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REVIEW

Forest Soil Bacteria: Diversity, Involvement in Ecosystem Processes, and Response to Global Change

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SUMMARY The ecology of forest soils is an important field of research due to the role of forests as carbon sinks. Consequently, a significant amount of information has been accumulated concerning their ecology, especially for temperate and boreal forests. Although most studies have focused on fungi, forest soil bacteria also play important roles in this environment. In forest soils, bacteria inhabit multiple habitats with specific properties, including bulk soil, rhizosphere, litter, and deadwood habitats, where their communities are shaped by nutrient availability and biotic interactions. Bacteria contribute to a range of essential soil processes involved in the cycling of carbon, nitrogen, and phosphorus. They take part in the decomposition of dead plant biomass and are highly important for the decomposition of dead fungal mycelia. In rhizospheres of forest trees, bacteria interact with plant roots and mycorrhizal fungi as commensalists or mycorrhiza helpers. Bacteria also mediate multiple critical steps in the nitrogen cycle, including N fixation. Bacterial communities in forest soils respond to the effects of global change, such as climate warming, increased levels of carbon dioxide, or anthropogenic nitrogen deposition. This response, however, often reflects the specificities of each studied forest ecosystem, and it is still impossible to fully incorporate bacteria into predictive models. The understanding of bacterial ecology in forest soils has advanced dramatically in recent years, but it is still incomplete. The exact extent of the contribution of bacteria to forest ecosystem processes will be recognized only in the future, when the activities of all soil community members are studied simultaneously.

KEYWORDS bacteria, decomposition, ecosystem processes, forest ecology, global change, litter, nutrient cycling, soil

INTRODUCTION

Forests represent one of the largest and most important ecosystems on Earth, covering more than 40 million km^2 and representing 30% of the total global land area (1). Forest ecosystems are found in most of Earth's biomes and harbor a large proportion of the global diversity. For example, temperate and boreal forests occupy most of the land surface of the Northern Hemisphere and contain 46% of all trees on Earth—0.66 and 0.74 trillion, respectively (2). Due to their global extension, the processes occurring in these two biomes are of global importance, and an understanding of the composition and function of their microbiomes is thus essential (Fig. 1).

Forests typically represent important carbon (C) sinks with large amounts of recalcitrant organic matter in their soils, especially the temperate forest soils, which receive tons of litter per hectare yearly (3). The presence of large trees distinguishes forests from grasslands, wetlands, and agricultural areas in multiple ways (4). Trees represent a multitude of habitats, such as the phyllosphere or rhizosphere, but they also substantially affect the remaining parts of the ecosystem. This is mainly because, as the dominant primary producers, they supply the bulk of the C that enters the ecosystem, and while some of this C is in the form of simple organic molecules, a significant fraction, such as the complex biomass of wood, litter, or roots, is composed of recalcitrant biopolymers (4). Trees also largely contribute to the spatial heterogeneity of forest ecosystems by multiple means, including the penetration of soils by various guilds of roots, generation of patches of litter and ground vegetation, and changes of the morphology of the terrain during uprooting or the production of deadwood (4, 5).

Temperate forests extend approximately from latitudes 25°N to 50°N, gradually changing into boreal forests further north (6). The southern limit of boreal forests is understood as the latitude at which conifers are competitively excluded by temperate tree species with higher rates of photosynthesis. There is, however, no distinct boundary between the two biomes but rather a broad transition zone that includes a mix of coniferous and deciduous tree species (7). Temperate forests are characterized by temperature ranges between −30 and 30°C, with hot summers and cold winters and with 750 to 1,300 mm of precipitation per year. Boreal forests—or mountainous forests in the temperate zone—face lower temperatures, with cold winters lasting more than 6 months and average summer temperatures of around 10°C. Despite the lower precipitation levels (300 to 900 mm of rain per year), boreal forests are typically moist because of the reduced evaporation at low temperatures. In addition, other factors, such as elevation, substrate, drainage, physical soil properties, and nutrient availability, are also responsible for the distribution of forest types on landscape scales.

