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Environmental drivers of microbial community composition in a temperate forest

Environmentální faktory ovlivňující složení mikrobiálních společenstev v lese mírného pásu

Dissertation

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Declaration

I hereby declare that I am the author of this dissertation, all the sources and literature are properly cited and the content of this thesis or its major part was not previously used for obtaining of the same or other academic degree.

Prohlášení

Prohlašuji, že jsem doktorskou práci zpracovala samostatně a že jsem uvedla všechny použité informační zdroje a literaturu. Tato práce nebyla předložena k získání jiného nebo stejného akademického titulu.

Prague, June 12th 2022   Tijana Martinović

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Abstract

Recently, much attention has been focused on the importance of forests to the global carbon cycle. Microorganisms are a critical component of the carbon cycle in forests, participating in important ecosystem processes and degrading various carbon compounds, from simple to highly recalcitrant compounds. However, most studies in this regard have focused on fungi. Only in recent years has it become known that bacteria are also capable of degrading complex plant polymers in soil, and that their contribution to the carbon cycle may be as important as that of fungi. Furthermore, our knowledge of the temporal dynamics of both fungal and bacterial communities is limited, as well as their response to different environmental drivers. The main objective of this dissertation was to fill these knowledge gaps by (1) quantifying the rate of temporal turnover of fungal and bacterial communities in soils of temperate forests, (2) describing the factors that shape fungal communities in spruce and beech stands during their long-term development (stand age), (3) assessing the contribution of fungi and bacteria to the utilisation of different carbon sources in forest soils, and finally (4) describing the development of bacterial communities in response to clearcutting of a spruce stand. The study of microbes responsible for important ecosystem processes, including decomposition and carbon cycling, is of great importance for a possible prediction of the carbon balance response to forestry practices in the context of climate change.

Křtiny forest, Czech Republic, 2017

Abstrakt

V poslední době se do popředí zájmu dostává úloha lesů v globálním koloběhu uhlíku. Mikroorganismy jsou klíčovou součástí koloběhu uhlíku v lesních ekosysémech, kde se účastní důležitých ekosystémových procesů. Jedním z nich je degradace uhlíkatých sloučenin, od jednoduchých po velice obtížně rozložitelné, přičemž většina studií se zaměřovala na houby. Teprve nedávno se ukázalo, že i bakterie jsou schopné rozkládat komplexní rostlinné polymery v půdě a že v koloběhu uhlíku mohou hrát stejně důležitou úlohu jako houby. Kromě toho máme velmi omezené znalosti o časové dynamice houbových a bakteriálních společenstev a o tom, jak na ně působí různé faktory prostředí. Hlavním cílem této dizertace je zodpovědět na výše naznačené otázky (1) určením rychlosti obratu houbových a bakteriálních společenstev v půdách lesů mírného pásma, (2) popsáním faktorů ovlivňujících strukturu houbových společenstev smrkového a bukového porostu v průběhu jejich dlouhodobého vývoje, (3) určením podílu hub a bakterií na rozkladu různých uhlíkatých sloučenin v lesní půdě a (4) popsáním vývoje bakteriálních společenstev v reakci na vykácení smrkového porostu. Výzkum mikroorganismů zajišťujících klíčové ekosystémové procesy včetně rozkladu a koloběhu uhlíku je zásadní pro pochopení budoucího vývoje uhlíkové bilance v rámci lesnických praktik v době probíhajících klimatických změn.

Křtiny forest, Czech Republic, 2017

List of abbreviations

C   carbon

N   nitrogen

SIP   stable isotope probing

ECM   ectomycorrhiza

HTS   high-throughput sequencing

ITS   internal transcribed spacer

OTU   operational taxonomic unit

PCR   polymerase chain reaction

1   Introduction

Forests are critical to the global carbon cycle and have a direct feedback on global climate through the flux of greenhouse gasses: both consumption and production. Soil microorganisms mediate numerous ecosystem processes, and recent studies show that the composition of these communities and their biomass are altered by a range of environmental factors, including forestry, posing a challenge for future adaptation of forest management practices. Many studies that have aimed to study important ecosystem processes in forests, such as the decomposition of complex organic matter in soils, have focused on fungi. Studies of bacteria are much rarer, and few studies to date have attempted to examine the relative contributions of both fungi and bacteria to important ecosystem processes.

The main novelty of this dissertation, therefore, lies in a new approach to quantifying turnover rates of fungal and bacterial communities across temporal (and spatial) scales, with repeated sampling at very specific and defined sites representing the first such attempt (**Publication I**). In addition, the respective roles of fungi and bacteria in utilising different carbon sources in forest soils were revealed, using a combination of recent methodological advances - stable isotope probing and high-throughput sequencing (**Publication III**). This work analysed additional environmental factors, such as forest stand age and forest management, that are important for soil microbial community assembly and contribute to the overall understanding of microbial community composition and importance in temperate forest soils (**Publications II, IV**).

This work consists of several experiments performed in the Training Forest Enterprise Masaryk Forest Křtiny of the Mendel University in Brno (Křtiny forest, Figure 1). The Křtiny forest covers a total area of 103 km^2 of temperate mixed forest (16°15' E, 49°15 N) and is located north of Brno in the Czech Republic. With an altitude ranging from 210 to 575 m, a mean annual temperature of 7.5 °C, and a mean annual precipitation of 610 mm, this forest is characterised by a variety of conditions. The forest stands consist of about 54% deciduous and 46% coniferous trees (mainly *Fagus sylvatica*, *Quercus petraea* agg, *Picea abies*, *Pinus sylvestris* and *Carpinus betulus*) ranging for pure monospecific stands to ones with a diverse tree layer. The different environmental

conditions and composition of the stands make the area suitable for characterising microbial communities in temperate forests.
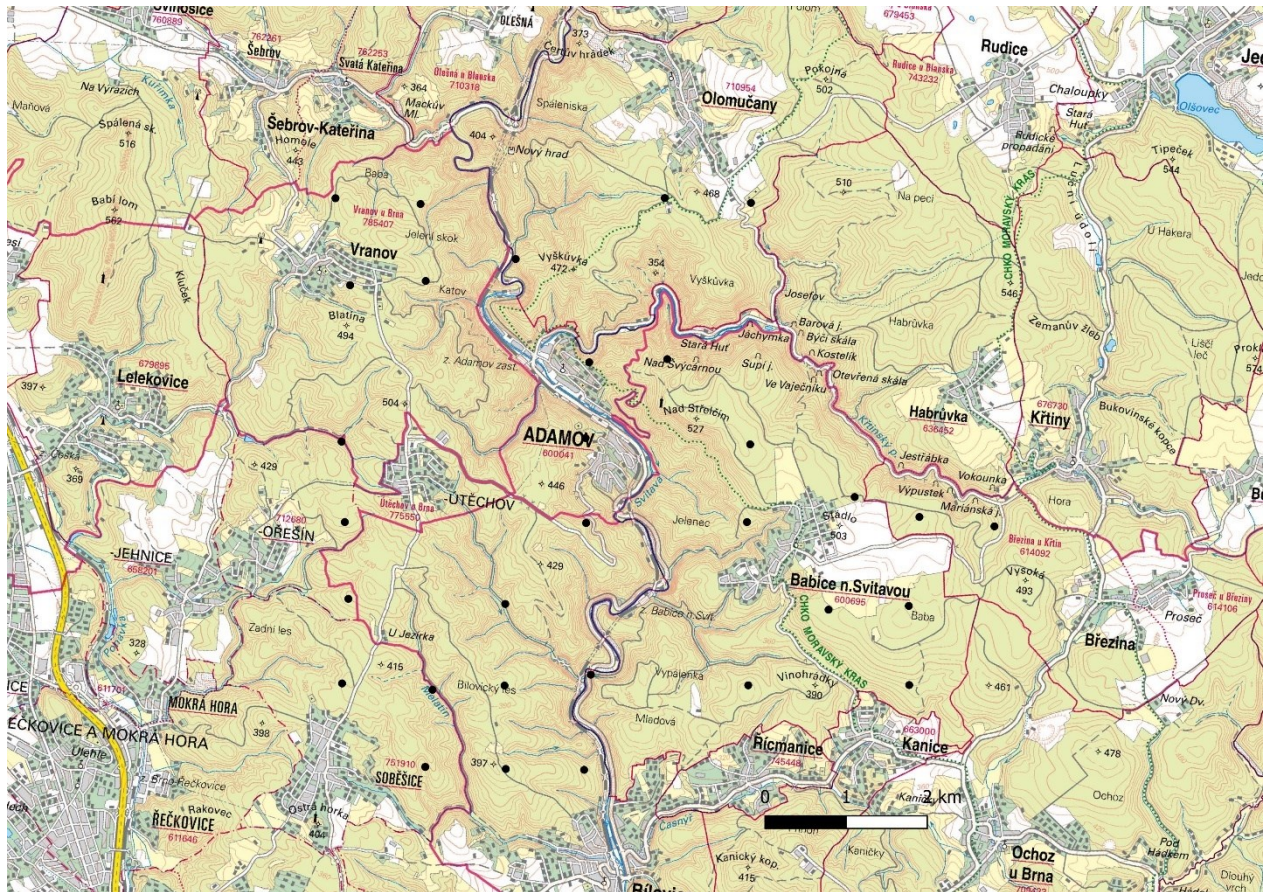

Figure 1. Selection of the research sites in Křtiny forest (from Publication I)

2 Literature overview

2.1 Soil microbial communities and their role in temperate forest ecosystems

Forests cover 31% of the global land area (Keenan et al., 2015). As one of the largest terrestrial carbon reservoirs, forests are of great importance for carbon sequestration and greenhouse gas fluxes. The processes carried out by microorganisms in the forest soil are therefore of critical importance to the global carbon cycle and consequently to global climate (Lal, 2004; Pan et al., 2011).

