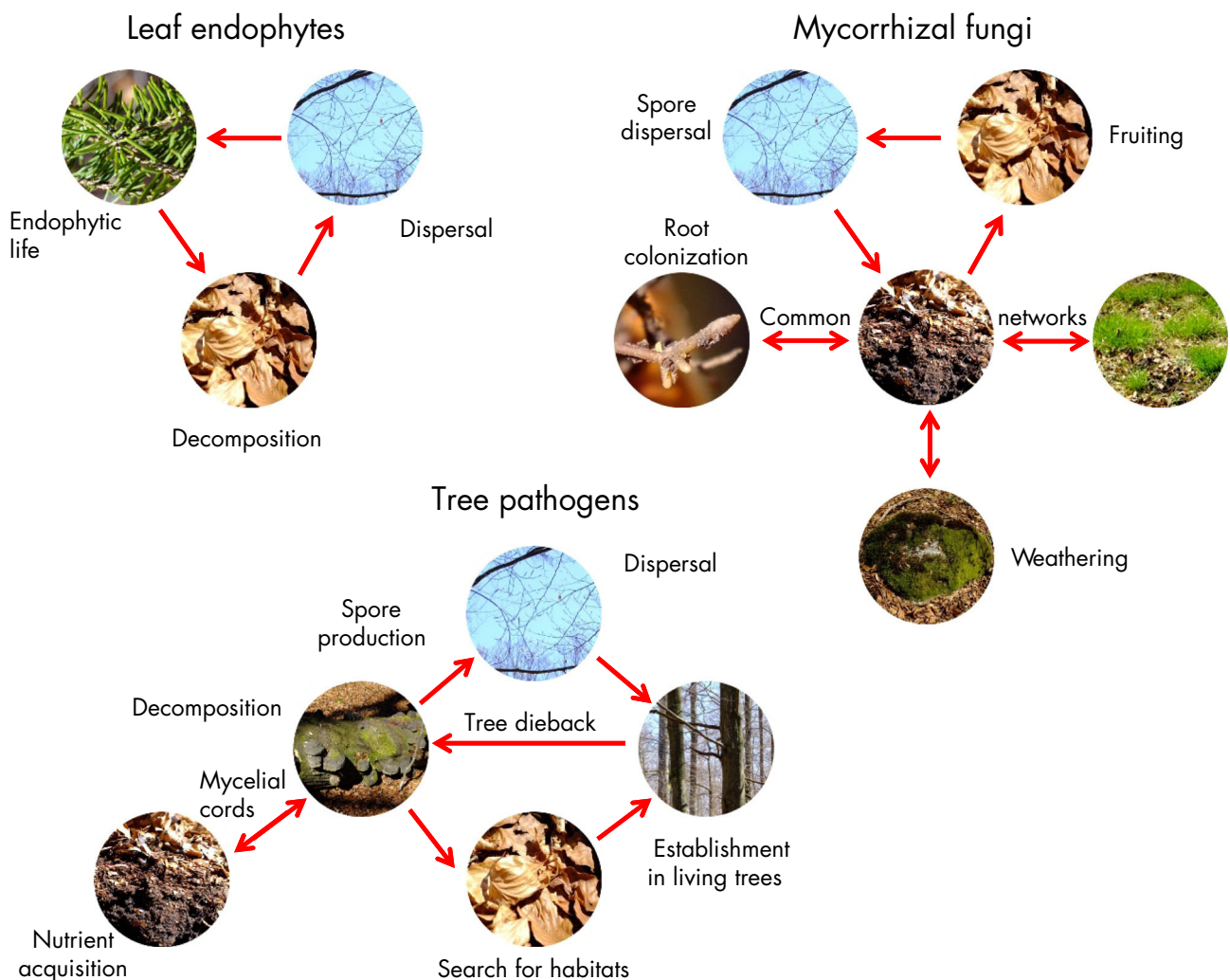
Figure 4. Connections between the microbiomes of multiple habitats mediated by fungi. Due to their filamentous growth and spore dispersal, fungi are better connectors of habitats than bacteria.

vertebrates inhabiting forests possess specific microbiomes and act as vectors spreading microorganisms in the ecosystem.