Temperate forests are composed of a large variety of deciduous trees, while coniferous trees dominate temperate forests at higher altitudes but also occur frequently in plantation forests (8, 9). Boreal forests exhibit a reduced tree diversity with a larger proportion of coniferous trees (10).

Although temperate and boreal forests fulfill several important ecosystem services, their role as large C sinks has gained specific interest in recent decades, especially in the context of global change. Recent approximations indicate that the current C stock stored in forests worldwide is approximately 861 Pg, of which 44% is in soil, 42% in above- and belowground biomass, 8% in deadwood, and 5% in litter (11). Of the global stock of C stored by forests, boreal forests contain 32% and temperate forests another 14%, indicating that their importance for global C sequestration is equivalent to that of tropical forests (11). The large amount of stored C has the potential to influence the feedback between the climate and the global C cycle (12). In this sense, global change, including both climate change and other changes linked to human activities, has been recognized as a major threat to forests (13). Over the millennia, human overexploitation has been the most important risk for forests, and the C balance of forests is largely affected by human activities, including deforestation, the management of production forest, reforestation, afforestation, and others (11, 14). Other disturbances that are associated with climate change and atmospheric drivers are also affecting the C

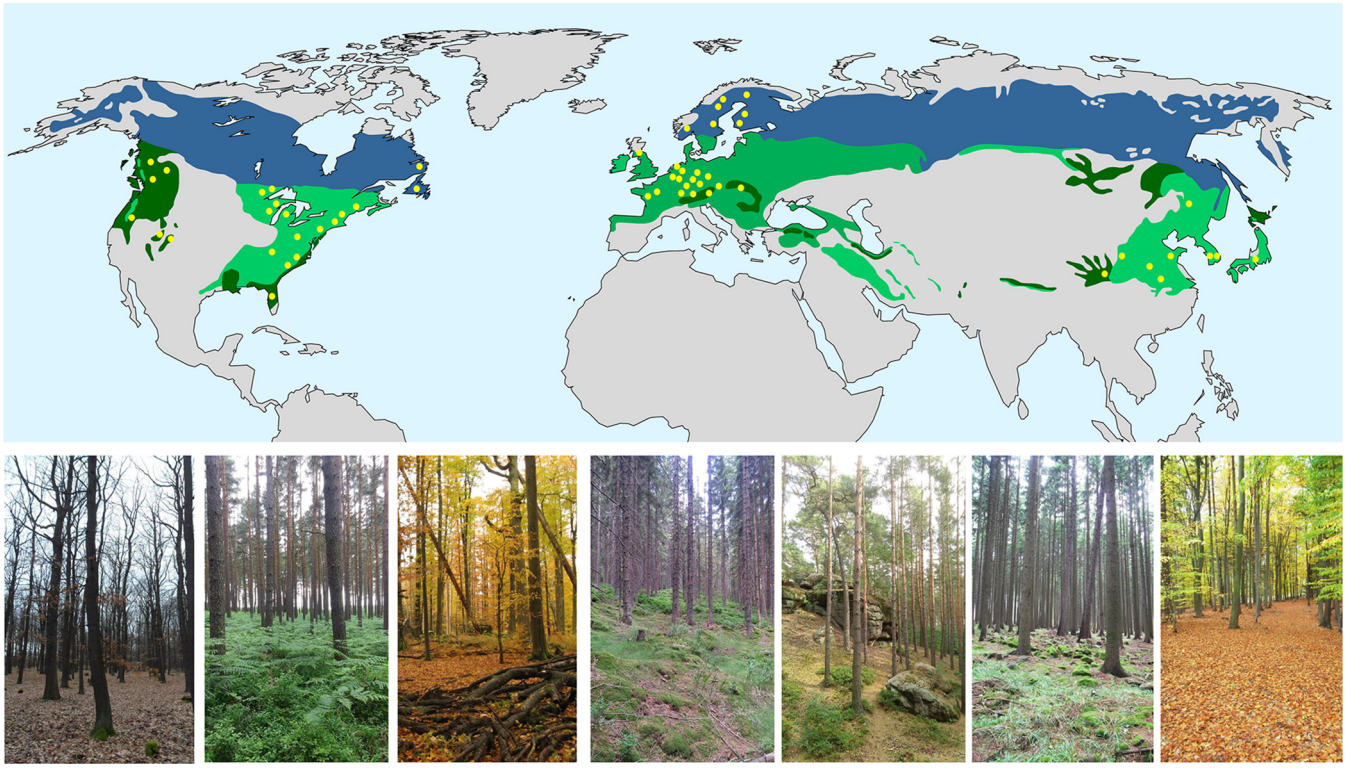

FIG 1 Distribution of temperate and boreal forests in the Northern Hemisphere. Natural areas of deciduous and mixed temperate forest (light green) and evergreen coniferous forest (dark green) are shown in green, and natural areas occupied by boreal forests are shown in blue. The regions in which microbial communities inhabiting soil have been studied are shown as dots. The bottom images show forest ecosystems dominated by *Quercus*, *Pinus*, *Fagus*, and *Picea* trees.

balance of forests. In this sense, the effects of increasing temperature, persistence of droughts, recurrence of fires, or expansion of native and invasive forest pests together with the increasing loads of nitrogen (N) and carbon dioxide affect forest nutrient cycles to a level where forests may potentially become net sources rather than sinks of CO_2 (12, 13, 15). Therefore, a better understanding of the role of forests in C fluxes that are largely dependent on the activity of bacteria and fungi has been highlighted as an essential prerequisite for projecting future predictions of the health of our planet (16).