Although temperate forests account for about 16% of the world's forest area, they are one of the most important biomes on Earth and contribute greatly to the global carbon budget (FAO & UNEP, 2020). These forests occur within temperate bioclimatic zones - areas in the mid-latitudes between the tropical and polar regions. Distinct temperature and precipitation regimes provide suitable environments for a variety of species in temperate forests, as they are critical for nutrient cycling, climate regulation, and water supply. Because soil organic matter (SOM) represents the largest pool of C in forests, temperate forest soils play a role in mitigating excess atmospheric C (Trivedi et al., 2013).

Temperate forests provide niches for a diverse community of fungi, both saprotrophic and mycorrhizal. The forest topsoil consists of several complex plant polysaccharides (e.g. cellulose, hemicellulose, pectin) and polymers of other nature including lignin, while fungal biomass contains ß-glucans and chitin (Brabcová et al., 2016). Fungi produce a variety of enzymes that can decompose even the most recalcitrant plant biopolymers. They also play a critical role in carbon sequestration and distribution in the soil, all of which are reasons why fungi are the commonly studied microbes in these environments (Eichlerová et al., 2015; Lladó et al., 2017). However, the respective roles of fungi and bacteria should be rather studied in the context of their complex interactions. While fungi liberate nutrients by degrading more complex compounds and leaving the residues for bacterial utilisation, bacteria are important for nitrogen fixation and cycling (Lladó et al., 2017; Reed et al., 2011; Starke et al., 2021). Only in the last decade has it become known that bacteria are also capable of degrading complex plant polymers in the soil, such as

cellulose and hemicellulose, through their own enzyme machinery (López-Mondéjar et al., 2018; Štursová et al., 2012), and that their contribution to the carbon cycle in soils may be as important as that of fungi (Žifčáková et al., 2017). In addition, there is a specific bacterial community associated with mycorrhizosphere, such as bacteria in soil mycelial mats (Kluber et al., 2011), or mycorrhiza helper bacteria that are important for the functioning of mycorrhizal associations (Frey-Klett et al., 2007; Labbé et al., 2014). In summary, studying bacteria alongside fungi is often necessary to understand their relative importance in decomposition processes in forest ecosystems.

2.1.1 Soil fungal communities

As one of the most diverse groups of organisms on Earth, fungi perform some of the key ecosystem functions (Hawksworth and Lücking, 2017). Recent methodological advances have greatly improved our knowledge of fungal diversity in many ecosystems, as well as their functional properties (Nguyen et al., 2016). Fungal communities in forest soils are composed of several groups with different ecological strategies (Figure 2). These fungal characteristics, defined as ecological guilds, provide information on the potential role of each group in ecosystem functioning and how these specific characteristics are relevant to providing ecosystem services (Põlme et al., 2021; Talbot et al., 2015). Three major ecological guilds of soil fungi can be distinguished: saprotrophic, symbiotic, and plant pathogenic fungi.
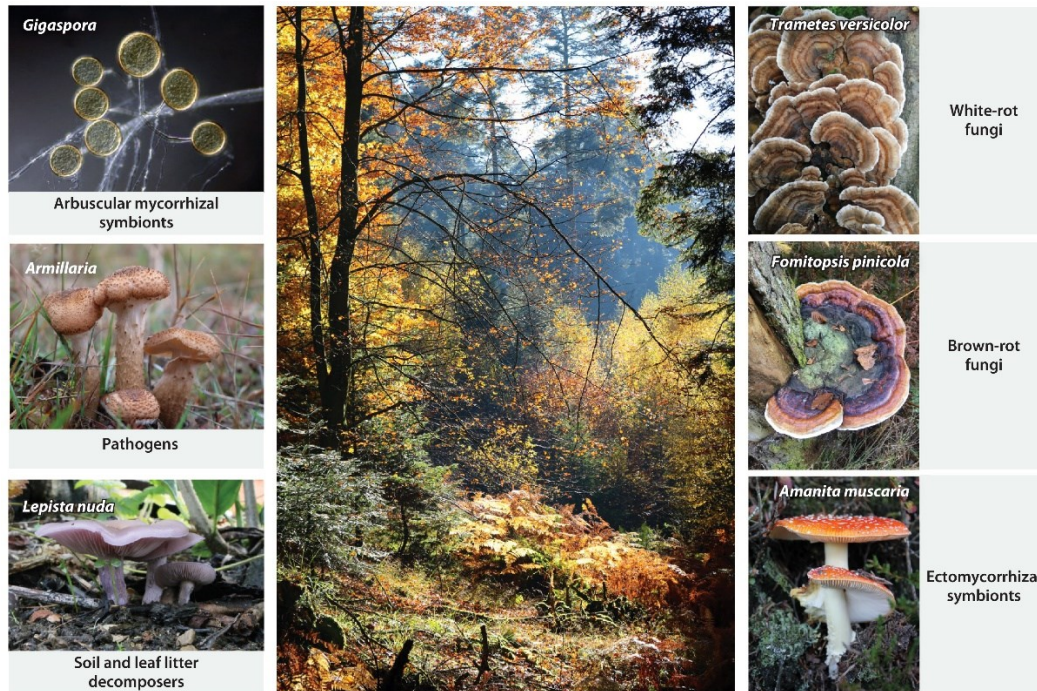
Figure 2. Major ecological guilds of forest fungi. (Lebreton et al., 2021)

In temperate forest soils, saprotrophic fungi are one of the most studied ecological guilds of fungi, contributing to the soil microbial biomass and wood and SOM decomposition processes (Baldrian and Valásková, 2008; Joergensen and Wichern, 2008). Owing to their efficient enzymatic machinery, these fungi have developed different strategies for degradation of complex carbon sources and are considered most proficient decomposers even of lignocellulose, which is usually difficult for other organisms to degrade (Baldrian et al.; Lebreton et al., 2021). Saprotrophic fungi involved in decomposition of compounds of wood and plant origin are most typically fruiting body forming Agaricomycetes (phylum Basidiomycota) and fungi belonging to phylum Ascomycota, and in temperate forests genera that are commonly found include, for example, *Mycena*, *Pleurotus*, *Trametes* (Mfombep et al., 2013; Voříšková et al., 2014).

Saprotrophic fungi play a key role in wood and plant substrate decomposition processes (Baldrian and Valásková, 2008), but also fungal mycelium decomposition (Brabcová et al., 2016; Fernandez et al., 2016). Saprotrophic microfungi, in particular (fungi that do not form large multicellular fruiting bodies), mainly from the phyla Ascomycota and Mucoromycota, appear to exhibit high

production of chitinases (Baldrian et al.; Beidler et al., 2020; Halder et al., 2019). Microfungi are cosmopolitan and have enormous dispersal potential, and many representative genera (e.g., *Penicillium*, *Mortierella*) seem to utilise variety of substrates of both plant and fungal origin (Algora Gallardo et al., 2021; López-Mondéjar et al., 2018).

Unlike saprotrophs, mycorrhizal fungi depend on their plant hosts – almost all tree species form mycorrhizal associations with fungi. As symbionts, mycorrhizal fungi gain access to C from the photosynthates of their hosts in exchange for nutrients (i.e. nitrogen and phosphorous) from the soil. These fungi also contribute directly to soil C enrichment by mediating the belowground distribution of C from plant roots into the soil (Clemmensen et al., 2013; van der Heijden et al., 2015). In temperate forests, most tree species form ectomycorrhizal associations, however arbuscular mycorrhiza are also present (Carteron et al., 2021; Soudzilovskaia et al., 2015).

Ectomycorrhizal (ECM) fungi colonise root tips of host trees and use the C provided by plants to extend their extracellular mycelium into the soil, where it serves as a site for nutrient exchange between symbiotic partners (Stuart and Plett, 2020; Zak et al., 2019). The central role of ECM fungi in mobilising organic N trapped in SOM and regulating soil C dynamics makes them essential for C and N dynamics of temperate forest ecosystems (Lindahl and Tunlid, 2015; Zak et al., 2019). Because they evolved from free-living saprotrophs (Strullu-Derrien et al., 2018), some ECM fungi have the enzymatic capacity to directly degrade organic matter, potentially competing with free-living saprotrophs for organic nutrients (Averill et al., 2014; Shah et al., 2016). Among typically abundant ECM fungal genera in temperate forests are basidiomycetes *Russula*, *Lactarius*, *Rhizopogon* or ascomycetes – for example *Cenococcum, Tuber* (e.g. Iotti et al., 2010; Milović et al., 2021; Twieg et al., 2007; Voříšková et al., 2014b; Wang et al., 2012).

Based on the current knowledge on these two important ecological guilds of fungi, understanding the interactions between saprotrophic and ectomycorrhizal fungi, and their response to both biotic and abiotic environmental factors is essential in providing protection and ways for forest trees to adapt to changing conditions, both local and global.

