Factors Affecting Soil Microbial Processes

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Abstract Soil is one of the most abundant environments on the Earth, where microbial processes take place, thus understanding the soil microbial processes in the context of factors influencing their environment is crucial. Soil microbial processes control soil nutrient cycling, foremost carbon cycling; therefore they affect global climate change. Organic and inorganic forms of carbon of natural or anthropogenic origin are sequestered via microbial activity into so-called soil organic matter that can be preserved in the soil for many decades. Soil microbial processes, such as carbon cycling, can be described by models emphasizing either the importance of physicochemical factors or the involvement of microbes. Balancing the carbon intake (e.g., photosynthesis) and output (e.g., decomposition) is one of the most important microbial tasks in the soil. Soil microbial processes are mediated by enzymes and thus are affected by environmental factors affecting enzymatic activities, such as temperature, water content, pH, and seasonality, but also by factors affecting diversity and abundance of microorganisms, such as nutrient availability, amount of soil organic matter, or presence of the symbiotic tree. Some microbial processes, such as N mineralization, are influenced more by abiotic factors (temperature and moisture) than the diversity of the microbial community since many groups of microbes are involved in this redundant process.

Keywords Mineralization · Physicochemical factors · Soil organic matter · Microbial activity

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Abbreviations

°C	Degrees of Celsius
Al	Aluminum
C	Carbon
Ca	Calcium
CDI	Climate decomposition index
CH_4	Methane
CO_2	Carbon dioxide
Cu	Cuprum
CUE	Carbon use efficiency
DNDC	DeNitrification-DeComposition
DOC	Dissolved organic matter
H	Hydrogen
LIDET	Litter decay study
Mn-peroxidase	Manganese peroxidase
N	Nitrogen
N_2O	Nitrous oxide
NH_4	Ammonium
NO	Nitric oxide
NO^-_2	Nitrite
NO_3	Nitrate
NPP	Net primary production
NSP	Net secondary production
O	Oxygen
P	Phosphorus
S	Sulfur
SMP	Soil microbial processes
SOM	Soil organic matter

1 Introduction

Soil is defined by Merriam-Webster dictionary as "the superior layer of earth that can be plowed and in which plants grow," but soil is much more than that. Soil ecosystem is composed of various microhabitats that differ in physicochemical gradients and represents discontinuous environmental conditions. Due to its heterogeneity, soil serves as a medium for the growth of plants, microbes, and diverse organisms. The soil is made up of organic remains, so-called soil organic matter (SOM), clay, and rock particles. One of the soil functions is to maintain global biogeochemical cycles, which affects other biotic and abiotic components of ecosystems. Soil processes are retroactively controlled by biotic components, such as plant and microbial communities, and abiotic factors, such as temperature, water content, pH, etc.

The knowledge of the interplay between external factors and soil microbes in simplifying SMP (soil microbial processes) is critical in our understanding of how global climate changes could affect processes of the terrestrial ecosystem. There is still a significant gap in our understanding on how different biotic and abiotic factors and their interaction influence or regulate SMP, which could be due to the complexity of SMP and technical obstacle to study soil microbial community (Hackl et al. 2005; Brockett et al. 2012).

For the purposes of this chapter, we will consider four processes mediated by microbes involved in C and N cycling: SOM degradation, C sequestration, nitrification, and denitrification. These SMP are mediated by microbial enzymes, of which activity and production can be affected by external factors, such as temperature, pH, water, seasonality, and interactions among organisms.

Enzymes are one of the key drivers of soil biological process, such as organic matter degradation, mineralization, or recycling. Activity of hydrolytic enzymes, ligninolytic oxidases, and peroxidases has a direct effect on the transformation rates of soil biopolymers into substrates which are easily available to microorganisms and plants. Thus, studying soil enzyme activities is useful for evaluating the functional diversity of soil microbes, soil organic mass turnover (Kandeler et al. 1999; Yadav et al. 2017; Datta et al. 2014), or fertility of soil.

Soil enzymes are the main indicator of soil quality and health due to their quick response and sensitivity to external environmental factors (Dick 1994; Dick et al. 1996; Datta et al. 2017b). Simultaneous measurement of multiple enzyme activities can be served as a suitable indicator of soil microbial activities (Bolton et al. 1985). Such as β-glucosidase activity, catalyzing the hydrolysis of cellulose to glucose and dehydrogenase activity may be particularly useful enzymes for soil quality monitoring because of their central role in C cycling (Ceccanti et al. 1993; Doi and Ranamukhaarachchi 2009; Pathan et al. 2017).

2 Importance of Soil Organic Matter (SOM) in C Sequestration

One of the most abundant microbial processes in soil mediated by extracellular enzymes is degradation of either plant litter, microbial necromass, or other inputs, including leachates and exudates from different sources. There is a consortium of microorganisms that are degrading and utilizing the majority of C compounds created by NPP (net primary production). NPP turnover supplies energy and forms blocks for heterotrophs to build their biomass termed NSP (net secondary production). NSP could be used in the process of decomposition which takes days to decades and depends on temperature, moisture, and the quality of the live and senesced biomass.