While plants are the key drivers of C uptake from the atmosphere in forests, forest microorganisms contribute greatly to the C balance in these ecosystems. They play an important role as decomposers, symbionts, or pathogens, influencing the C turnover and retention and the availability of other nutrients (17–19). Microbial communities are vital in mediating the biogeochemical cycles, and an understanding of their role in ecosystem processes is essential for the prediction of the forest response to future environmental conditions (8, 17, 20).

Fungi are the most well-studied microbes in temperate and boreal forest soils that harbor abundant and diverse communities of saprotrophic and mycorrhizal fungal taxa (12, 21, 22). Fungi are considered the main decomposers in forest soils because of their ability to produce a wide range of extracellular enzymes that allow them to efficiently degrade the recalcitrant fraction of dead plant biomass (23–25). Moreover, mycorrhizal fungi play a pivotal role in the mobilization and sequestration of N and P in the forest soil and are also responsible for significant soil transport of C (26–29). It is not surprising that most of the research on forest soil ecology so far has focused on fungi (18, 19). This traditional emphasis on fungi, however, is slowly shifting with an increasing appreciation of the role of bacteria as the other major component of forest ecosystems (19).

Bacteria represent another important, though less explored, integral part of the microbial community in forest soils. For example, recent findings indicate that bacteria commonly harbor genes encoding plant cell wall-degrading enzymes (30) and contrib-

ute significantly to the decomposition of organic matter (31–35). In addition, bacteria are the major natural agents responsible for N fixation in forest ecosystems (36) and for other ecosystem processes, such as mineral weathering leading to the release of inorganic nutrients (37). The roles of bacteria and fungi, however, should not be viewed as separate. The high abundance of fungal biomass in forest soils has multiple consequences for bacteria, including the creation of specific niches in the soil patches colonized by mycorrhizal fungi (i.e., the mycorrhizosphere) and soil mycelial mats (38, 39), provision of nutrients via organic matter decomposition (40), and an increase in soil connectivity by fungal mycelia that allow certain bacteria to move across the environment (41). Conversely, the functioning of mycorrhiza is modulated by mycorrhiza helper bacteria (MHB) (42).