Besides beneficial fungi, such as saprotrophs and ECM fungi that contribute significantly to key soil processes, soil-borne pathogens are important sources of biotic stress in the rhizosphere and

roots of plants (Delgado-Baquerizo et al., 2020). Plant pathogenic fungi affect plant diversity and influence the abundance and functioning of plant species in many ecosystems (Domínguez-Begines et al., 2020). In forest soil, plant roots are colonised by a wide range of fungi, depending on the root exudates and other compounds coming from the roots (Hartmann et al., 2009). Fungal pathogens that associate with parent tree also affect the growth and performance of the seedlings. Several factors are known to influence the composition of root-associated fungi, including host genotype, root carbohydrates or plant defence mechanisms (Domínguez-Begines et al., 2020).

2.1.2 Soil bacterial communities

Although bacteria are often less studied in temperate forest ecosystems compared to fungi, they are an essential component of the forest soil microbial community and contribute to important ecosystem processes. Contrary to fungi, their small size allows them to inhabit a wide range of microenvironments, while the ability to form spores offers protection and resilience to many soil bacteria.

Forest soils harbour highly diverse bacterial populations, typically containing the five most common bacterial phyla: Acidobacteria, Actinobacteria, Proteobacteria, Bacteroidetes, and Firmicutes (Lauber et al., 2009; Lladó et al., 2017). Since most bacteria cannot be cultured from the soil environment (Hahn et al., 2019), it has proven difficult to determine their ecological characteristics. Advances in "omics" culture-independent methods have somewhat improved our understanding of bacterial ecology, but this aspect remains largely unexplored. Nevertheless, based on the environmental conditions of their habitat, we can distinguish between two broad groups of soil bacteria: fast-growing and slow-growing bacteria. Opportunistic (r-strategists) bacteria prefer nutrient-rich environments and are characterised by rapid turnover. In temperate forests, fast-growing Proteobacteria seem to be particularly enriched where they inhabit topsoil, and contribute to litter decomposition (Lladó et al., 2017; López-Mondéjar et al., 2015). Stress-tolerant (K-strategists) bacteria (e.g. Acidobacteria) are more typical of nutrient-poor environments, where they grow slowly while often outcompeting other groups in obtaining nutrient sources (Fierer et al., 2007; García-Fraile et al., 2015).

Because of the filamentous nature of fungi, which enables them to colonize substrates efficiently, and their ability to produce a variety of extracellular enzymes, microbial ecologists have traditionally considered them the major players in the decomposition of organic matter and have underestimated the role of bacteria in the decomposition process (Bani et al., 2018; Buée et al., 2009b; De Boer et al., 2005). However, in the recent years it is becoming clearer that bacteria contribute significantly to SOM decomposition, commonly having a range of cellulolytic genes (Berlemont and Martiny, 2015; Žifčáková et al., 2017), but also play a vital role in N cycling in forest ecosystems (Starke et al., 2021). During the decomposition of plant litter in forest topsoil, the bacterial biomass and diversity typically increase (Urbanová et al., 2014). While many Proteobacteria and Bacteroidetes seem to preferentially use simple C substrates in fresh litter (Fierer et al., 2007), in later decomposition stages mycolytic bacteria from these phyla seem to utilise fungal biomass – another important nutrient source for forest soil bacteria (Brabcová et al., 2016; Tláskal et al., 2016). As lignin and cellulose become the main compounds found in litter as the decomposition progresses, an increase in cellulolytic bacteria typically occurs (Purahong et al., 2016; Tláskal et al., 2016). Bacteria in forest topsoil play an important role in wood decomposition as well, especially in initial phases of decay, where members of Acidobacteria, Actinobacteria, Proteobacteria and Firmicutes are common inhabitants (Johnston et al., 2016; Kielak et al., 2016).

In temperate forests where sharp stratification is present in soils, different bacteria occupy the soil layers and are horizon-specific, in line with their ecological strategies (Figure 3). While Acidobacteria, Actinobacteria and Proteobacteria dominate the organic horizon, rich in plant-derived organic matter and mineral horizon with a lower content of organic matter, mineral soil provides a niche also for Firmicutes and Chloroflexi (Lladó et al., 2017; López-Mondéjar et al., 2015).
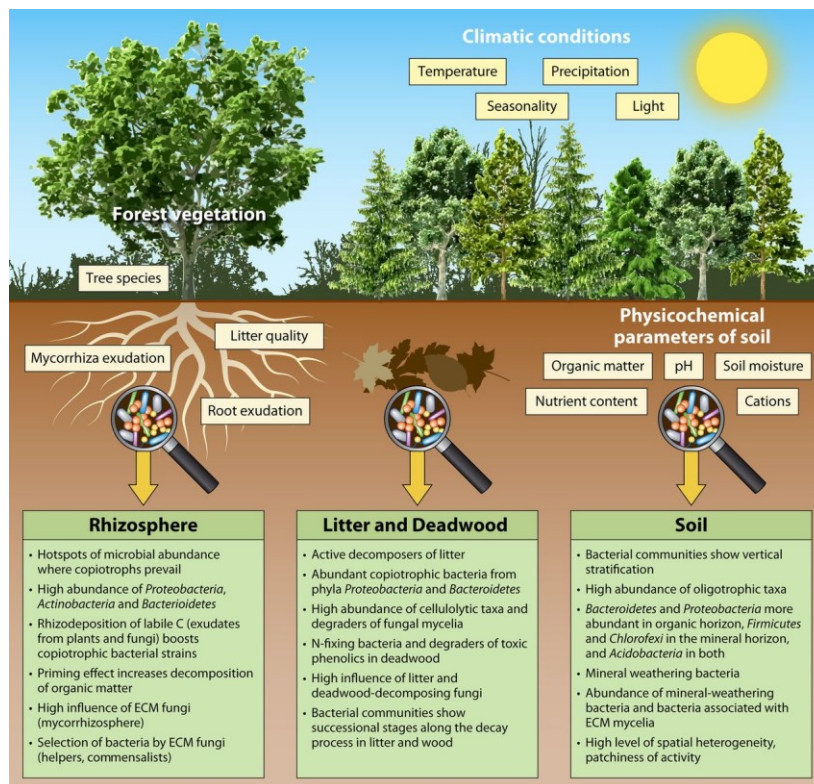
Figure 3. Bacterial communities in forest soils and their ecological traits. From Llado et al., 2017

In a recent effort to classify soil bacteria into ecological or substrate-specific guilds, bacterial strains were isolated from *in situ* decomposing litter incubated with different substrates (Algora et al., 2022). High levels of bacterial specialisation have been observed, suggesting an active role for substrate-specific bacteria in the utilisation of biopolymers in forest topsoil.

2.1.3   Microbial decomposition of various carbon sources in temperate forest soils

Microbial utilisation of different C sources defines their functional niche in the environment. Their characterisation is therefore an essential step in determining the functional role of individual microorganisms in the ecosystem-level C cycling. C fluxes in forest ecosystems are mainly determined by the activity of primary producers that fix atmospheric CO_2 and turn over each year. Plant litter and dead wood consist of a mixture of recalcitrant and complex polymers such as cellulose, hemicellulose, and lignin. In addition, plants also supply large amounts of C to the soil in the form of root exudates – mainly sugars, amino acids, and carboxylic acids (Sasse et al., 2017;

Shen et al., 2020), and mineralisation of this simple labile C has been found to account for a significant proportion of stable SOM (Schmidt et al., 2011; Sokol et al., 2019). In addition to C of plant origin, microbial biomass is also abundant in forest soils and represents a large and important pool of organic matter with a faster turnover than plant litter (Brabcová et al., 2018).

Microorganisms are key players in recycling and turnover of soil organic matter, contribute greatly to C fluxes in soils, and have the potential to influence the feedback between climate and the global C cycle (Schaeffer et al., 2012; Trivedi et al., 2018). Therefore, predicting how soils will respond to future environmental conditions is impossible without understanding the role of soil microbes in the C cycle (Graham et al., 2016). Even though both fungi and bacteria contribute to the assimilation and mineralisation of C from major complex sources in soil, their specific roles and quantitative contributions of different guilds of the soil microbiota to decomposition processes and C flux in soils are a constant point of debate (Kramer et al., 2016; López-Mondéjar et al., 2018; Rousk and Frey, 2015). Recent studies have suggested that decomposition processes rely on complementarity between different groups of metabolically distinct taxa. Along these lines, Bhatnagar et al. (2018), analysing the decomposition of different litter types, found that fungal taxa are organised into functional guilds of decomposers for cellulose and lignin. Similarly, other authors demonstrated a high degree of specialisation and substrate preference among fungal decomposers when assessing the degradation of individual biopolymers of plant and fungal origin in forest soils (Algora Gallardo et al., 2020). In contrast, another study showed that decomposer communities in forest soils are dominated by both fungal and bacterial generalist taxa and that guilds of specialised decomposers are not as abundant as expected (López-Mondéjar et al., 2018). In conclusion, determining the microbial utilisation of different C sources in the soil, including labile and recalcitrant C pools, and the functional role of each microorganism is an essential step in understanding C turnover in the ecosystem (Morrissey et al., 2017; Pepe-Ranney et al., 2016; Wang et al., 2021). This is particularly important with respect to soil C pools that are not derived from plant biomass and whose fate in C flux has not yet been studied in detail, such as C from components of microbial biomass or from labile compounds of root exudates.