A small fraction of plant (NPP) and heterotrophic decomposer constituents (NSP) are converted into soil organic matter (SOM) that could be persevered for many decades and is an imperative and stable C pool, making up a significant proportion

of terrestrial C stocks. Although SOM is mostly a small fraction of the soil, it regulates air and water availability for plant root growth and provides the resistance against wind and water erosion. Organic matter content in different soils ranges from 0.2% to 80%, respectively, in desert and peat soils. In temperate regions, it ranges between 0.4% and 10.0%, with soils of humid region averaging 3–4% and those in semiarid areas 1–3%. Soil C stocks are created in a process called carbon sequestration, during which CO_2 is removed from the atmosphere via photosynthesis and stored soil carbon pool in the form of SOM. The different elements of NPP added to the soil differ significantly as a source of energy and nutrients reflecting their biochemical composition and physical availability to the microorganisms (Wardle and Giller 1996).

The SOM can be separated into two fractions depending on their biological degradability: (1) rapid to medium turnover fraction and (2) recalcitrant fraction with slow turnover. The first one is composed of soluble compounds with small molecular mass and serves as immediate C sources for the soil biota, thus contributing to nutrient cycling. The latter fraction is a complex combination of humic and fulvic acids with different high molecular weight organic molecules attached to soil inorganic particles, represents sequestered C and thus the energy reservoir, and improves soil structure as well (Simpson et al. 2007; Schmidt et al. 2011). Carbon polymers, including hemicellulose, pectins, and cellulose, make up to 50% of NPP inputs in terrestrial environments. These components are structural part of plant cell wall and contain macronutrients, mainly N and P. Cytoplasmic components of plant cells, for example, sugars, organic acids, amino compounds, and proteins, provide energy and essential nutrients for decomposition and form up to 10% dry weight of the plant. After the degradation process, a small fraction of C NPP and NSP is preserved in soil in the form of humic substances by metabolism process or associate with other soil minerals and protected by soil aggregates. SOM thus comprised of distorted decayed plant residues, soil microbes, soil fauna, and by-products of degradation, such as humic substances. Humic substances are results of long oxidation and reduction, causing the material to be increased in C and H but depleted in O content, compared to the original one. During decomposition, N content of humic substances is increased because N compounds react through radical coupling with other compounds, and thus humic substances consist of 50–55% C, 5% H, 33% O, 4.5% N, 1% S, and 1% P. Metals and micronutrients, such as Al, Ca, Zn, and Cu, are also exist but in much smaller amounts. The dominance of aliphatic compounds derived from microbial cell walls in SOM (Schurig et al. 2012) suggests that microbial biomass contribute significantly to stable C pools.

Fungi and bacterial share on total soil biomass is approximately 90% (Rinnan and Bååth 2009), and thus turnover of their necromass is evaluated to contribute as much as 80% to the preservation and accumulation of SOM (Liang and Balser 2010). Throckmorton et al. (2012) hypothesized that cellular biochemistry of different microbes determines the form and amount of C designated to form stable SOM. Martin and Haider (1979) suggested that C stored in SOM is mainly of fungal origin compared to other microbial groups, due to their composite cell walls and pigments that are resistant to decomposition. Rinnan and Bååth (2009) supported this hypothesis by the fact that fungi have higher C-use efficiency (CUE) compared to bacteria that can lead to higher involvement of fungal C to stable SOM. Yet, the overlapping ranges

of CUEs for some soil fungi and bacteria question this theory (Six et al. 2006). The composition of the bacterial cell wall is likely to influence its decomposition by soil microorganisms because Gram-positive bacteria contain more peptidoglycan, which is associated with slower decomposition, than Gram-negative bacteria. Though the structure of peptidoglycan in cell wall differs among bacterial species and with growth conditions, what makes it difficult to predict is its decomposability (Vollmer et al. 2008). Due to the limited field-based assessment on comparing bacterial and fungal turnover, our understanding is scarce on the contribution of different microbial groups to SOM (Strickland and Rousk 2010). Throckmorton et al. (2012) reported that the involvement of various cellular biochemistry of main microbial groups contributed evenly to maintaining of SOM, but the results were more dependent on the abundance of microbial groups rather than their unique cellular biochemistries.

Among others, the decomposition processes are regulated by temperature, moisture, soil disturbance, xenobiotics, the quality of SOM as a microbial substrate (Smith and Paul 1990; Smith 1994; Molaei et al. 2017a, b), and microbial community composition (Aber et al. 1990; Couteaux et al. 1995; Fassnacht and Gowerr 1999; Park and Matzner 2003; Pregitzer et al. 2004).