It is only recently that advances in analytical methods have allowed us to assess the role of bacteria in the complex forest ecosystem and to address the important questions that previously remained unanswered, such as the following. Which habitats do bacteria inhabit, and what are the major drivers of their abundance and diversity? What is their role in nutrient cycling and the C balance? How do they interact with other forest organisms? How do they respond to climate change, and how does this response affect ecosystem processes? The aim of this review is to answer these questions for temperate and boreal forests to summarize the present knowledge about the role of bacteria in ecosystem processes and about their response to global change, as well as to motivate further research in the bacterial ecology of forests.

BACTERIAL COMMUNITIES IN FOREST ECOSYSTEMS

Forest ecosystems provide a broad range of habitats for bacteria, including soil and plant tissues and surfaces, streams, and rocks, among others, but bacteria seem to be especially abundant on the forest floor, in soil and litter (4). Five phyla, *Acidobacteria*, *Actinobacteria*, *Proteobacteria*, *Bacteroidetes*, and *Firmicutes*, appear to be abundant in most soils (43). In addition to pH, which seems to be the most important driver of the bacterial community composition in soils, organic matter content, nutrient availability, climate conditions, and biotic interactions (especially the effect of vegetation) affect the composition of bacterial communities (43–47). The spatial variation of these parameters is responsible for the presence of hot spots of microbial activity with increased abundance and activity in the soil, such as in and on plant debris, including litter and deadwood, or on and around plant roots (48–50). Each of these niches has specific properties and, consequently, a specific bacterial community (Fig. 2).

Bacterial Communities on Plant Litter and Deadwood

Due to the activity of primary producers, dead plant biomass—litter and deadwood—represents the most important C sources for forest soil microbes. The estimated 10^{11} tons of fallen leaf litter that accumulates yearly on the forest floor surface and its transformation are of great importance for the cycling of C and other nutrients (51–53). The litter habitat is dominated by a diverse community of fungi that have traditionally been considered to be key players in litter decomposition. In addition to fungi, recent studies have demonstrated an active role of bacteria in litter transformation. In the litter of coniferous forests, bacteria incorporated relatively more cellulose-derived C than that incorporated by fungi (31). Cellulose-C was accumulated mainly by *Betaproteobacteria*, *Bacteroidetes*, and *Acidobacteria*. Similar results were found in different pine forest soils in North America, where members of the *Proteobacteria* (*Burkholderiales*, *Caulobacteriales*, *Rhizobiales*, and *Xanthomonadales*), *Bacteroidetes* (*Sphingobacteriales*), and subdivision 1 *Acidobacteria* accumulated the most cellulose-derived C (32). Recently, studies of deciduous forests reported that at least 10% of litter bacteria are able to decompose cellulose. Many of these bacteria belong to the *Proteobacteria*, *Actinobacteria*, *Bacteroidetes*, and *Acidobacteria*, but members of other phyla are also active (33, 54). Considering the frequency of cellulolytic genes in bacterial genomes (30), bacterial involvement in decomposition seems to be a relatively common trait.