2.2 Spatial and temporal distribution of microbial communities in forest soils

While it is known that community dynamics generate both spatial and temporal patterns, a concept well illustrated by the example of many plant species (Chun and Lee, 2019; Verstraeten et al., 2013), microbial communities have been explored primarily at the spatial scale (Kivlin and Hawkes, 2020). The spatial distribution of microbial communities depends on their ability to disperse and the availability of their specific niches. Microbial communities differ significantly with respect to these two factors. Fungi (especially mycorrhizal fungi) have less efficient dispersal abilities than bacteria, which makes their spatial distribution variable (Kasel et al., 2008). The dispersal patterns of fungi that form large mycelial networks follow the patterns of larger organisms determined by the rules of island biogeography (Peay et al., 2010). Fungal species that produce spores are able to spread rapidly and survive for years under unfavourable conditions, while mycelia of other fungal groups (e.g. saprotrophic fungi) may spread only vegetatively in the soil (Cairney, 2005; Fernandez et al., 2013). Recent studies also show that the distribution of bacterial communities in soil is not random but influenced by different environmental factors depending on the phylum (Karimi et al., 2018).

Microbial community structure and abundance may also be a consequence of soil vertical stratification in forest ecosystems (Jumpponen et al., 2010; Lladó et al., 2017; Voříšková et al., 2014). This strong vertical stratification is mainly caused by the decomposition of organic matter in the litter. Usually, the decrease in organic matter quality in the deeper soil horizons is accompanied by a decrease in microbial diversity, biomass, and activity (Lindahl et al., 2007; Lladó et al., 2017; Šnajdr et al., 2008; Tedersoo et al., 2003). In general, litter exhibits high abundance of saprotrophic fungi, while abundance of ectomycorrhizal fungi increases with depth (Baldrian et al., 2012; Lindahl et al., 2007; O'Brien et al., 2005). Compared to fungi, bacterial communities in litter are often characterized by faster temporal dynamics and higher diversity (Baldrian et al., 2012; Santonja et al., 2018; Urbanová et al., 2015). Bacteria are horizon-specific, dependent on nutrient availability and the ability to utilize recalcitrant carbon sources (Lladó et al., 2017; López-Mondéjar et al., 2015). Because of this diversity in the ecology of both fungi and bacteria, their distribution in soils varies, making it important to study the drivers of the distribution of the different microbial groups and their ecological importance.

Though spatial patterns in microbial communities have been reported in the literature at both local (e.g., Bahram et al., 2015; Karimi et al., 2018; Pasternak et al., 2013) and global scales (e.g., Lozupone and Knight, 2007; Põlme et al., 2014; Tedersoo et al., 2014; Větrovský et al., 2019), much less is known about species turnover and temporal dynamics of microbial communities. Recent methodological advances have led to an accumulation of studies on time series of microbial communities (Buscardo et al., 2018; Goldmann et al., 2020a, 2020b; Stevenson et al., 2014; Wang et al., 2019), however, these focused mainly on intra-annual seasonality. Temporal dynamics of microbial communities is a rather complex concept and understanding this process and the drivers behind it is central to improving the incorporation of soil microbiomes into ecological forecasts and models.

2.3   Main drivers of microbial community composition in forest soils

Fungal communities in litter are primarily determined by the dominant tree species and litter composition (Bahnmann et al., 2018; Kivlin and Hawkes, 2016; Santonja et al., 2018), abiotic factors (e.g., soil pH, moisture, nutrient availability) are also important factors in deeper soil horizons (Bahnmann et al., 2018; Burke et al., 2019) (Figure 4). Burke et al. (2019) showed that it is indeed site-specific chemical factors that drive (temporal) variation in soil fungal communities, rather than climate. Moreover, Goldmann et al. (2020b) showed that temporal fluctuation of arbuscular mycorrhizal communities in grasslands is rather independent of abiotic factors. This suggests that fungal communities are structured differently depending on their ecological guild.

To explain the distribution of bacteria in soil, it is necessary to recognise that soil is a complex collection of microniches that have different physiochemical properties, at different levels. Since bacteria tend to inhabit these small niches, they are mainly driven by the properties of their immediate environment (Lladó et al., 2017). Several studies indicated that the soil pH is the most important driver of the bacterial community composition in forest soils (e.g. Jeanbille et al., 2016; Lauber et al., 2009; Norman and Barrett, 2016). In addition, soil moisture can affect the physical properties of the soil matrix, which in turn affects the distribution of bacteria and nutrients and consequently the rate of important soil processes (Brockett et al., 2012) (Figure 4).
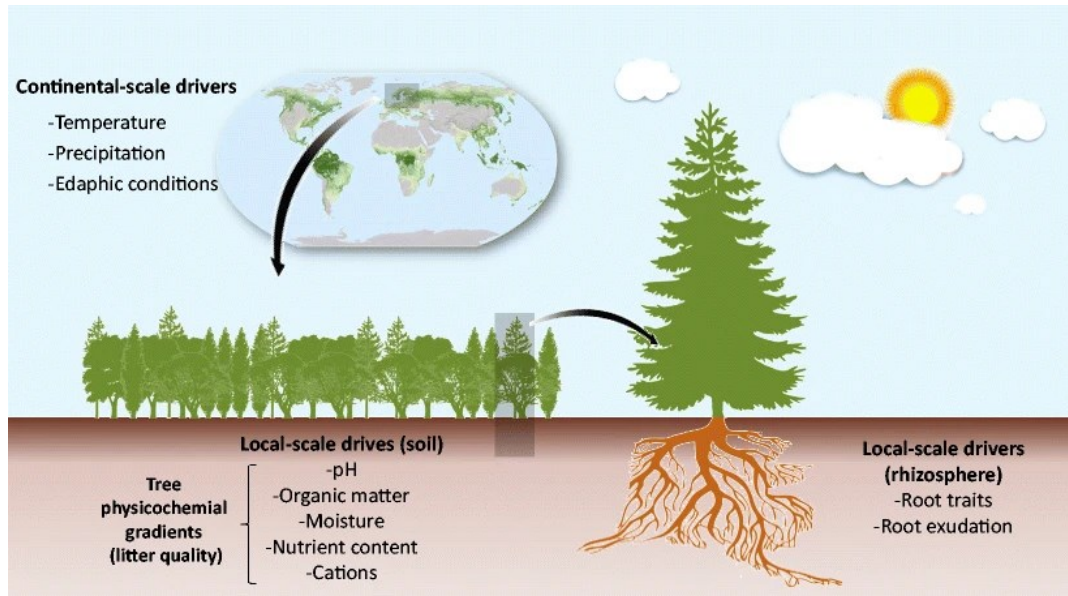
Figure 4. Major drivers of microbial communities in soil (Llado et al., 2018)

In Křtiny forest, where the experiments of this dissertation took place, several studies on the distribution of fungal communities were conducted. Bahnmann et al. (2018) showed that stand type is an important driver of fungal communities. In both litter and soil, the dominant tree type was found to influence fungal communities. However, in soil, stand type was a significant driving factor only for ECM fungal communities. In addition, a study on yeasts in temperate forests (Mašínová et al., 2017) demonstrated that yeast communities were mainly influenced by soil pH and moisture, but also by tree species composition. Finally, the effects of *Picea abies* stand clearcutting on fungal community succession were investigated (Kohout et al., 2018), showing that fungal communities change dynamically over time and contribute to decomposition of root litter - a hotspot of decomposition and fungal biomass. Thus, the experiments in this dissertation represent a natural extension of the studies conducted in this forest, examining bacterial communities in addition to fungi.

3 Aims of the Thesis

This dissertation consists of a combination of experiments involving environmental sampling, community analysis, and the use of "omics" techniques and stable isotope labelling to track soil C flux, but also to ask essential questions about temporal and spatial variation in microbial communities and other environmental factors that influence their composition.

Our present understanding of the microbial response to environmental drivers and the consequences on microbe-mediated biogeochemical processes is rather limited. To predict such a response, we should first study the temporal stability or turnover of microbial communities under current conditions in undisturbed soils. This knowledge would serve as a basis for further studies and prediction of the microbial response to climate change and their overall contribution to greenhouse gas fluxes. In addition, we lack deeper knowledge of local drivers of microbial communities as well as the ability of microbial taxa to utilise different forest soil substrates in an everchanging environment. Temperate forests are of global importance because they harbour some of the largest and oldest organisms in the world and also represent an important source of timber and wood products, with a potential for sustainable management. In this context, our knowledge of microbial response to disturbances, particularly those caused by anthropogenic activities (e.g., forest management) in temperate forests, is also scarce, and research of this aspect would provide a basis for future adaptation of such practises to maintain sustainability and provision of ecosystem functions. Overall, a systematic approach to the study of both fungi and bacteria is needed to understand their respective roles in ecosystem processes and their response to changing environmental factors, the primary motivation for this dissertation.

The main aims of this PhD. thesis were:

1) To quantify the temporal turnover rate of fungal and bacterial communities in temperate forest soil (**Publication I**)
2) To track the incorporation of C from compounds of different recalcitrance into the biomass of fungi and bacteria (**Publication II**)
3) To examine how the stand age affects fungal biomass and relative abundance of the major ecological guilds of fungi (**Publication III**)

4) To complement previously published data on fungal community succession following the clearcutting, by assessing the response of bacterial communities to this common forest management practice, and their potential role in root decomposition (**Publication IV**)

4   Experimental Part

4.1   List of publications

During my PhD studies, I co-authored 10 papers, some of which are still under review at the time of writing and the others, although related, do not fit the specific objectives of this dissertation (e.g., Unuk et al., 2019; Fernandes et al., 2022). Therefore, this dissertation represents a selection of relevant publications that are either already published (Publications I and III) or currently under review (Publications II and IV).