Habitat connections

Although forest habitats appear to be distinct in their properties, many microbial taxa inhabit several of them, either subsequently or at the same time. This appears to be especially common for filamentous fungi that, unlike the unicellular bacteria or yeasts, are able to explore multiple habitats during their search for novel niches, and then connect and exploit them by the translocation of nutrients or water (Boddy and Watkinson 1995; de Boer *et al.* 2005; Guhr *et al.* 2015). The lifecycles of fungal foliar endophytes, tree pathogens and mycorrhizal fungi demonstrate how diverse habitats can be connected by fungi (Fig. 4).

Many fungal foliar endophytes are recovered from living tree leaves or needles as asymptomatic inhabitants with limited biomass. However, many of them can actively initiate litter decomposition, as they are able to benefit from their presence in senescent leaves before the arrival of soilborne saprotrophs (Muller *et al.* 2001; Žifčáková *et al.* 2011; Voříšková and Baldrian 2013; Peršoh 2015; Szink *et al.* 2016). It is proposed that the endophytes of leaves that are shed by deciduous trees in autumn

persist as saprobes in litter or dead wood over winter, sporulate and then re-invade living leaves, as indicated by their presence in both litter and live leaves (Unterseher, Persoh and Schnittler 2013). There are indications that some of these endophytes may even spend some part of their lifecycle in the aquatic environment (Selosse, Vohník and Chauvet 2008). Although the mode of re-entry into the foliar structures of their hosts is unknown, spore dispersal via the atmosphere seems to be most likely (Fig. 4).

Saprotrophic fungi can use deadwood as a resource that provides them C and energy to spread in the soil and colonise the next deadwood resources or, in the case of pathogens, the roots of living trees (Rayner and Boddy 1988; Baldrian 2008). Wood decay is promoted by the translocation of N and P into this nutrient-poor substrate by the mycelial cords of the fungi (Wells and Boddy 1995; Bebber *et al.* 2011; Philpott *et al.* 2014). A sufficient nutrient supply allows the fungi to fruit and produce large numbers of spores that are transported by air. The wood of trees is typically entered through wounds by mycelia germinating from spores, but even the wood of living trees with no symptoms of fungal presence often contains several parasitic or saprotrophic wood-decaying fungal taxa (Fig. 4). The presence of saprotrophic fungi in wood tissues may allow them to

rapidly colonise wood when the tree dies or to develop into parasites when it is stressed (Parfitt *et al.* 2010). Wood-decomposing saprotrophic basidiomycetes, such as *Phanerochaete velutina* or *Hypholoma fasciculare*, also extend their mycelia into soil and are able to decompose litter during the search for deadwood (Baldrian 2008). In a similar way, the root pathogen *Heterobasidion annosum* can live as a saprotroph on deadwood in stumps and spread through soil to infect living trees (Piri 1996). Interestingly, wood-rotting fungi have also been recovered from tree needles (Žifčáková *et al.* 2011).