3 Models of Soil Microbial Processes (SMP) Involved in SOM Degradation Are Either Process- or Organism-Oriented

C flux is directly or indirectly controlled by soil organisms through the degradation process. The relative contributions of microbes to CO_2 release vs. C storage in soil are of great interest. The CUE of the organism is the amount of CO_2 lost per unit of energy gained, and environmental conditions can impact CUE (Six et al. 2006). Nutrients in specific ratios or their lack can modify the amount of energy spent to decompose SOM. Nutrient availability, substrate quality, and temperature (del Giorgio and Cole 1998) impact the CUE of soil organisms. Cotrufo et al. (2013) suggested that microbial efficiency should be modeled as a function of substrate characteristics, community structure, and environment. This would widen our understanding of soil microbiota impact on CO_2 flux, SOM retention, C pool composition, and assembly, as well as an improved our knowledge of energy transformations in the microbial community. Multicompartmental models of SOM decomposition dynamics can be either "process-oriented" or "organism-oriented" (Paustian 1994).

Organism-oriented models, also known as "food web models," emphasize diverse functional or taxonomic groups of soil organisms in the description of the flow of organic matter and nutrients (Moore and de Ruiter 2012). Instead of concentrating on the specific organism's activity or group, process-oriented models emphasis on the processes mediating the transformations of organic matter and nutrients.

Most of SOM decomposition dynamics models start by modeling litter decay on the soil surface. The assumption of these models is that plant litter comprises both readily decomposable fraction and recalcitrant fraction composed of cellulose and

lignin. Hence, the SOM and litter decay can be divided into different pools based on stabilization mechanisms, bioavailability, and biochemical and kinetic parameters, consisting of small "active" pool with a rapid turnover rate and larger pool with slow turnover rates from decades to thousands of years. Plant lignocellulose ration is positively correlated with plant biomass recalcitrant fraction to decomposition. Many litter decay models work with microbial community as variable and also presume that the majority of plant lignin (>70%) will be transformed into organic material. Plant residue decay is well described by first-order rate kinetics that suggests that inoculation of soil microbes is not limiting factor for degradation rate.

LIDET (litter decay study) (Parton et al. 2007) data was used to assess global ecosystem models. Bonan et al. (2012) have used LIDET data (litter decay data) from study of Parton et al. (2007) to determine global ecosystem models and reported that models should also consider the initial litter N, lignin, labile C content, and effect of climate decomposition index (CDI) to precisely characterize litter decomposition dynamics. The most correlated variable was CDI since it embraces the seasonal patterns of temperature and moisture. From other factors influencing the results of model, the starting N content had a strong impact on N dynamics. Microbial N immobilization during the initial phase of decay (>50% of initial C remaining) was more favorable when N litter content was low (<0.8% N), while high N litter content (>1.5% N) resulted in the immediate release of simultaneous C and N during litter decay.

Many models (Schimel 2001) have coupled soil C decay to microbial biomass and physiology and contain the influence of microbial activity on SOM decay rates as well (Allison et al. 2010). General hypothesis in these models is that extracellular enzymes regulate the decomposition of SOM to dissolved organic matter (DOC) and that DOC availability regulates depolymerization of SOM. Another assumption in these models is that the production of enzymes is equivalent to the amount of microbial biomass. These models utilize Michaelis-Menten equation with the maximum reaction rate, microbial uptake (V_{max}), and half-saturation constant (K_m) being the primary input variables that can represent enzyme reaction rates and microbial uptake of DOC. Other soil environmental factors (water, temperature, soil pH, N, and P) can affect the enzymes production rate and their influence on the decomposition rate of SOM pools (Sinsabaugh and Shah 2012).

Additional relevant factor in substrate-enzyme-microbe models is the ratio of microbial growth to C processing costs known as microbial C-use efficiency (CUE). Substrate-enzyme-microbe models presume that CUE is influenced by the soil environmental variables and the SOM pool, whereas conventional SOM models usually use fixed values for CUE. Thus, conventional SOM models can be improved by counting the influence of soil environmental factors, microbial activity, and enzyme production on CUE.

Nevertheless, how will soil microbial communities react to external variables is also influenced by the type of soil ecosystem. When soil microbial community from the different forests was compared with different climate zones, it was reported that SMP is significantly influenced by soil water content (Brockett et al. 2012). In contrast, it was shown that soil organic carbon one of the main factors affecting

soil microbial community function and structure under different types of vegetation (Grayston and Prescott 2005; Yao et al. 2006; Franklin and Mills 2009; Katsalirou et al. 2010). Other studies suggest that soil chemical properties, such as soil C/N ratio (Fierer et al. 2009), nutrient status (Lauber et al. 2008), and soil pH (Rousk et al. 2009), are highly correlated with soil microbial community composition and functioning. Some other studies suggest that composition soil microbial community in forest significantly influenced by the chemistry of plant litter (Ushio et al. 2008; Strickland and Rousk 2010) and spatial pattern of soil properties (Ushio et al. 2010) and these changes in the composition have a direct impact on the functioning of soil microbes.

Moreover, Tilman (1995) reported that biodiversity is regulating the SMP rates and if aboveground species diversity increase could lead to an increase in ecosystem stability. Klironomos et al. (2000) suggested that the presence/absence of arbuscular mycorrhizal fungi changed the relationship of plant biodiversity to aboveground productivity. Diversity and C cycling are significantly correlated to each other during a decrease in diversity, and when diversity increases, C cycling increased. Nevertheless, with high diversity, species-specific traits became more influential than numbers of species. Microbial community functioning can also alter soil chemistry directly via processes, which increase nutrient availability, such as P solubilization and N fixation, and/or alter SOM decomposition rates.