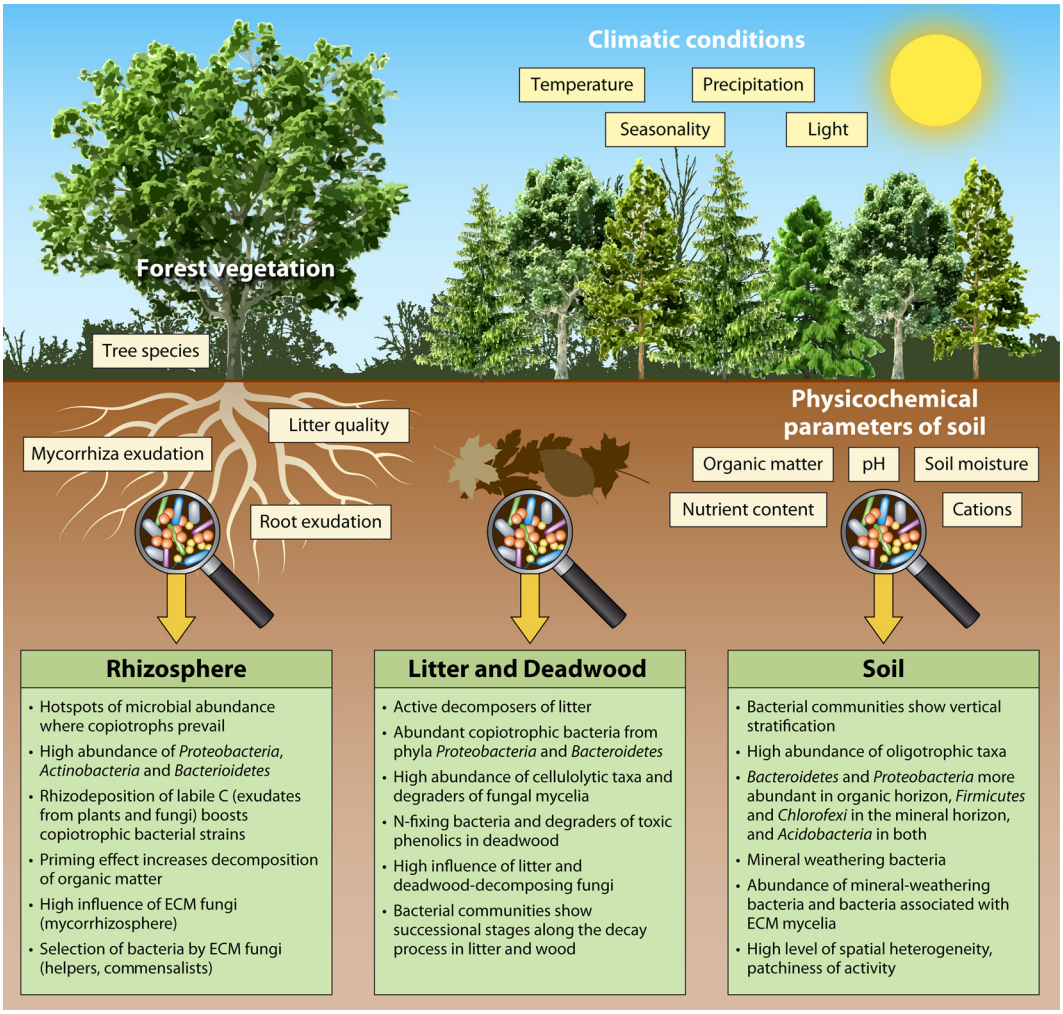

FIG 2 Drivers of bacterial community composition in forest soils and features of bacterial ecology in the rhizosphere, litter/deadwood, and soil compartments of the forest floor.

While the acidic soils of coniferous forests harbor mainly *Proteobacteria*, *Acidobacteria*, and *Actinobacteria* (8, 55), in temperate deciduous forests, litter bacterial communities seem to be especially enriched with *Proteobacteria* and *Bacteroidetes* (45, 56, 57). Indeed, significant differences in the chemical structure of litter and root exudates among tree species influence soil bacterial communities through changes in substrate chemistry (45, 58, 59). Litter quality, which includes the quantity of nutrients, tissue structure, and the C/N ratio, varies between tree species and results in varying litter decomposability (60–62). Higher litter quality is typically associated with faster litter turnover and the liberation of exchangeable basic cations, such as Ca^{2+} and Mg^{2+}, helping to maintain low levels of soil acidification (63–65). When trees typical of temperate and boreal forests were ranked in order of increasing acidification ability of their litter, conifers appeared to be the most acidifying, followed by beech, oak, and birch. Maple, hornbeam, ash, and lime comprised the group with the least acidifying forest trees (59). These effects of litter quality on soil nutrient status and pH indirectly drive the bacterial community composition of forest soils and its activity (66–68).