Publication I: Temporal turnover of the soil microbiome composition is guild-specific

Martinović, T., Odriozola, I., Mašínová, T., Doreen Bahnmann, B., Kohout, P., Sedlák, P., Merunková, K., Větrovský, T., Tomšovský, M., Ovaskainen, O., Baldrian, P., 2021. Temporal turnover of the soil microbiome composition is guild-specific. Ecology Letters 24, 2726–2738. doi:10.1111/ELE.13896

Journal: Ecology Letters, IF$_{2021}$ 9.492

Publication II: Stand age affects fungal community composition in a Central European temperate forest

Odriozola, I., Martinovic, T., Bahnmann, B.D., Ryšánek, D., Mašínová, T., Sedlák, P., Merunková, K., Kohout, P., Tomšovský, M., Baldrian, P., 2020. Stand age affects fungal community composition in a Central European temperate forest. Fungal Ecology 48, 100985. doi:10.1016/j.funeco.2020.100985

Journal: Fungal Ecology, IF$_{2021}$ 3.404

Publication III: Microbial utilization of simple and complex carbon compounds in a temperate forest soil

Martinović, T., Mašinová, T., López-Mondéjar, R., Jansa, J., Štursová, M., Starke, R., Baldrian, P. 2022. *Submitted for publication*

Journal: Soil Biology and Biochemistry, IF2021 7.17 (in revision)

Publication IV: Bacterial community in soil and tree roots of *Picea abies* shows little response to clearcutting

Martinović, T., Kohout, P., López-Mondéjar, R., Algora Gallardo, C., Starke R., Tomšovský, M., Baldrian, P. *Submitted for publication*

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4.1.1 Publications summary

While the spatial distribution and composition of microbial communities in many forest types is widely known at both local and global scales, our knowledge of the temporal dynamics of microorganisms is much more limited. A few studies that have examined soil microbial community composition using time series indicate their complex temporal dynamics. In the **Publication I**, the accurate quantification of the temporal turnover rates of bacteria and fungi in soils of temperate forests represents one of the first such attempts on a timescale greater than one year. The rate of turnover was not uniform across fungal guilds and bacterial phyla, indicating the importance of guild-level resolution to understand patterns of microbial community assembly and response to environmental factors.

Because the focus was on the relatively well-defined fungal guilds, this research was extended to include the role of stand age as a potential environmental factor in fungal community development (**Publication II**). ECM community composition was shown to respond to stand age, and the effects of stand age on fungal community decomposition appear likely to be the result of changes in nutrient supply, independent of plant community composition or forest age.

Different groups of organisms may respond differently to soil nutrient availability, depending on the substrates they prefer. To further explore this concept of substrate preference and potential versatility in utilising different carbon sources, soil from Křtiny forest was incubated with ^{13}C-labelled carbon substrates of various recalcitrance (**Publication III**). Both soil fungi and bacteria can utilise a wide range of C substrates. However, we know from previous studies that fungi can play a central role in determining bacterial community composition in many processes involving these substrates. **Publication IV** therefore focused on bacterial succession during forest development in a distinguished environment of a *P. abies* forest following clearcutting that leads to even-aged forest stands – complementing previously published data on fungi from the same sites.

Publication I: Temporal turnover of the soil microbiome composition is guild-specific

Both spatial and temporal variation are important components in structuring microbial communities. However, accurate quantification of temporal turnover rates of fungi and bacteria has not been performed. In this study, we repeatedly sampled bacterial and fungal communities at specific sites over several years to describe their patterns and temporal turnover rates. We show that microbial communities are subject to temporal change, with change in soil being somewhat faster for fungi than for bacteria, and bacterial communities changing more rapidly in litter than in soil. Our results show that temporal turnover differs between ecological guilds within fungi and phyla within bacteria. While some microbial guilds show uniform responses across regional sites, others exhibit site-specific evolution with weak general patterns. These results suggest that guild-level resolution is important for understanding the structure and dynamics of microbial communities and their responses to environmental factors.

Publication II: Stand age affects fungal community composition in a Central European temperate forest

To better understand the processes driving changes in fungal community structure during succession in temperate forests, samples were collected from the soil, rhizosphere, and roots of *Fagus sylvatica* and *Picea abies* stands of different ages (1-137 years). ITS2 amplicon sequencing and ergosterol quantification were used to examine how fungal community composition and productivity differ by forest age. While forest age had no significant effect on ergosterol content, fungal community composition changed with forest age, particularly the ECM fungal guild. However, other ecological fungal guilds did not appear to change with stand age. These results suggest that the effect of stand age on fungal community composition may be due to changes in nutrient supply that are independent of plant community composition or forest age.

Publication III: Microbial utilisation of simple and complex carbon compounds in a temperate forest soil

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Microorganisms in soil mediate various ecosystem processes, but few studies have attempted to address the relative contributions of fungi and bacteria to these processes. The aim of this experiment was to track the incorporation of carbon in forest soils into the biomass of fungi and bacteria using stable isotope probing. After incubation of microcosms supplied with ^{13}C substrates of varying complexity, substrate respiration rates were determined. Phospholipid fatty acids were used as a proxy for microbial biomass. Microbial taxa incorporating ^{13}C into their biomass were identified by ^{13}C-DNA separation and amplicon sequencing. After 1 week of incubation, the highest respiration was observed in microcosms with labelled citric acid and glucose, and the lowest with chitin. A significant increase in chitin respiration rate was observed after 3 weeks, as well as the increase in total and ^{13}C microbial biomass. In addition, a distinct microbial community was observed in the microcosms containing ^{13}C-chitin, clearly indicating that both fungi and bacteria were involved in the decomposition of chitin. The results showed that both specialized and generalist taxa were present in all microcosms, suggesting that numerous microbial taxa are capable of utilizing different carbon sources. Compounds with low molecular mass were more readily respired, while carbon from more complex biopolymers was more incorporated into the microbial biomass.

Publication IV: Bacterial community in soil and tree roots of Picea abies shows limited response to clearcutting

Martinović, T., Kohout, P., López-Mondéjar, R., Algora Gallardo, C., Starke R., Tomšovský, M., Baldrian, P.

In this study, we investigated changes in bacterial community structure in response to clearcutting of forests. Roots, rhizosphere soil, and soil samples were collected from a *Picea abies* stand over a two-year period after clearcutting, and the results of 16S rRNA sequencing were compared to data obtained prior to harvesting. While there was no clear difference in community structure between the rhizosphere and topsoil in the first few months after clearcutting, the bacterial communities associated with the roots were distinct and underwent more profound changes over time. The early stages of root decomposition were characterized by the presence of Actinobacteria, whereas the relative abundance of Proteobacteria (mainly Burkholderia) increased in the later stages. In addition, bacterial communities on decomposing roots differed markedly from those on live roots prior to clearcutting. Our results suggest that cessation of tree root activity resulted in changes in root bacterial communities as well as soil bacterial communities at the later stages of postharvest sampling. Clearcutting can cause both changes in microbial community structure and declines in microbial biomass, and the effects appear to be pronounced for both fungi and bacteria.

4.2 Methods

The experimental work in the scope of this dissertation is based on a combination of the following methods.

Environmental (soil) sampling (Papers I, II, III, IV)

DNA extraction (Papers I, II, III, IV)

PCR amplification of fungal ITS2 region (Papers I, II, III)

PCR amplification of bacterial 16S rRNA region (Papers I, II, IV)

Amplicon sequencing (Illumina MiSeq) (Papers I, II, III, IV)

Biomass quantification (ergosterol) (Paper III)

Quantitative PCR (Paper II)

Bioinformatic analyses of amplicon sequencing data (Papers I, II, III, IV)

Multivariate statistics and diversity analyses (Papers I, II, III, IV)

5   Discussion

This dissertation is based on four publications aiming to reveal patterns in microbial community composition both in time and space and in response to various environmental factors. Altogether, this work contributes to our understanding of the composition and ecology of fungi and bacteria in the topsoil of temperate forests.

Fungal and bacterial communities in soil showed differences in composition between the years studied in **Publication I** (Figure 5). In contrast, the fungal and bacterial communities in the litter did not show clear temporal patterns. Consistent with community structure, there were also differences in the rate of community turnover over time between fungi and bacteria and between soil and litter. Soil fungi, which exhibited a strong temporal pattern in community structure, had the highest rate of temporal community turnover, followed by litter bacteria and soil bacteria. In all studied communities, species replacement was the main driver or temporal turnover, while species loss/gain had little effect, in line with earlier research that showed that diversity can remain stable even when there is species community turnover (Brown et al., 2001).