ECM fungi inhabit plant roots and the rhizosphere, and most of them extend into the bulk soil, although to a varying extent depending on their mycelial structure, the so-called exploration type (Agerer 2001). They can even utilise organic N in decomposing deadwood or litter (Tedersoo *et al.* 2003; Rajala *et al.* 2011; Urbanová, Šnajdr and Baldrian 2015) and mine rock surfaces for mineral nutrients to be delivered to their plant hosts (Landeweert *et al.* 2001; Schmalenberger *et al.* 2015). Mycelia of ECM fungi may connect their host to soil or nutrient patches by their mycelia (e.g. Lindahl *et al.* 1999). Forest trees with mycorrhizal roots and ground vegetation may be even connected by ECM fungi with appropriate mycelial morphology into common mycelial networks that link their roots and rhizospheres with the nutrients in soil or weathered rock (Högberg *et al.* 1999; Simard *et al.* 2012). Such networks appear to be resilient to the random loss of participant trees and to soil water stress, but may depend on large trees or fungal genets that represent hubs (Beiler, Simard and Durall 2015). Networks transport soil water, nitrogen and phosphorus, and carbon provided by tree primary production (Simard *et al.* 2012). For example, C assimilated by mature spruce was shown to be traded over to neighbouring beech, larch and pine trees via overlapping root spheres. Isotope mixing signals indicated that this interspecific, bidirectional transfer, assisted by common ECM networks, accounted for 40% of the fine root carbon (Klein, Siegwolf and Körner 2016). Seasonally, mycorrhizal fungi colonise litter (Voříšková *et al.* 2014), produce fruiting bodies on the forest floor and disperse as spores by air movement or depend on invertebrates that disperse their spores from hypogeous fruiting bodies (Fig. 4). Mycelial networks of ECM fungi have also been proposed to connect soil and deadwood and to act in N translocation between these habitats in one or the other direction (Rajala *et al.* 2012; Hoppe *et al.* 2015). Mycelial networks also provide the means for communication: for example, the defoliation or budworm infestation of *Pseudotsuga menziesii* led to the allocation of carbon and stress signals to *P. ponderosae* seedlings via their ECM connection (Song *et al.* 2015).

In different habitats, ECM fungi have to adapt their physiology to the habitat properties (Table 1), to differentiate functionally. Theoretically, fungi that grow as root symbionts and benefit from the photosynthesis of their hosts in summer should be able to switch to full saprotrophy in winter, when their tree host does not provide sufficient C. However, there are no ECM fungi that assimilate significant amounts of soil or litter C because all of their evolutionary lineages lost the ability to utilise biopolymers (Kohler *et al.* 2015). Their decomposition abilities vary but are typically confined to mining for N contained in organic matter (Lindahl and Tunlid 2015; Shah *et al.* 2016).

Almost no information exists regarding habitat sharing in bacteria, but it is highly probable that such sharing also exists where habitats offer similar niches, such as in the litter and soil (Baldrian *et al.* 2012; Urbanová, Šnajdr and Baldrian 2015). In this respect, it should be noted that bacteria may use fungal hyphae or cords to move through the environment (Kohlmeier *et al.* 2005;

Warmink *et al.* 2011), and fungal networks thus likely promote habitat sharing by bacteria. The above examples indicate that there seems to be a complex network of connections between forest habitats, the importance of which has so far not been fully appreciated, where live or dead trees act as hubs providing carbon.

FORESTS AS DYNAMIC ECOSYSTEMS

Forest ecosystem processes are dynamic at a wide range of temporal scales, and the dynamics of processes is habitat specific (Table 1, Fig. 5). For example, the utilisation of root exudates by soil microbes takes minutes to hours, whereas the growth response and sharp increase in respiration by forest soil microbes following precipitation or disturbance occurs on the scale of a few hours to days (Aanderud *et al.* 2015). On the other hand, decomposition of fine roots occurs over the course of months, litter decomposition occurs over the course of years and some coarse woody debris are decomposed only after >50 years. Rock weathering occurs over even longer time scales, as well as the effects of uprooting on soil morphology and chemistry (Rajala *et al.* 2011; Šnajdr *et al.* 2011; Šamonil *et al.* 2013b; Hendricks *et al.* 2016).

Importantly, most ecosystem processes affect multiple habitats at the same time, such as those that affect trees, which represent multiple microbial habitats themselves (Fig. 5). It is these ecosystem-level processes that cannot be properly understood without considering the whole ecosystem microbiome. They include, for example, temperature or moisture seasonality, disturbances of various intensity, such as forest fires or insect invasions, and stand development after disturbance or as a result of management.