Morris and Blackwood (2015) suggested that availability of a diverse range of organic compounds to varied organisms with a wide range of enzymes could lead to functional redundancy of the microbial community. Experimental studies over the last years have challenged this assumption. Strickland et al. (2009) found differences in C mineralization rates on a community level, using diverse communities, proposing that each combination of microbial communities provided a unique set of metabolic physiologies resulting in different rates. These studies are also supported by metagenomic approaches evaluating metabolic gene diversity (Röling et al. 2010). Changes in the composition of soil microbial community are prone to result in changes of microbial functioning, thus altering SMP (Waldrop and Firestone 2006). For example, increased abundance of microbes producing hydrolytic enzymes that facilitate C acquirement will support the primary metabolism (Cusack et al. 2011), but rise in the production of oxidative enzymes, mainly by saprophytic fungi, will result in higher decomposition of complex compounds (Sylvia et al. 2004). An understanding of the interplay between the function and structure of the microbial community is necessary for estimating the effect of shifts in the structure of microbial community on changes in SMP (Weand et al. 2010). The ability to identify specific soil microbial features driving SOM transformations will expand our mechanistic understanding on how soil C sink and C sequestration work (Lucas et al. 2007; Acosta-Martınez et al. 2010). Soil bacterial community regulates SOM storage in soil by the increase in the C acquisition activity. In contrast, saprophytic fungi are active in SOM turnover because they produce enzymes involved in the oxidation of C compounds.

A wide variety of soil microorganisms are able to produce extracellular enzymes, and some of these enzymes indicate the presence of certain microbial groups (Baldrian 2009). For example, ligninolytic enzymes, such as lignin peroxidase and

Mn-peroxidase, are produced only by saprotrophic Basidiomycetous fungi (Hofrichter 2002; Baldrian 2008; Datta et al. 2017a). Enzymes involved in cellulose and lignin decomposition are the most widely assayed enzymes (Cusack et al. 2011). Other commonly assayed enzymes produced by a wide variety of microorganisms are those involved in the hydrolysis of proteins, chitin, and peptidoglycan, making organic N, S, and P accessible for microorganisms (Caldwell 2005). It was discovered that the relative abundance of particular arbuscular mycorrhizal fungi and Gram-negative bacteria was correlated with activities of hydrolytic enzymes involved in acquisition of C by microorganisms (cellobiohydrolase and β-glucosidase), whereas the relative higher abundance of the saprophytic fungi was associated with the specific activities of enzymes involved in lignin (phenol oxidase and peroxidase) and chitin (N-acetylglucosaminidase) degradation (Colpaert and Laere 1996; Courty et al. 2008, Miller et al. 1998; Burke et al. 2011). On the other hand, Gram-positive bacteria were positively associated with cellobiohydrolases that are involved in cellulose degradation (Waldrop et al. 2000; Bell et al. 2009). It was found that bacteria respond most quickly to additions of simple C compounds such as sugars, starch, and amino acids, while fungi and filamentous bacteria – actinomycetes – dominated when complex C compounds such as lignin and cellulose were added to the beech litter (Moller et al. 1999; Datta et al. 2017c).

Other factors related to the soil fertility, such as SOM content, NH_4, NO_3 and C to N ratio, were correlated with the structure of the soil microbial community. Bacteria are usually found SOM rich soils, while the richness of saprophytic fungi rises with degrade soil (Grayston et al. 2004; Grayston and Prescott 2005; Franklin and Mills 2009; Katsalirou et al. 2010; Wu et al. 2011). The C to N ratio in litter and soil was positively correlated with the occurrence of saprophytic fungi (Högberg et al. 2006; Fierer et al. 2009; You et al. 2014). Abundance of bacteria is high clay soil, while the abundance of saprophytic fungi decreased in clay-rich (Högberg et al. 2006; Lamarche et al. 2007; Fierer et al. 2009; You et al. 2014). Some recent studies suggested that the soil microbial community structure is significantly affected by soil pH (Högberg et al. 2006; Sinsabaugh et al. 2008). On the other hand, it was showed that composition of plant community is a better predictor of variations in microbial community composition than the soil properties, which is mostly due to dependence of litter quality and amount on the plant species, which in turn affects soil physico-chemical properties (Mitchell et al. 2010; Thoms et al. 2010).

4 Interplay Between Photosynthesis and Decomposition

The relative rates of C uptake via photosynthesis vs. C release in the process of autotrophic and heterotrophic respiration = decomposition represent the fluxes in the global C cycle in terrestrial ecosystems. The rates of SMP are significantly impacted by interactions among soil microorganisms and by their interactions with plants. For example, mycorrhizal symbiosis between fungus and plant increases photosynthetic rates, mainly under stress conditions such as water or nutrient restrictions.

Decomposition rates are influenced by competition for resources among decomposers, predation on decomposers, and changes in living conditions.