Differences in fungal community structure also existed among ecological guilds. The temporal trend observed in the soil fungi was present only in the saprotrophic soil community, while the ECM fungi in soil did not show any temporal patterns in community structure. One of the possible explanations would be the stochasticity of recolonization of the annually emerging fine roots of trees. Compared to saprotrophic fungi, the activity of ECM fungi is largely reduced during winter in temperate regions; therefore, their communities must re-establish each season. The supply of C to new roots in spring may result in some ECM fungal taxa taking up a disproportionate share of the resources, dominating in the soil and leading to high temporal variability in the ECM fungal community. This stochasticity in mycorrhizal fungal community establishment appears to be important (Dumbrell et al., 2011), and our study supports this idea.
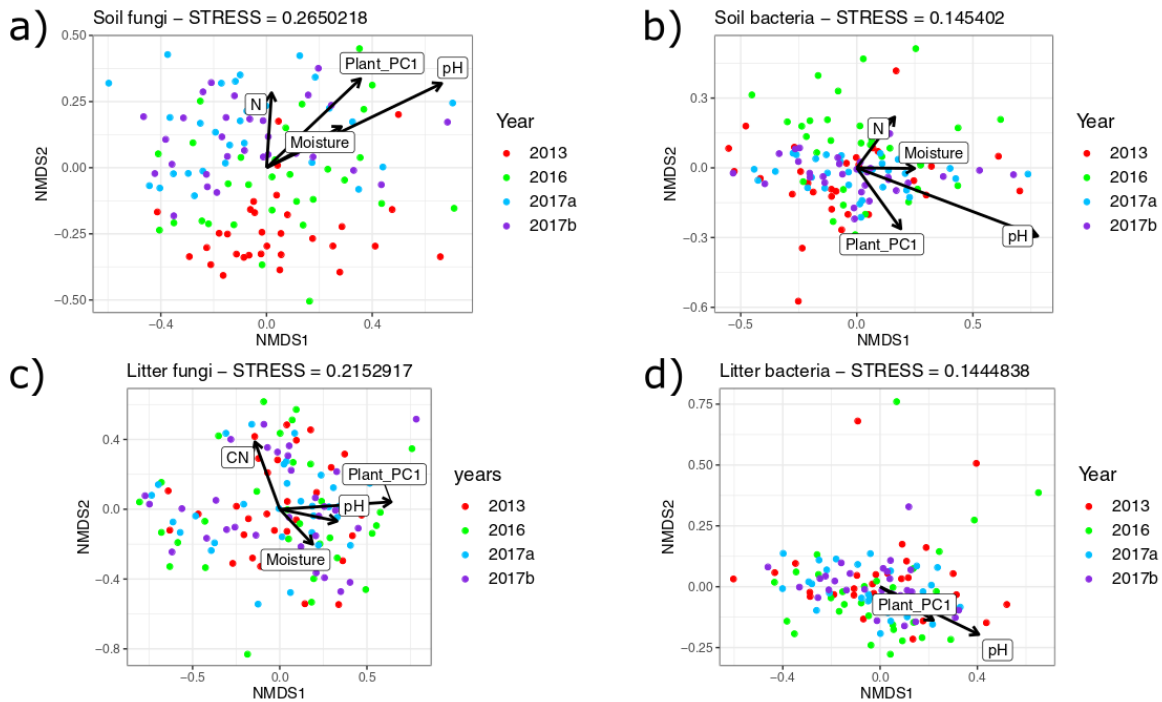
Figure 5. NMDS ordination plots of fungal and bacterial communities: soil fungi (a), soil bacteria (b), litter fungi (c), and litter bacteria (d). (Publication I)

Similar to the fungal ecological guilds, differences in the community structure of the individual phyla were also evident in the soil bacteria. The annual effect seemed to be present in the soil Proteobacteria and possibly a little in the Bacteroidetes and Verrucomicrobia, but the rest showed no specific trends in community structure with respect to time. As with the litter fungi, none of the bacterial groups in the litter showed directional change between years. Of the bacterial phyla in the soil, the Planctomycetes and Verrucomicrobia showed the slowest changes over time, which can be explained by their slow growth rates (Lladó et al., 2017). Growth rate is one of the obvious potential drivers of community change over time, but it seems that a faster growth rate of bacteria does not necessarily lead to a faster change in their communities. This could be due to the high proportion of dormant bacteria in the soil (Lennon and Jones, 2011), which exhibit relatively slow community turnover. Bacterial species belonging to other phyla in the soil had slightly higher turnover rates, and overall, the bacterial phyla in the litter had higher turnover rates than the bacterial phyla in the soil.

In summary, turnover rates among fungal guilds or bacterial groups were not consistent. While some ecological guilds showed uniform responses at regional sites, others responded more to site-specific factors such as temperature or precipitation, and did not show general patterns.

Because of the importance of site-specific factors in development of soil microbial communities, a study was conducted on the effects of forest stand age (**Publication II**). Forest stands of different ages play diverse roles in ecosystem processes, including C accumulation and nutrient turnover (Clemmensen et al., 2013). Fungal species are important mediators of these processes, so understanding how fungal communities evolve is central to better predicting changes in ecosystem function during forest succession (Clemmensen et al., 2015; Kyaschenko et al., 2017). Previous studies have shown that forest age can influence fungal community composition (especially the ECM community) (e.g., Hagenbo et al., 2018; Kyaschenko et al., 2017; Wallander et al., 2010). In our study, the importance of stand age on fungal community composition was extended to a more representative, heterogenous forest landscape dominated by spruce and beech stands. It was also shown that the effects of stand age apply to fungal communities in roots as well as bulk soil and rhizosphere.

While stand age had no effect on fungal abundance, ECM fungal composition was most strongly affected by stand age, consistent with previous studies (Hagenbo et al., 2018; Kyaschenko et al., 2017; Wallander et al., 2010) (Table 1). Of the other fungal guilds, only plant pathogens were affected, and only in roots, suggesting that the root-associated fungal community may be more susceptible to changes in stand age compared to soil communities. Rhizosphere is different from the bulk soil, as it receives increased amounts of small molecular mass compounds as root exudates (organic acids, amino acids and carbohydrates) (Buée et al., 2009a; Zhalnina et al., 2018), and harbours different fungal communities, also demonstrated in this study. Although we expected the relative abundance of fungal guilds to change with stand age, we found no significant effect of stand age on the relative abundance of any fungal guild. The reason for this may be that there was no relationship between soil nutrient and plant composition and stand age in this study. Nevertheless, it appeared that even very young forest stands harboured a similar proportion of ECM fungi as older stands, suggesting rapid recovery of the ECM fungal community,

as shown in the study by Kohout et al. (2018) from the Křtiny forest, which examined fungal community succession after clearcutting of spruce.

Ecological guild	Effect	Soil			Rhizosphere			Roots		
		Df	*P*-value	Adj. R^2	Df	*P*-value	Adj. R^2	Df	*P*-value	Adj. R^2
Whole community	Stand age	1	0.049	0.019	1	0.037	0.014	1	0.116	-
	Environment	1	n.s.	-	1	0.006	0.025	1	0.021	0.026
	Plant	1	0.006	0.031	1	0.001	0.066	2	0.001	0.078
Saprotrophs	Stand age	1	n.s.	-	1	n.s.	-	1	n.s.	-
	Environment	1	n.s.	-	2	0.028	0.038	2	0.027	0.05
	Plant	1	0.038	0.053	1	n.s.	-	1	n.s.	-
Ectomycorrhizae	Stand age	1	0.015	0.032	1	0.011	0.029	1	0.029	0.03
	Environment	1	n.s.	-	1	0.015	0.027	1	n.s.	-
	Plant	2	0.001	0.152	2	0.001	0.122	1	0.002	0.058
Endophytes	Stand age	1	n.s.	-	1	n.s.	-	1	n.s.	-
	Environment	1	n.s.	-	1	0.017	0.092	1	n.s.	-
	Plant	2	0.001	0.082	1	n.s.	-	2	0.001	0.214
Plant pathogens	Stand age	1	n.s.	-	1	n.s.	-	1	0.039	0.028
	Environment	1	n.n.	-	1	n.s.	-	1	n.s.	-
	Plant	1	n.s.	-	1	n.s.	-	1	0.001	0.215

Table 1. Effects of stand age, environment, and plant community composition on fungal communities in soil, rhizosphere and roots. (Publication II)

Although it has been previously proposed that changes in soil chemistry (Kyaschenko et al., 2017; Wallander et al., 2010) and ground vegetation (Harantová et al., 2017; Urbanová et al., 2015) are linked to the effect of stand age, based on our study, it seems more likely that the effect of stand

age is related to changes in the nutrient supply that hosts provide to root-associated fungi, in line with other studies (e.g., Parrent and Vilgalys, 2007; Prescott and Grayston, 2013).

Many ecosystem processes depend on the resilience of microbial communities when suppressed by these changes in nutrient supply, as well as their ability to use different nutrient sources to maintain productivity. The results of our study (**Publication III**) showed that both fungi and bacteria were able to utilise various C sources from forest soil. We confirmed the previously proposed concept of C use preferences of soil bacteria and fungi, according to which both groups are involved in the use of soil C from different sources, regardless of their complexity (López-Mondéjar et al., 2018). Moreover, we complemented this concept by introducing pure carbon compounds, both labile citric acid (alongside glucose), as a proxy for root exudates, and recalcitrant chitin, as the main component of fungal biomass. We showed that fungi and bacteria utilise chitin equally efficiently, and while bacteria might dominate the initial phase of fungal biomass degradation (Brabcová et al., 2018), they most likely mainly utilise components other than chitin. In fungi, we showed guild-specific substrate preferences, with yeasts generally utilising simple carbon sources such as glucose and citric acid, and saprotrophic fungi and moulds being efficient in utilising recalcitrant carbon sources.