As mentioned above, the microbial communities of all habitats are dynamic and change in composition over time. The temporal variability of fungal communities was found to be higher in topsoil compared with lower soil horizons, which can be explained by different levels of environmental heterogeneity or the faster turnover of microbial biomass in the nutrient-rich organic soil horizon (Bahram, Peay and Tedersoo 2015). While diurnal fluctuations in microbial activity driven by the photosynthetic activity of trees has been rarely addressed and seems to be rather minor due to a time delay between photosynthesis and allocation to roots (Betson *et al.* 2007; Högberg *et al.* 2008), seasonality in the temperate and boreal zones has been frequently addressed and has been demonstrated to be important, as discussed above for individual habitats. Cold and dark winters and warm summers with longer photoperiods affect the development and production of foliage, the activity of tree roots and rhizospheres, the production of mycorrhizal mycelia and, consequently, microbial activity in the roots, rhizospheres, litter and soil, and in the foliage (Kaiser *et al.* 2011; Rasche *et al.* 2011; Peršoh 2015; Žifčáková *et al.* 2016). In soil, seasonality also likely affects competition between ECM and saprotrophic fungi and thus the contribution of these two functional groups to soil organic matter turnover (Fernandez and Kennedy 2016; Shah *et al.* 2016). Seasonality also affects ground vegetation development and activity, input of allochthonous nutrients into streams, photosynthetic production in lakes and changes to the water table in wetlands. Biochemically, temperature differences affect the decomposition rate through the acceleration of enzymatic processes with temperature (Baldrian *et al.* 2013a). Some short weather events such as precipitation or snowmelt most likely represent hot moments of activity in certain habitats (Kuzyakov and Blagodatskaya 2015), e.g. when nutrients, enzymes or even
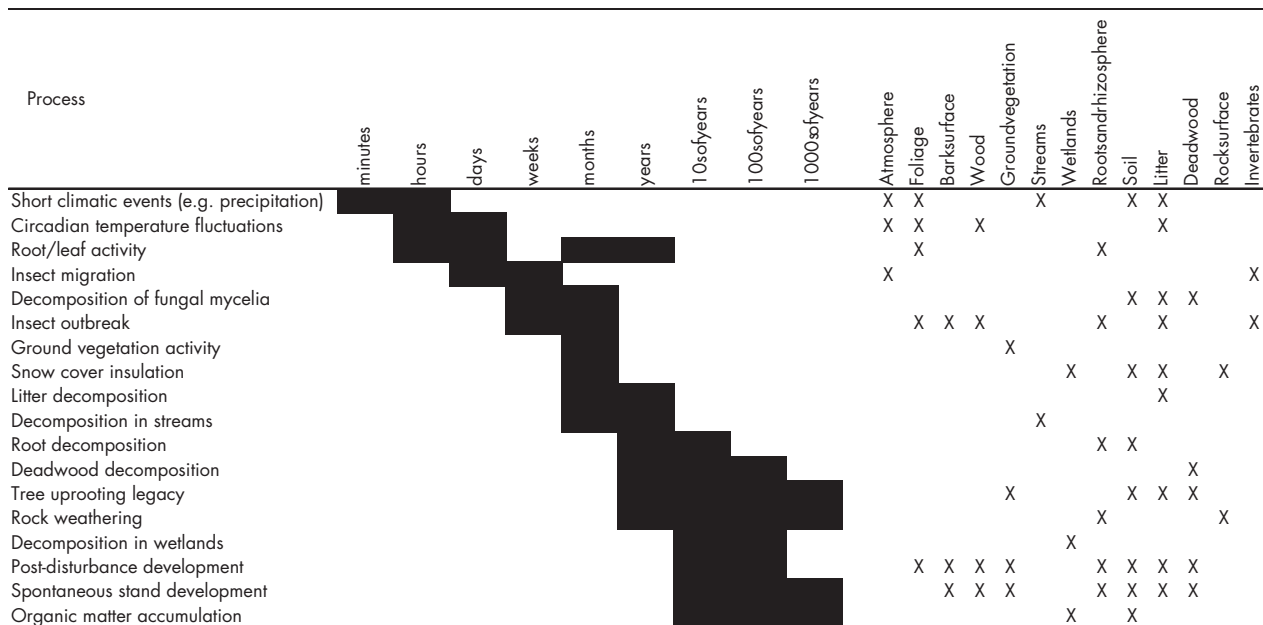
Process	minutes	hours	days	weeks	months	years	10s of years	100s of years	1000s of years	Atmosphere	Foliage	Bark surface	Wood	Ground vegetation	Streams	Wetlands	Roots and rhizosphere	Soil	Litter	Deadwood	Rock surface	Invertebrates
Short climatic events (e.g. precipitation)	█	█								X	X				X			X	X			
Circadian temperature fluctuations		█	█							X	X		X						X			
Root/leaf activity			█	█	█	█					X						X					
Insect migration		█	█							X												X
Decomposition of fungal mycelia				█	█													X	X	X		
Insect outbreak					█	█					X	X	X				X		X			X
Ground vegetation activity					█	█								X								
Snow cover insulation					█											X		X	X		X	
Litter decomposition					█	█													X			
Decomposition in streams					█	█									X							
Root decomposition						█	█										X	X				
Deadwood decomposition						█	█													X		
Tree uprooting legacy							█	█						X				X	X	X		
Rock weathering								█	█									X			X	
Decomposition in wetlands						█	█									X						
Post-disturbance development							█	█	█		X	X	X	X			X	X	X	X		
Spontaneous stand development							█	█	█		X	X	X				X	X	X	X		
Organic matter accumulation								█	█								X		X			