Decomposition and photosynthesis are key ecosystem processes; thus, individual plant species differentially impact the composition of the soil food webs (Bezemer et al. 2010; Rout and Callaway 2012; Wolfe et al. 2008; Shamina et al. 2018) as well as N turnover rates, which were influenced by plant diversity (Bezemer et al. 2010). Vice versa, the alterations of the microbial community can decrease the flow of nutrients to plants and thus decrease the flow of energy to the microbial community as well.

4.1 Effect of Seasonality on SMP

In terrestrial ecosystems, microbial communities are significantly influenced by dominant primary producers – plants. Plants provide not only novel niches for the microbial communities to thrive but most importantly C and N for microbial growth in the form of plant detritus used by saprotrophs, root exudates available for the symbionts, and root-associated microbial communities. Energy input into soil microbial communities highly rely on NPP. Thus the amount of microbial biomass that can be supported in soil depends on plant contributions through root exudates, leaf, or root litter. In temperate zone, photosynthesis associated with the rhizodeposition of easily decomposable C compounds into the soil, either directly or through the root-associated mycorrhizal fungi, is limited to the vegetation period of spring and summer (Ekblad and Högberg 2001). Approximately 30% of the NPP is allocated to roots and soil via root exudates (Beidler et al. 2014). The allocation of C into the soil via plant roots shows several-fold seasonal changes corresponding to the change in intensity of photosynthesis throughout the year (Högberg et al. 2010). Seasonality can be found in plant carbon balance that is positive in the summer due to higher photosynthesis than respiration but negative in winter due to respiration and low photosynthesis (Ryan 1991). Carbon in the form of root exudates derived from plant photosynthates is rapidly consumed by microorganisms, which highlights short-term dynamics in degradation by microbial soil communities (Bellemain et al. 2012). Ten to fifty percent of all assimilated C of plant origin is translocated into mycelia of ectomycorrhizal fungi. Thus they play a role in soil carbon storage, and carbon sink in the boreal forest is driven by these fungi (Orgiazzi et al. 2016).

Seasonality that is represented by changes in plant growth, temperature, and precipitation affects the structure and abundance of microbial community (Högberg et al. 2010; Kaiser et al. 2010; Voriskova et al. 2013). Such seasonal changes in the composition of microbial community and function were observed in the mixed temperate forest (Zhang et al. 2014) and in the Arctic ecosystem (Mundra et al. 2015). One of these changes was the dominance of saprotrophic fungi in spring that was correlated to spring fine root turnover (Satomura et al. 2006), and ectomycorrhizal ones in late summer, when the maximal growth of spruce fine roots occurred (Stober et al. 2000) in temperate (Jumpponen et al. 2010; Voriskova

et al. 2013; Wallander et al. 2001) and boreal forests (Davey et al. 2012; Santalahti et al. 2016). Fungal richness and diversity increased more than three times between spring and summer in *Quercus petraea* forest soil (Voriskova et al. 2013). The increase in fungal richness in the Arctic environment was found to correlate with the increase in soil temperature (Mundra et al. 2015), which was showed to be a growth-limiting factor for ectomycorrhizal fungi in these environments (Robinson 2001; Timling and Taylor 2012). Spring snowmelt was correlated to the decrease of fungal biomass and increase of Gram-positive bacteria and Actinobacteria biomass in the soil of Alpine tundra soil, while the Gram-negative bacteria were abundant in summer in the same environment (Bjork et al. 2008). In contrast to the fungal community, bacterial community structure in the soil was responsive to a summer peak of rhizodeposition in a temperate oak forest (Lopez-Mondejar et al. 2015). Seasonal shifts of the relative abundances of individual bacterial groups were found in the alpine soils (Lipson 2007; Kuffner et al. 2012) and were connected to C fluctuations in plant roots. A metaproteomic study in coniferous and deciduous forest showed that the fungi to bacteria ratio have increased in spring compared to winter (Schneider et al. 2012). It was also found that fungi produced more than half the transcribed enzymes involved in SOM degradation, especially in summer in the temperate coniferous forest (Zifcakova et al. 2015, 2017). Enzymes involved in breakdown of complex polysaccharides (endocellulases and endoxylanases) and those decomposing fungal cell wall (N-acetylglucosaminidases) were more active in summer, while cellobiohydrolases involved in cellulose degradation were active in spring (Baldrian et al. 2013). Results of Zifcakova et al. (2017) showed increase in the transcription of enzymes that involved fungal biomass turnover in summer, whereas expression of other compounds such as starch or trehalose is increased during the winter season. Seasonality has a significant influence on gene in soil compared to litter and transcription of the ligninolytic, and cellulolytic enzyme increased during the summer than the winter. Winter communities of microorganisms produced more cellulases and amylases and thus were able to decompose complex carbon substrates, as indicated by decreased mineralization of SOM, while summer communities were able to utilize glucose more effectively since there was the higher availability of dissolved organic carbon in summer than in winter (Koranda et al. 2013). In temperate forest, seasonal differences in the enzyme pools with maxima in summer were found for N-mineralization and denitrification enzymes, but the pool of β-glucosidases enzymes present in most microorganisms did not show any regular seasonal pattern (Rastin et al. 1988; Bohlen et al. 2001) but their transcription varied between summer and winter season (Pathan et al. 2017). Activities of phenol oxidases and peroxidases were highest in late summer, while activities of cellulases and proteases peaked in winter in beech forest soil (Kaiser et al. 2010). The structure of the fungal community of cellulases producers was different in the summer and winter, and it was also suggested that lignin breakdown starts later in summer with the increase of Basidiomycota in metaproteomic data (Schneider et al. 2012). At least in the tundra, the main factor influencing seasonal differences in enzyme activities was temperature (Wallenstein et al. 2009). The total annual enzyme activity in the boreal coniferous forest was 7–32% in winter while 68–93% in summer (Wittmann et al. 2004). Overall, there are evidences not only for