Although both fungi and bacteria were able to degrade all substrates, bacteria were found to be less specialised (Figure 6). More than 50% of the ^{13}C-enriched taxa (species accumulating C from the added sources) belonged to slow-growing Acidobacteria, Actinobacteria, Alphaproteobacteria, or Verrucomicrobia. Actinobacteria are known to degrade plant-derived polysaccharides in forest soils (Morrissey et al., 2016), and though the vast majority of these very common slow-growing bacteria (Lladó et al., 2019) were enriched in plant biomass and hemicellulose, some were not enriched at all (e.g., *Mycobacterium*, *Solirubrobacter*). While slow-growing bacteria appeared to use all substrates well, there was no evidence that fast-growing bacteria (e.g., Bacteroidetes, Betaproteobacteria) (Lladó and Baldrian, 2017) preferred compounds with low molecular mass. Some fast-growing Bacteroidetes even showed some degree of specialisation on more recalcitrant substrates (e.g., *Chitinophaga* on chitin, *Mucilanibacter* on chitin, plant biomass and its components) (Figure 6). However, it is important to note that the relative abundance and enrichment of these taxa decreased between day 7 and

day 21 of incubation, consistent with their fast-growing lifestyle. It should be emphasized that ^{13}C enrichment does not necessarily imply substrate decomposition – it may be the result of cross-feeding, and some observed taxa may be opportunists or cheaters (Algora Gallardo et al., 2021; López-Mondéjar et al., 2018), which is the most likely explanation for these results.
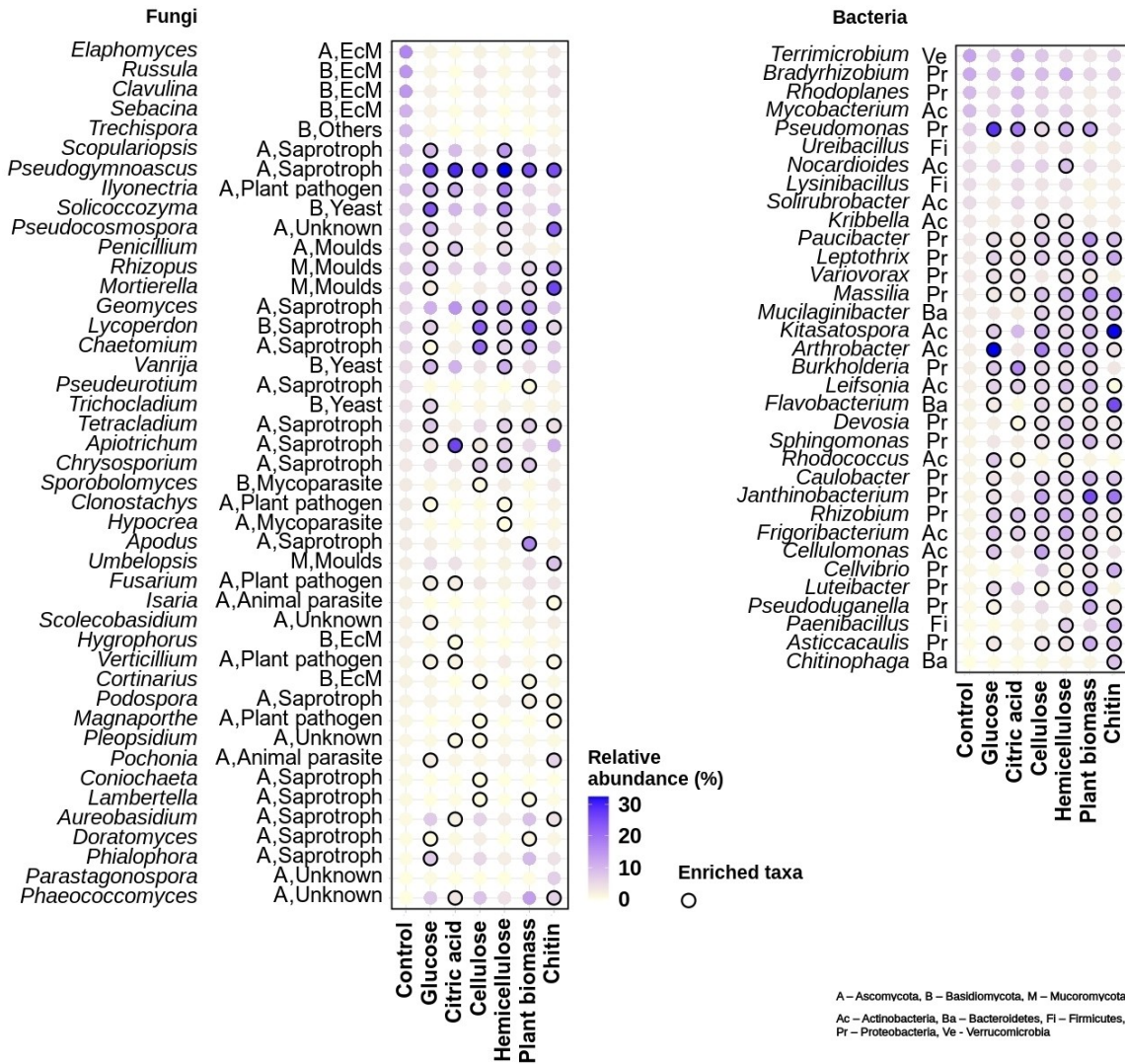

Figure 6. Fungal and bacterial genera accumulating carbon from ^{13}C-labelled substrates added to forest soil. (Publication III)

Guild-specific substrate preferences were observed among fungi. Although fungal community composition appeared quite similar between total plant biomass and cellulose, hemicellulose

appeared to harbour a distinct community that included a greater proportion of yeasts. The relatively high abundance and enrichment of some yeasts on hemicellulose (e.g., *Vanrija*, *Soilicoccozyma*) can be explained by their ability to degrade hemicellulose components (Mestre et al., 2011; Yurkov, 2018). Hemicellulose microcosms were dominated by saprotrophic fungi, many of which were also enriched (Figure 6) and known to have enzymatic potential for hemicellulose degradation (Baldrian et al.; Talbot et al., 2013), theoretically making their decomposition products available to yeasts.

Though both fungal and bacterial decomposers were able to degrade recalcitrant carbon sources in the forest soil, our results suggest that fungi accumulate more carbon from plant biomass components – cellulose and hemicellulose – consistently with previous findings (López-Mondéjar et al., 2018). Overall, our results showed that simple C substrates that are typically contained in root exudates (glucose and citric acid) are primarily used for generating energy rather than incorporation into microbial biomass, pointing to the distinct role of root exudates in forest soils.

As root exudates and C delivered to ectomycorrhizal fungi play an important role in influencing C and nutrient dynamics in ecosystems, their removal can have a major impact on root-associated microbial communities, potentially extending to the surrounding soil. Following deforestation, belowground microbial communities are affected not only by reduced root exudate inputs and consequential increases in root litter, but also by changes in associated environmental parameters such as temperature and moisture (Holden and Treseder, 2013; Lado-Monserrat et al., 2016; Purahong et al., 2014).

Dynamic development of fungal communities was demonstrated after clearcutting of a spruce stand in the Křtiny forest (Kohout et al., 2018), where the disappearance of fungi living symbiotically with tree roots was accompanied by a relative increase in saprotrophic fungi. Similar observations were made in a spruce forest after tree death due to a bark beetle outbreak (Štursová et al., 2014). However, there was little change in bacterial community composition two years after clearcutting (**Publication IV**).

Bacterial communities in soil responded marginally to clearcutting, with changes most pronounced in the root compartment (Figure 7), in line with previously documented changes in

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bacterial communities in decomposing roots of *Pinus sylvestris* (Herzog et al., 2019). While the roots harboured a bacterial community that was significantly different from that of the rhizosphere or soil, bacterial succession on the roots was not as obvious or gradual as in the fungi from the same samples (Kohout et al., 2018). In this particular experimental setup, bacteria appear to have independent development. There may be several reasons for these observations. The two-year period may be too short to detect significant changes in bacterial community structure - they tend to respond to disturbances later than fungi, as the latter are more dependent on symbiotic hosts (Hartmann et al., 2012; Osburn et al., 2019). The relatively higher abundance of *Paenibacillus* and *Burkolderia* in the living roots (before clearcutting) compared to the rhizosphere and bulk soil (Figure 7) suggests the importance of these genera in the roots, perhaps for maintaining mycorrhizal association as mycorrhizal helper bacteria (Frey-Klett et al., 2007; Labbé et al., 2014). A significant increase in the relative abundance of *Paenibacillus*, a common endophyte (Ulrich et al., 2008), could possibly be due to increased nutrient availability in decomposing roots, similar to the almost immediate increase in the relative abundance of fungal endophytes (Kohout et al., 2018). Also, Actinobacteria, which were abundant in the root compartment as well, are known to degrade plant material in the soil similar to saprotrophic fungi and are therefore strong competitors on root litter (Sanaullah et al., 2016).

