



Review Paper

Ecology of the forest microbiome: Highlights of temperate and boreal ecosystems



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ABSTRACT

Due to land use history, most of the current temperate and boreal forests are developed on nutrient-poor and rocky soils, keeping fertile soils for agriculture. Consequently, the conditions occurring in forest ecosystems strongly differ from those of other terrestrial environments, giving importance to the access of nutritive elements and their recycling for the long-lasting development of forest ecosystems. In this review, we present an overview of the recent findings on the relationships between bacterial and fungal communities and their tree hosts at both the taxonomic and functional levels. We highlighted the common and different deterministic drivers of these microbial communities, focusing on the tree species effect, the different interfaces existing between the trees and their environment, the impact of tree by-products (decaying wood and litter), the impact of soil and seasonal changes, and lastly, the consequences of forestry practices. Depicting both taxonomic and functional diversity based on cultivation-dependent and -independent analyses, we highlight the distribution patterns and the functional traits characterizing bacterial and fungal communities. We also discuss the importance of bridging environmental microbiology to genomics and how to integrate the interactions between microorganisms for a better understanding of tree growth and health.

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1. Introduction

Forest ecosystems provide several key environmental services such as acting as carbon sinks, protecting biodiversity, protecting soils and providing wood resources (Pan et al., 2011). Their worldwide distribution, covering boreal to temperate and tropical regions, allows for the development of complex and distinct ecosystems. In this review, we mainly focus on temperate and boreal forest ecosystems. In both forest biomes, the distribution of forests is strongly related to land use history and soil characteristics. Indeed, easily manageable soils with high plant nutritional capacity have often been dedicated to crops and grasslands, while nutrient-poor and rocky soils have been abandoned to forests. In northern latitudes, climatic conditions also determine forest distributions, especially on frozen soils. These specific conditions strongly differentiate forest ecosystems from annual cultures and grasslands, especially as forests are usually non-amended and

unploughed. Forest ecosystems are also characterized by the existence of large perennial plants: the trees. Indeed, trees require decades to centuries of growth to complete their lifecycles or before harvesting. Consequently, their impact on soil parameters is important due to litter deposition, nutrient uptake and root exudation. Through these different processes, trees modify soil properties and thereby determine temperature (the canopy effect), aeration (oxygen consumption), porosity (root development) and water capacity (root uptake) of soil (Augusto et al., 2002). These specificities and the absence of ploughing allow for the development of soil horizons, which form a nutritive gradient along the soil profile. However, all of these modifications vary qualitatively and quantitatively depending on the tree species (i.e., the tree species effect) and the type of tree stand (i.e., pure vs mixed) (Andrianarisoa et al., 2010; Augusto et al., 2002, 2015). These differences are explained not only by the physiological and phenological characteristics of each tree species but also by their associated soil biota (microflora and micro- to macro-fauna; Geisen et al., 2016; Korboulewsky et al., 2016). In addition to soil properties and the tree species effect, forest composition and productivity are also determined by their local environment, especially climate, as

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well as forestry practices in the case of managed forests (Kaarakka et al., 2014; Gamfeldt et al., 2013; Gundale et al., 2014). Altogether, these data highlight the strong, complex and reciprocal links that exist between trees, soil, and climate. All these interactions determine soil chemistry and nutrient cycles as well as tree colonization, development and health. In this context, we can wonder how the soil biota and especially the forest microbiome (archaea, bacteria, fungi, protists) are impacted by these different factors and how they contribute to the functioning and homeostasis of forest ecosystems (Courty et al., 2010; Hacquard and Schadt, 2015; Prescott and Grayston, 2013; Uroz et al., 2011). Indeed, microorganism play an essential role in nutrient cycling, tree nutrition and plant health, due to their ability to directly mobilize and transfer to the plants the nutrients entrapped in organic matter and minerals, but also through the nutrients released during their consumption by other organisms in the soil food web. In this review, we summarize recent progress in understanding the distribution, function, and interactions of the microbial communities in boreal and temperate forest ecosystems in relation to different questions (Table 1). We mainly focus on bacterial and fungal communities, which are supported by broader genomic resources and literature compared to other microorganisms. To decipher the relative taxonomic and functional distributions of soil microbial communities, we partition the forest ecosystem into several reactive interfaces where nutrients are made available to microbial communities such as the soil, rhizosphere, mycorrhizosphere, phyllosphere, mineralosphere and decaying wood (Fig. 1).