the seasonal change in enzyme activities but also for seasonal shifts in abundance of saprotrophic and mycorrhizal fungi also shifts in the bacterial community composition.

4.2 Temperature Dependence of SMP

Correlation of SMP and temperature is complex because individual microbes vary in their optimal temperature, and thus diverse soil microbes may be active at various temperatures. At the top of it, divergent microorganisms have distinctive abilities to adapt to the temperature by changing their physiology, such as membrane fluidity and permeability and structural flexibility of proteins, including enzymes. Due to temperature dependence of enzymatic reactions and biological processes, temperature is one of the key factors affecting SMP. Rise in the temperature by 10 °C will increase the activity of most enzymes by 50 to 100% (Martinek 1969).

The relative temperature sensitivity of microbial activity can be indicated as a Q10 function that is essentially the change in activity proportional to change of temperature about 10 °C and is used to explain the temperature sensitivity of SMP, such as respiration of soil microorganisms. It is generally accepted that microbial activity at 30 °C is twice as high as at 20 °C and activity of soil microbes is usually greatest within 20–40 °C. The metabolic activity of the most microbes decreases drastically around 5 °C referred to as biological zero.

Though activity of microbes is lower at lower temperatures, SMP rates are much higher and more sensitive to temperature changes than predicted from mesophilic temperature range studies. For example, values of Q10 for decomposition of SOM, soil respiration, and N mineralization were quite high, near 8–10, when soil temperature was around 0 °C (Kirschbaum 2013). Microbial activity in SMP during cold periods with dormant plants and barren soil plays a crucial role in the winter losses of soil nutrients, such as N leaching and denitrification, especially during freeze/thaw cycles.

Due to the influence of temperature and moisture on microbes, it is clear that SMP will be modified with climate change; however, it is not yet certain which processes will decrease or increase. It is certain that alterations of nutrient's mineralization rates that are needed by plants and microbes will change ecosystem productivity. Whether the rates of SMP increase or decrease can depend on the changes in temperature and moisture and their impacts on microbial efficiencies but also on the selection of microbial species under the new conditions.

Net flux of CO_2 to the atmosphere is thought to rise over time under most models because microbial decomposition of SOM shall increase with higher temperature and moisture, predominantly in Arctic ecosystems. In the last 100 years, Earth global temperature is increased by 0.5 °C and will be increased by 1 °C–6 °C by 2100, predicted by different model studies. Even though it is only a few degrees' increases, global warming will intensely increase microbial decay rates of the SOM stored in the boreal forests and tundra regions, which contain 30% of the global soil C (Kirschbaum 1995).

Currently, there are studies available that are dealing with the relative contributions of soil microbes to C flux, C-use efficiency, the effect of elevated level of CO_2, and climate change on these fluxes. The main concern is that SOM decomposition is much more accelerated than in NPP representing the C input to SOM. Theory also implies that the decomposition of recalcitrant SOM compounds, such as cellulose and hemicellulose that are usually a rate-limiting step in CO_2 emissions, would become essentially easier at higher temperatures (Davidson and Janssens 2006). More CO_2 atmosphere can positively affect NPP via C fertilization and increased water use efficiency. In addition to losses in soil C, it is anticipated that rising CO_2 will increase emissions of CH_4 and N_2O formed by increased root growth and lowered soil water losses (van Groenigen et al. 2011).

Though, feedback mechanisms that are representative for all biogeochemical fluxes may inhibit the impacts of temperature changes. Soils are complex ecosystems affected by factors, such as change in soil water storage, nutrient cycling, and rainfall patterns that will have an impact on mostly on NPP.

Many of the environmental factors have an influence on decomposition by changing effective SOM (substrate) concentrations at the site of enzymatic reaction, where decomposition occurs. Thus one of the factors to consider in SOM decomposition rates are enzyme affinity levels. Other external factors that are considered in models of the effects of global warming on C cycling are kinetic and thermodynamic properties of extracellular enzymes.