Significant changes in community composition in soil were observed only in the final months after clearcutting, later in bulk soil than in the rhizosphere. Some bacteria, such as Actinobacteria and Proteobacteria, which were relatively abundant in soil, have rapid growth rates (Lladó et al., 2016), so they can recover relatively quickly after forest disturbance. Also, Actinobacteria generally show high stress tolerance (Evans and Wallenstein, 2014).
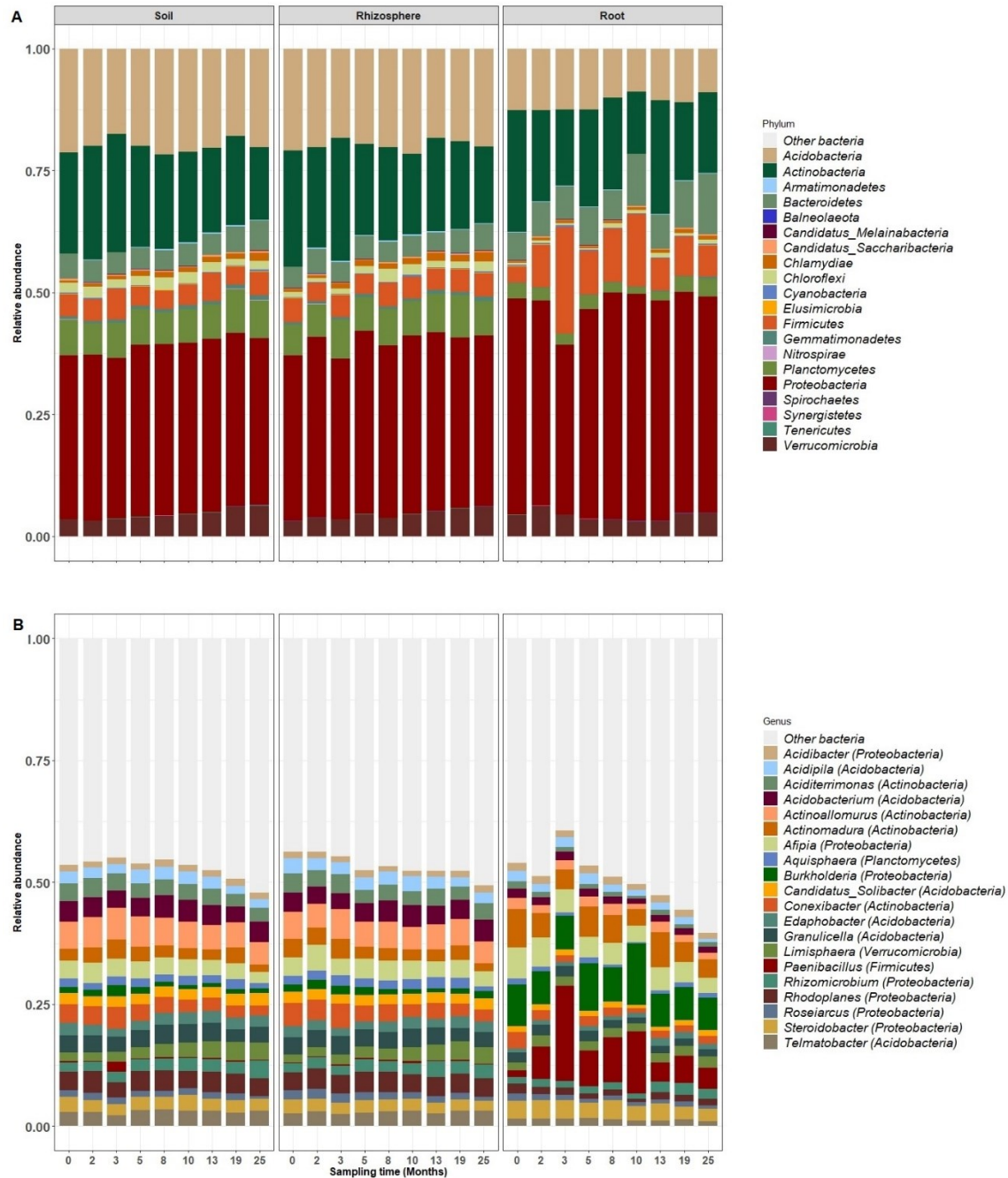
Figure 7. Relative abundance of bacterial phyla (A) and selected genera (B) in soil, rhizosphere, and roots of a *Picea abies* stand before (month 0) and after clearcutting. (Publication IV)

To get a better idea of the changes in bacterial communities, we also examined the potential nutritional groups of bacterial taxa in the soil and roots before and after clearcutting. Because decomposing roots were a substrate hotspot after clearcutting (Kohout et al., 2018), most OTUs

in the root compartment corresponded to bacteria previously isolated from a range of substrates. Roots contained more decomposers, especially of plant biomass components, compared to the rhizosphere and soil – the overall increase in OTU richness in roots after clearcutting was accompanied by an increase in OTUs with high similarity to bacteria enriched on plant or fungal cell wall biopolymers. In the early stages of root dieback (5-10 months after clearcutting), the activity of biopolymer-degrading enzymes was highest in the spruce roots (Kohout et al., 2018), and at the same time, roots contained the highest proportion of bacteria with a preference for utilisation of plant and fungal biopolymers. This suggests that bacteria may contribute to root decomposition or utilise the byproducts of fungal root decomposition. Together with the highest proportion of bacterial taxa with preference for lignin in roots, this result suggests that bacteria, in addition to fungi, play a role in fine root decomposition, as recently suggested (Fu et al., 2020). There was a large overlap between bacterial community composition in the living roots (before clearcutting) and decomposing roots (after clearcutting), suggesting that bacteria may associate equally well with both.

Maintaining the productivity of managed forests is extremely important, and the first step to better understanding how best to manage forests is to examine how microbial communities change in response to carbon availability and forest development. Although microbial communities were thought to have high potential for resilience to intensive timber harvesting (Busse et al., 2006; Hannam et al., 2006), recent evidence challenges this assumption and shows that ecosystem functions can be severely impacted (Pohjanmies et al., 2021), as can microbial community structure (Cao et al., 2020; Herzog et al., 2019; Lee and Eo, 2020). The relevance of this study also lies in the fact that, unlike the common approach of using root litter bags (e.g., Herzog et al., 2019), naturally decomposing roots were analysed, providing the first insight into the fate of living roots that naturally die when cut off from plant resources. However, based on the results of this study, in which bacterial community structure changed only slightly after clearcutting, long-term omics approaches are needed to explain specific patterns of change in bacterial communities. This would also improve our understanding of fungal-bacterial interactions and the potential consequences of forest management actions on the ecosystem,

ultimately leading to appropriate actions to maintain ecosystem functions and providing new insights for sustainable forest management in the long term.

Altogether, the results of this dissertation highlighted several interesting and novel points. Difference in temporal trends between fungi and bacteria was shown, where fungi had faster turnover rate compared to bacteria. The response was guild-specific, prompting us to explore microbial communities in this context. Among fungal guilds, ECM fungi are the most affected by the change in nutrient availability – either as a result of forest disturbances, demonstrated in previous studies, or in relation to stand age, as shown in this dissertation.

Moreover, studying bacteria alongside fungi gave us some clues about their potential interaction, and the overall role of bacteria in decomposition processes in forest soil. Bacteria proved capable of utilising also recalcitrant carbon sources from forest soils, as demonstrated by the SIP experiment. They also seem to play a role in lignin degradation, as many bacterial taxa with lignin preference were found in decomposing spruce roots after clearcutting.

6   Conclusions

This dissertation is based on four publications aimed at answering important and fundamental questions related to the establishment of microbial communities in soils of temperate forests and their role in the ecosystem. The experiments were conducted in the Křtiny forest near Brno in the Czech Republic.

The results of this thesis show that microbial communities in forest soils exhibit a temporal turnover that differs between litter and soil communities. The turnover rate also differed among ecological fungal guilds and bacterial phyla – some guilds responded regionally, while others responded mainly to site-specific factors, possibly short-term climatic conditions. These results highlight the importance of studying microbial communities at the guild level to predict their response to changing environmental factors. Among the important environmental factors affecting microbial communities in forest soils is stand age, the effects of which on fungal community composition and abundance have been studied. This study was extended by including two dominant tree species – beech and spruce – and three compartments – soil, rhizosphere, and soil – to examine whether the effects of stand age extend to soil and whether there are differences in fungal community composition between the two tree species. Stand age was particularly important for ECM fungi, which showed significant differences in composition along the age gradient. The results suggest that the change in nutrient supply from the plant to the root-associated fungi is most likely the cause of the effect of stand age, independent of soil chemistry or plant communities. Because nutrient supply also appears to be an important factor influencing microbial communities, substrate preferences of fungi and bacteria and their ability to use different C sources were examined as well. In addition, certain degree of specialisation and substrate preferences in fungi and bacteria was demonstrated, but also that many microbial taxa are able to utilise C from different substrates. Opportunists such as yeasts, moulds, and especially Proteobacteria mostly utilised less recalcitrant carbon sources such as glucose, cellulose, and hemicellulose. Finally, the results indicate that the simple C substrates, such as root exudate components-glucose and citric acid-are mainly used for respiration, i.e., energy production, while relatively little is incorporated into microbial biomass, indicating the differential use of these

components in temperate forest soils. These labile forms of C, derived from root exudates, represent a very dynamic source of C in the soil. Their absence from the soil as a result of forest disturbances, such as clearcutting, can lead to restructuring of microbial communities, and the effects appear to be more pronounced for fungi than for bacteria. However, there is relatively little information on the response of bacterial communities to clearcutting. Following clearcutting of a spruce stand in a Křtiny forest, roots represent the most dynamic compartment in which gradual changes in bacterial communities are evident. While the supply of fresh photosynthates is absent, the roots become a hotspot of decomposition and harbour many bacterial taxa with a preference for lignin, confirming their role in lignin degradation alongside fungi.

The results of this dissertation have improved our understanding of microbial community structure in soils of temperate forests. Bacteria were shown to play an important role in decomposition processes alongside fungi, indicating the importance of fungi-bacteria interactions in forest soils. However, this particular aspect deserves more attention and should be pursued further in continuation of this work. Advanced "omics" methods such as metatranscriptomics and metaproteomics would enhance our understanding of the respective functions of fungi and bacteria in forest soils and provide us with clues to their complex interactions, and how they respond to changing environmental factors. With this knowledge, we may suggest better solutions for sustainable forest management while maintaining ecosystem functions.

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