Figure 5. Time scales of selected processes occurring in forest ecosystems and the habitats that are affected.

microorganisms from litter or soil are transported vertically in the soil profile or washed into the streams and lakes by rain or during snowmelt.

With much lower frequency and varying probability, forest ecosystems are affected by large-scale disturbances that may reduce or remove the tree layer. Forest fires differ largely in their severity and thus effects. Large fires may remove much of the soil organic matter and often kill ECM trees. Microbial biomass is reduced by tens of percents (Dooley and Treseder 2012), but ECM fungi can survive severe fires in the form of propagules, although community composition and density can be changed in favour of fire-resistant taxa as shown in the coniferous forest after the California Rim Fire (Glassman *et al.* 2016). While forest fires affect microbiota mainly by heat-induced mortality in the short term, the long-term effects are largely due to altered vegetation cover (Hart *et al.* 2005). The fungal community shifts from being ECM dominated before the fire to AM dominated in the early post-fire stages with abundant ground vegetation. Subsequently, ECM abundance increases again with accumulating organic matter and tree development (Treseder, Mack and Cross 2004).

Insect invasions are the quantitatively most important disturbances of forest ecosystems (Peh, Corlett and Begeron 2015). Both defoliators and bark beetles can kill virtually all mature trees within large areas and represent an excellent example of processes affecting multiple forest habitats (Table 2) (Cullingham *et al.* 2011; Štursová *et al.* 2014). In the case of a bark beetle attack killing all spruce trees (Štursová *et al.* 2014), tree-associated habitats of foliage and living wood disappear instantly. At the same time, rhizodeposition stops, and shed leaves and dying roots increase the pool of litter in the short term but result in drastically reduced litter production in the following years. In the timeframe of a few years, the ground vegetation develops to form a thick, patchy, highly heterogeneous cover (Fig. 2) and the amount of deadwood increases by an order of magnitude. Soil experiences changes in chemistry such as a temporal increase in nitrate and a decrease in organic N content and complex changes in C and N availability over the