2. Distribution of bacteria and fungi

Because forest soils are comparatively less manipulated than agricultural soils, growth of trees over the long term allows for the creation of a large and dynamic set of microbial habitats. Indeed, soil horizons, tree root exudates, leaf litter and decaying wood can be considered as reactive interfaces where nutrient cycles are intensified and microorganisms are specialized. Moreover, environmental variations (seasons, forestry practices, fires, pathogen attack) strongly determine the distribution and abundance of forest soil microorganisms (Holden and Treseder, 2013). In this context, it is challenging to depict the forest microbiome as it results from the assembly of multi-scale habitats, and it is also difficult to predict the structure and composition of its microbiota according to environmental parameters (e.g., soil type, climate, management). Surprisingly, most published forest microbiome studies focus independently on either bacterial or fungal communities, but rarely on both. In this context, we present an overview of recent findings on the distribution and diversity of forest microbial communities, highlighting the few studies combining both bacterial and fungal analyses.

2.1. Taxonomic structure of forest bacterial communities

2.1.1. Impact of tree species

In contrast to the model plants that exist in crop and grassland systems, few biodiversity studies have investigated the potential relationships between tree species and soil bacterial communities (Table 1). Such limitations can be partly explained by the growth timeline of trees and by the difficulty in finding convenient experimental sites permitting the effects of such tree species to be evaluated. Indeed, in the natural environment, tree species are mixed while in plantation, rarely more than 2 or 3 species are associated with one another, limiting extensive studies. In this context, contrasting trends have been reported in the literature (Lauber et al., 2008; Lejon et al., 2005; Nacke et al., 2011a; Pfeiffer et al., 2013; Urbanová et al., 2015). In temperate forests with low

management influences, Urbanová et al. (2015) showed that among the seven tree species considered, some tree species such as *Alnus* and *Pinus* presented distinguishable soil bacterial communities. A detailed analysis of the distribution of the phylotypes detected revealed that the variations of structure of the soil bacterial communities observed between different the tree species were explained by only few phylotypes, which abundance varied significantly. In a comparison of different German experimental sites planted with beech and spruce trees, Nacke et al. (2011a) revealed significant differences in terms of bacterial structure and diversity according to tree species, with higher richness occurring below beech (3200–4800 OTUs) than below spruce (1700–2800 OTUs). Aside from potential geographical effects, the differences observed between these two studies may be due to the differences in tree species and types of forests examined. Indeed, Urbanová et al. (2015) characterized the bacterial communities in a mixed tree species forest while Nacke et al. (2011a) compared pure stands. In this context, the long-term observatory (LTO) of Breuil-Chenue (Morvan, France) permitted the disentanglement of the geographic effect from the tree species effect. Indeed, this LTO is characterized by mono-species blocks of six different tree species of the same age under the same management and planted on the same soil under the same climatic conditions (Ranger and Gelhaye, 2007). Comparing four of the tree species at this site, Lejon et al. (2005) revealed specific bacterial communities in the soil collected below each tree species, highlighting that tree species is a strong driver of the differentiation of soil bacterial communities. In addition to these *in situ* approaches, microcosm experiments based on the culture of young seedlings of different tree species have been used. Comparing different soil types planted with the same tree species (*Quercus phellos*, *Pinus taeda* and *Populus deltoides*) and maintained under the same conditions, Bonito et al. (2014) also highlighted an important host tree effect on soil bacterial communities, which was greater than the effect due to soil type. The resolution provided by their 16S rRNA pyrosequencing approach revealed that the root-associated bacterial communities associated with *Quercus phellos* and *Pinus taeda* were more similar to each other than to those of *Populus deltoides* despite the different soil types, suggesting that differences in these bacterial communities may be mainly related to tree species rather than soil properties. Using a similar microcosm approach, Pfeiffer et al. (2013) also observed differentiation of bacterial communities according to tree species. These authors suggested that this effect was due to leaf litter chemistry, which can strongly vary between different tree species. Finally, relative host specificity was addressed for leaf-associated bacterial communities. Sampling leaves from 56 different tree species, Redford et al. (2010) reported a huge diversity and variability of bacterial communities in the tree phyllosphere. Despite this relative variability, Redford et al. (2010) showed that the structure and composition of the bacterial communities were related to tree species. Indeed, Bacteroidetes and Betaproteobacteria appeared to be more abundant on gymnosperms (evergreen), while Actinobacteria and Gammaproteobacteria were more abundant on angiosperms (deciduous trees). Altogether, these observations highlight that bacterial communities are strongly shaped by the associated tree species. Such plant species effect was also evidenced for other plants such as wheat, maize, rape and barrel clover (Haichar et al., 2008). Nevertheless, it was also demonstrated that the tree species effect does not impact bacterial communities in the same way in mono-specific and mixed forests.

2.1.2. Tree-environment interfaces

In addition to this strong tree species effect, recent studies have highlighted that trees are not uniformly colonized by

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