The production of litter is not constant throughout the year; it is limited to a short autumnal period in deciduous forests. These and other aspects of seasonality in the temperate and boreal zones have been identified as key factors affecting the C input into the soil environment and its decomposition by soil bacteria. Cold and dark winters and warm summers with longer photoperiods affect the development and production

of foliage and, consequently, microbial community structure and activity in the litter and soil as well as in the foliage (69). Temperature differences affect decomposition rates by accelerating or decelerating enzymatic processes (55, 70). On a shorter time scale, selected weather events, such as precipitation or snowmelt, contribute to the mobilization of nutrients that are washed into the forest soil, and they represent periods of high microbial activity, especially of fast-growing r-strategists (50).

During decomposition, the chemical composition of litter changes with the gradual removal of cellulose, hemicellulose, and lignin (58, 71). In contrast to fungi, bacteria inhabiting the phyllosphere of living leaves do not seem to be largely involved in litter decomposition and are quickly replaced by other taxa (72). *Proteobacteria* and *Bacteroidetes* are considered to be copiotrophs that preferentially consume the labile pool of organic C (73) and are thus typical for freshly fallen litter. The fresh litter is also characterized by the quantitative dominance of fungi. The biomass of bacteria increases gradually during decomposition (58, 74), as does their diversity (57, 72). During decomposition, the abundance of mycophagous bacteria coincides with the peak of fungal biomass in the fresh litter. In this stage of decomposition, potentially mycolytic bacteria in *Quercus* litter represent as much as 40% of the total community (72), highlighting the importance of the fungal biomass as a nutrient source. Bacterial taxa that associate with decomposing fungal mycelia represent a distinct subset of the bacterial community, including members of the genera *Pedobacter* and *Chitinophaga* (*Bacteroidetes*) and *Pseudomonas*, *Variovorax*, *Ewingella*, and *Stenotrophomonas* (*Proteobacteria*) (75). With ongoing litter decomposition, the share of cellulolytic bacteria gradually increases (72).

Importantly, a large proportion of plant inputs into forest soils are derived from organs other than leaves, including fine roots, seeds, and twigs (76). While it has been shown that this type of litter represents an important source of soil organic matter (SOM) C (52, 77), bacterial communities associated with this substrate remain unexplored.

In addition to litter, coarse deadwood is also an important structural component of forest ecosystems, especially in unmanaged forests. Wood debris represents a rich yet recalcitrant source of organic matter, mainly due to its physical impermeability and high lignin content. These characteristics benefit filamentous, macroscopic fungi (78), which are consequently the dominant decomposers of deadwood. However, bacteria are also important inhabitants of decaying wood, especially during the initial phases of decay (79, 80). The physicochemical properties of wood that are tree specific, such as the density, pH, and water and N content, determine the composition of bacterial communities (80, 81). *Proteobacteria*, *Acidobacteria*, *Actinobacteria*, and *Firmicutes* belong to the most abundant phyla (79, 80, 82). Because fungal decomposition changes the properties of wood substantially via the removal of easily available C, acidification, and the production of fungal mycelia, bacteria that can thrive at an acidic pH and utilize C from fungal mycelia are positively selected (80, 83, 84). As observed for litter decomposition, the bacterial community in deadwood shows successional development with wood decay. The assembly of the bacterial community appears to be a stochastic process during the initial stage of wood decay, and the bacterial abundance in fresh wood is very low, with $<0.2 \times 10^9$ 16S rRNA copies g^{-1}. During decomposition, the bacterial abundance increases, reaching levels as high as 3×10^9 to 13×10^9 16S rRNA copies g^{-1} in highly decayed *Picea abies* wood, with a density of 0.15 g cm^{-3} (80). While the involvement of wood-associated bacteria in wood biopolymer decomposition versus the use of substrates liberated by fungal decay remains largely unexplored, recent studies support a role for bacteria in other important processes, including the degradation of toxic wood compounds and N fixation. Genera such as *Burkholderia*, *Phenylobacterium*, and *Methylovirgula*, which are abundant in the middle and late stages of wood decomposition, are known to degrade aromatic compounds and to use methanol as a sole carbon source (79, 82). Moreover, the N-fixation ability of bacteria that are abundant during the late stages of wood decomposition (such as the members of the *Rhizobiales*, which may account for 25% of all bacteria in this phase) offers the possibility of mutualistic interactions with fungi that provide C via wood decomposition