Temperature indeed affects the kinetics of enzymatic reactions but also changes microbial community composition. 5 °C increase in temperate forest soil influences relative abundance of the bacterial community which leads to high bacterial to fungal ration (DeAngelis et al. 2015). Microbial communities react to global warming, and other ecosystem disturbances through resistance, which is facilitated by the plasticity of microbial traits, or via resilience as the community returns back to its initial compositions of species after the stress is gone (Allison and Martiny 2008). Changes in the composition of soil microbial communities are thought to mediate changes in SMP, assuming that a special group of soil microorganisms is different in their functional traits or control a rate-limiting step of SMP (Schimel and Schaeffer 2012). For example, specific microbial groups govern ecosystem functions such as methanogenesis (Bodelier et al. 2000), denitrification (Bakken et al. 2012; Salles et al. 2012), N fixation, and nitrification (Isobe et al. 2011). Changes in the richness of one group of microorganisms that regulating specific processes can have a straightforward impact or influence on the process rate, conversely, some processes occurring at a cruder scale, for example, N mineralization, are more correlated with abiotic factors (temperature and moisture) than composition of microbial community as wide variety of microorganisms is involved in these processes (Hooper et al. 2005).

4.3 Nitrification and Denitrification Models of SMP

Soil macronutrient cycles are strongly connected via microbes' nutrient demands at the time of decomposition, so few of the multicompartmental models of SOM decomposition focusing on C cycle are also able to predict the fluxes of other macronutrients such as N, P, and S. Flows within the N cycle are mainly driven by N fixation (capture of atmospheric N_2 to forms usable for the microbes), mineralization (represented by nitrification and ammonification) of organic N from plant and animal necromass and biomass, and gaseous loses via denitrification and ammonia volatilization. The microbes drive important processes in N cycle, so mutualistic relationships between plants and soil microorganisms, such as *Frankia* (phylum *Actinobacteria*) and *Rhizobium* (class *Alphaproteobacteria*), are very important. In soil systems, where organic N is not yet available, microbial N fixation delivers the initial N source allowing plants to grow. With the increase in plant production, the most N in the ecosystem will originate from the decomposition of plant litter by microorganisms. Such accessible N can either be assimilated by plants or by soil microorganisms via immobilization process when N becomes part of microbial rather than plant cells.

The DNDC (DeNitrification-DeComposition) model simulates plant growth and soil processes (Li et al. 1992) and has few submodules. The nitrification submodule simulates the nitrification rate, the turnover rates of nitrifiers, as well as N_2O and NO productions and is controlled by temperature, moisture, ammonium, and DOC (dissolved organic carbon) concentrations. Denitrification submodule is influenced by soil temperature, moisture, and substrates (DOC, NO^-_3, NO^-_2, NO, and N_2O) concentrations and can predict changes in denitrification process, as well as changes in the size of the population of denitrifiers. The fluxes of N_2O and NO^- induced by denitrification are calculated dynamically from soil aeration status, gas diffusion, and substrate limitation. As a source of NO^-production in soils, chemo-denitrification is often considered, and it is dependent on soil pH and nitrite availability. Nitrification occurs mainly in the aerobic fraction of soil, while denitrification is preferred in the anaerobic environment. Denitrification rates can be expressed by Nernst (redox potential) and Michaelis-Menten (enzyme kinetics) equations. When the anaerobic conditions in soil are common and favorable, few processes can happen: (1) more substrates (DOC, NO^-_3, NO^-_2, NO, or N_2O) will be allocated to the N pool, (2) rates of sequential denitrification reactions will increase, and (3) the intermediate product gases (N_2O, NO, etc.) will take longer to diffuse from the anaerobic to the aerobic fraction, increasing the rate of N gases being reduced to N_2. The overall effect will be the loss of N from the soil. If N is limiting nutrient in the soil, the microbes will "win" the competition for N between plants and

microbes, which will limit the amount of N available for plants and thus decrease NPP and litter quality (van der Heijden et al. 2008). The most of nitrogen found naturally in soil was a product of either N fixation by free-living or symbiotic microbes or of microbial decomposition of organic materials. This does not apply nowadays because anthropogenically generated N is entering soil ecosystems via fertilization and pollutant dispersal and this has resulted in two times increase in the amount of N available for plants. Such nitrogen additions boost soil respiration, reduce microbial biomass, and change enzyme activity in many studied soils, implying significant effect of these N supplements on the soil microbe functions (Ramirez et al. 2012).

4.4 Importance of Soil Water Content in SMP

Another factor influencing not only N and C cycles but all SMP is the soil water content. Soil water influences not only the moisture available to microorganisms and osmotic pressure but also soil aeration status, the solubility of organic materials, and the pH as a function of the soil solution. Physically, water is a transportation agent by mass flow but also a solvent, where enzymatic and chemical reactions happen. Water retention in soil is facilitated by water adsorbing via hydrogen bonding and dipole interactions to soil particles, and thus it is a function of the size of pores in the soil. In soils, where water content is non-limiting, biological activity depends mainly on the temperature, which can be predicted by standard Arrhenius theory. However, when soils dry out, moisture becomes a greater determining factor of SMP than temperature. It is likely that moisture and temperature do not impact the microbial activity in a linear manner, but in complex, nonlinear fashion that reflects the responses of individual microorganisms and their enzyme activities.