mid-term that affect microbial nutrient cycling (Kaňa, Tahovská and Kopáček 2012; Štursová *et al.* 2014; Kaňa *et al.* 2015). Streams and lakes in the affected catchments temporarily change in chemistry, such as in the content of nitrate and base cations (Oulehle *et al.* 2013). Stand damage also leads to greater air movement, a reduction in mean moisture content and increased desiccation, especially during hot summer days (Bässler *et al.* 2016). At the microbial community level in the litter and soil, disturbance is followed by a rapid decrease in fungal biomass and a slight decrease in bacterial abundance. Root-symbiotic fungi in litter and soil are replaced by saprotrophs, and later by wood-inhabiting taxa spreading from deadwood, while enzyme activities drop as a consequence of limited C input (Štursová *et al.* 2014). Furthermore, bark beetle-deforested stands are subject to changes in the functional guilds of lignicolous fungi, including decomposers and lichen symbionts. Due to a higher deadwood volume, lichenous species with larger and more complex growth forms and fungi with large, perennial fruiting bodies are favoured and lichen diversity increases (Bässler *et al.* 2016). The community of bacteria changes in composition as well, mostly due to changes in nutrient availability and overall chemistry (Mikkelson, Lozupone and Sharp 2016). The effects of defoliation by leaf-feeding insects have similar effects to bark beetle-induced tree dieback. For example, defoliation caused by birch-feeding moths caused dramatic shifts in the functional and taxonomic community composition of root-associated fungi. Differentially defoliated mountain birch roots harboured distinct communities as a consequence of an increase in soil nutrients and a decreased amount of host trees with green foliar mass. ECM abundance and richness declined with increasing defoliation intensity, while the proportion of saprotrophic and endophytic fungi increased (Saravesi *et al.* 2015). Development of natural stands that are subject to disturbances may proceed for a long time. Based on a metastudy of temperate and boreal forests, the recovery of diversity after disturbance of old growth forests took an average of 90 years for ECM fungi and 180 years for epiphytic lichens, while the diversity of non-saproxylic insects decreased slowly over time to reach the values of the

Table 2. Changes in forest habitats following bark beetle-induced tree dieback. Based on Cullingham *et al.* (2011), Bässler *et al.* (2016), Kaňa, Tahovská and Kopáček (2012), Kaňa *et al.* (2015), Karst *et al.* (2015), Mikkelson, Lozupone and Sharp (2016), Oulehle *et al.* (2013) and Štursová *et al.* (2014).

Habitat	Development following insect invasion
Insects	High levels of bark beetle reproduction, dispersal of microbes (especially symbionts), change in insect community with stand desiccation
Foliage	Rapid defoliation—habitat disappears over a short term
Living wood	Slow dieback—transition to standing snags (habitat transition into deadwood)
Roots/rhizosphere	Slow dieback—input of root litter (habitat disappears over time)
Litter	One-time accumulation as a result of defoliation, very low input in years following invasion
Soil	Changes in chemistry over time, replacement of fungal root symbionts by saprotrophs, relative increase in bacteria and change in their community composition
Bark	Accumulation on forest floor within a few years after tree dieback
Deadwood	Increase in size as a result of tree dieback, changes in functional guilds of lichens and wood-associated fungi
Ground vegetation	Change in composition and increase in biomass in response to higher light penetration
Streams and lakes	Changes in chemistry due to nutrient leaching and changes in soil base saturation

climax ecosystem (Spake *et al.* 2015). In a boreal forest, soils of young stands (50 years since fire) are dominated by ECM fungal mycelia that decompose rapidly, while at later stages (up to 5000 years), the mycelia of stress-tolerant ERM that are difficult to decompose prevail. For this reason, the rates of organic matter decomposition decrease and C accumulation increases with the successional age of the forest (Clemmensen *et al.* 2015).

A similar course of development is typical after the clearcutting of tree plantations. Successive development of newly established stands causes increasing tree biomass and changes in the abundance of ground vegetation. Microbial activity, biomass and community composition, as well as soil invertebrates, respond to this development (Chauvat, Zaitsev and Wolters 2003). ECM fungi seem to be largely affected, while the effects on bacteria and archaea appear to be more moderate (Jurgensen *et al.* 1997; Hartmann *et al.* 2009; Štursová *et al.* 2014). Following the clearcutting of coniferous trees, ECM fungi re-establish rapidly, but their community composition on young seedlings is different from that on mature trees (Jones, Durall and Cairney 2003). Changes in ECM communities continue with stand development and reach a peak in biomass at the intermediate stages of stand development (Wallander *et al.* 2010). The ratio of ECM and AM fungi also changes during forest stand development, depending on plant community assembly, climate and edaphic factors (Dickie *et al.* 2013).