Even though the many microbes are capable of tolerating soil stress by accumulation of amino acids and polyols (osmolytes) or altering their outer membrane, soil microbes are significantly affected by rapid dry-wetting cycles and undergo osmotic shocks and induce cell lysis. Following such catastrophic event, there is often a peak in the activity of surviving microbes, called the Birch effect, which is caused by mineralization of the released content of microbial cells.

Further, the lack of soil moisture amplifies the differences in temperature sensitivity of bacterial and fungal community (Briones et al. 2014). Another difference between fungi and bacteria toward the effect of moisture is that bacterial communities respond rapidly to moisture pulses, while the slower-growing fungal community delays in their feedback (Bell et al. 2008; Cregger et al. 2012; Cregger et al. 2014). On the other hand, fungal communities may shift in dominant representatives even with small changes in soil moisture availability (<30% reduction in water holding capacity), while the representatives of bacterial communities do not change. These observations indicate a higher plasticity of fungal community during wet-dry cycles

(Kaisermann et al. 2015), but soil communities that are adapted to wet-dry cycles or to low water availability will show less functional and compositional changes (Evans et al. 2011). The soil moisture plays a crucial role in S and N cycles as well. For example, sulfur (*Thiobacillus* sp.) and ammonium oxidizers (*Nitrosomonas* sp.) are less tolerant of water stress than are the ammonifiers (*Clostridium* sp., *Penicillium* sp.). Ammonium can pile up in dry soils at the water potentials when ammonification is still possible, but nitrification is restricted, which results in decreased soil pH affecting SMP but also changing the microbial community composition.

4.5 Soil pH as One of the Factors Influencing SMP

A measuring of pH of soil solutions presents a necessary approach allowing to predict of reactions of microbes involved in SMP and enzyme activity in soil. Although pH is easily measured in soil solution, it could be difficult to interpret due to concentrations of cations that are sorbed to the negatively charged soil surfaces and are 10–100 times higher than ones of the soil solution. It has implication for enzyme activity measurements in soil because enzyme sorbed to colloid surfaces in soil have 1–2 pH units' lower optimum as the same and not sorbed enzyme (Marfo et al. 2015 Lojkova et al. 2015).

Although certain microbes can alter pH by acidifying soil in their vicinity to the disadvantage of competitors, the most diverse composition of soil bacterial populations is found near-neutral pH. Acidity, on the other hand, enhances the activity of soil fungi, and it explains why fungi dominate in forested soils, which are acidic, while bacteria usually prevail in rangeland soils and in mildly acidic subhumid to semiarid prairie. Fungi can tolerate low pH and are able to decompose recalcitrant compounds, unlike bacteria, which are thought to be limited by low pH and less enzymatic equipment and have higher requirements for some nutrients and lower tolerance of environmental changes (Allison and Martiny 2008). A pH was found to be the most important factor in determining bacterial community composition (Högberg et al. 2006), and thus *Acidobacteria* and *Alphaproteobacteria* are highly abundant in acidic soils (Bryant et al. 2008; Jones et al. 2009; Baldrian et al. 2011; Shen et al. 2013), but on the other hand, the amount of *Bacteroidetes* and *Actinobacteria* increase with more basic pH (Lauber et al. 2008; Lauber et al. 2009; Jeanbille et al. 2015). In addition, the abundance of *Acidobacteria* in soil is negatively correlated with the dissolved organic carbon availability, which indicates they are slow-growing oligotrophs and are most probably adapted to nutrient limitation (Naether et al. 2012; Garcia-Fraile et al. 2015). *Acidobacteria* were suggested to be very adaptable to environmental modifications due to the high metabolic versatility that allows them to use even highly complex C substrates originated from SOM (Rasche et al. 2010; Naether et al. 2012).

5 Conclusions

Overall, the research suggests the existence of complex interactions between the abiotic and biotic factors that affect the functioning of soil microbial communities in SOM transformations via changes in the allocation of plant-derived C to microbial communities and through modifications of the fungal and bacterial community structure activities.

Particularly, it was found that both soil water and temperature are important drivers of changes in soil microbial community structure (Hackl et al. 2005; Djukic et al. 2010; Brockett et al. 2012). The presence of soil water was positively correlated with the abundance of Gram-negative bacteria, while soil temperature was positively linked with the abundance of saprophytic fungi but negatively with the bacterial community abundance (You et al. 2014). Structure of the soil microbial community was also profoundly affected by SOM, fine root mass, clay content, and C/N ratio. In addition, the relative abundance of Gram-negative bacteria, saprophytic fungi, and actinomycetes was enough to explain most of the variations in the soil enzymes activities involved in SOM transformations (You et al. 2014). The abundance of fungi was found to be associated with activity of enzymes involved in C oxidations, while the abundance of bacteria was linked to activity of extracellular enzymes participating in C transformation (You et al. 2014; Zifcakova et al. 2017). Research findings demonstrate the existence of complex interplay among soil physiochemical properties, soil microenvironment, and plant traits in the decomposition of SOM via regulations in microbial communities. Moreover, external factors that affect the structure of soil microbial communities have also direct/indirect impact on their functioning in soil microbial processes.

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