OPEN QUESTIONS AND FUTURE RESEARCH NEEDS

Despite the fact that forest microbial ecology research has slowly begun to create an integrated view of forest ecosystem processes mediated by microorganisms and their diversity, it is far from being complete, and our present knowledge suffers from several caveats. On the microbial community level, these include:

(1) the incomplete or biased description of microbial communities

Despite considerable progress, our ability to describe microbial community composition is so far incomplete. For example, the Archaeorhizomycota were only recently demonstrated to be frequent inhabitants of forest soils, and the same may be the case for other fungi belonging to basal lineages (Rosling *et al.* 2011; Větrovský *et al.* 2016). Their absence in surveys was likely due to biases in the most frequently used molecular markers (Ihrmark *et al.* 2012; Baldrian *et al.* 2013b; Větrovský *et al.* 2016). Even less is known about the communities of protists and viruses, although metagenomic and metatranscriptomic results show that they may be both important and diverse (Vainio *et al.* 2015; Žifčáková *et al.* 2016).

(2) imbalanced focus on different groups of microorganisms

Extensive information exists on ECM fungi in forest soils and saprotrophic wood-decomposing taxa in deadwood due to their presumed importance. Far less is known about bacteria in both environments. Still, most recently published studies address only bacteria or only fungi, and rarely both.

(3) lack of quantitative abundance data

Current molecular surveys make it simple, although not always reliable, to describe the diversity and composition of microbial communities. Unfortunately, in many papers, a clear definition of the explored habitat is missing, as well as an estimate of the relative proportions of certain taxa or functional groups within the ecosystem. The same is true for estimates of microbial abundance in terms of biomass or cell counts. Even less complete is our understanding of turnover rates, for example, in the cases of mycorrhizal roots and fungal mycelia (Ekblad *et al.* 2013; Brabcová *et al.* 2016; Fernandez *et al.* 2016) or the turnover of bacterial cells (Hungate *et al.* 2015).

(4) difficulty in identifying active microbes and their functions

Many microbes may be inactive or dormant in the environment (Lennon and Jones 2011). For example, much of the DNA extracted from decomposing wood likely belongs to inactive taxa that were replaced in succession (Rajala *et al.* 2011), and the active (RNA based) and total microbial communities in litter and soil differ, with the former being much more dynamic (Baldrian *et al.* 2012; Žifčáková *et al.* 2016). Still, the ability to identify individual communities does not allow us to infer much about ecosystem-level functioning because the ecology of many dominant taxa, especially unculturable bacteria and archaea, is completely unknown (Baldrian *et al.* 2012). It was recently demonstrated that high-throughput culturing is able to yield isolates of dominant microorganisms and that their nutritional requirements and decomposition abilities can be determined in culture (Lladó *et al.* 2016; López-Mondéjar *et al.* 2016). However, despite

apparent feasibility, these approaches are considered too laborious and are therefore rarely used. Studies of microbial expression (Damon *et al.* 2012; Žifčáková *et al.* 2016) and metaproteomic studies (Schneider *et al.* 2012) are so far limited, and their ability to assign functions and taxonomy to sequences is currently inadequate.

At the ecosystem level, our understanding is limited mainly due to

(5) a highly variable level of exploration of individual habitats and biomes

The uneven level of description of individual habitats is estimated in Table 1. For some of them, only a handful of studies are available. The information is highly unbalanced towards temperate and boreal forests, with results from other biomes almost missing, such as in the case of deadwood microbiota (Seibold *et al.* 2015).

(6) an absence of studies focusing on ecosystems as a whole

The available data that consider individual habitats are difficult to integrate because they come from different study sites and the insufficient data from certain habitats cannot be extrapolated to the biome level. This is also impossible without proper ecosystem descriptions (Fig. 3).

There is a clear need for intensive studies on stands that consider multiple habitats and the relationships between them, even if such studies are descriptive. As demonstrated above, most ecosystem-level processes affect multiple habitats and all microorganisms present, to a certain extent so that the "ecosystem microbiome" concept appears to be more appropriate rather than the limitation of experimental question to a single habitat. With the currently available analytical and molecular tools in hand, integrative surveys have become feasible. The focus on ecosystem-level microbiology should thus represent an important field of future work in microbial ecology.

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