(82). Despite these initial studies, little is still known about the community dynamics of wood-inhabiting bacteria or their interactions with wood-decaying fungi (81). Considering that multiple bacteria are able to utilize cellulose and other recalcitrant plant polymers and that the fungal biomass is highly abundant in deadwood, the involvement of bacteria in the decomposition of lignocellulose and fungal mycelia appears to be highly probable.

Bacteria in Forest Soils

Forest soils are among the most diverse microbial habitats on Earth, in which bacteria are the most abundant group of microorganisms (4, 85). Forest soils are characterized by a sharp vertical stratification resulting from the decomposition of litter-derived organic matter and the weathering of the mineral matrix. The decreasing content and quality of organic matter with soil depth are accompanied by decreases in microbial biomass, respiration, and activity of extracellular enzymes. For example, in a *Quercus petraea* forest soil, organic matter decreased 10-fold, bacterial biomass 8-fold, and enzyme activity 5-fold to 20-fold across the top 5 cm of the soil profile (86). The temperate forest soil profile typically comprises the organic horizon, representing a mixture of processed, plant-derived organic matter and soil components, and the mineral soil horizon, with a lower content of organic matter, originating from both the decomposition of organic matter and exudation from abundant tree roots. The bacterial communities are horizon specific, although they display a high level of taxon overlap (56). For example, the organic and mineral horizons in a temperate *Quercus* forest are dominated by *Acidobacteria* (accounting for 40 to 50% of all sequences), together with members of the *Actinobacteria*, *Proteobacteria*, and *Bacteroidetes* (56). Bacterial communities in coniferous forest soils also differ among horizons. Although *Acidobacteria*, *Proteobacteria*, and *Actinobacteria* are most abundant in organic as well as mineral horizons, the organic horizon is richer in *Proteobacteria* and *Bacteroidetes* (8, 87), which have been proposed to preferentially utilize easily accessible carbon substrates (73, 88). In contrast, communities in the mineral soil harbor a larger proportion of *Firmicutes* and *Chlorofexi* organisms that are more adapted to the use of recalcitrant carbon substrates and inorganic nutrients.

The high abundance of *Acidobacteria*, *Actinobacteria*, and *Proteobacteria* across forest soils (87, 89–92) appears to indicate their functional importance. These three phyla also dominated the active fraction of a *P. abies* soil, comprising $>$80 to 90% of rRNA molecules, and were responsible for the bulk of bacterial transcription (8, 55).

The soil bacterial community composition has been shown to display biogeographical patterns on a continental scale that are predictable but differ from the well-studied plant and animal community patterns (44). The first comprehensive study indicated that the soil pH is the most important driver of the bacterial community composition, and this observation was confirmed in multiple studies that focused specifically on forest soils (43, 93–97). Whereas *Acidobacteria* and *Alphaproteobacteria* are abundant in acidic soils (8, 96, 98, 99), the abundances of *Bacteroidetes* and *Actinobacteria* increase with a rising pH (43, 94, 100).

The preference of bacterial taxa for niches with certain nutrient contents and organic matter quality is indicative of their ecological strategy. The abundance of *Acidobacteria* was initially negatively correlated with the C availability in soils, corroborating the idea that *Acidobacteria* are slow-growing oligotrophs that have adapted to resource limitations (73, 101, 102). However, the present results show that members of the *Acidobacteria* inhabit soils across a wide range of C contents, representing, on average, 20% of all bacteria; their abundance may exceed 60% in acidic forest soils where both the content of organic matter and the allocation of C by tree roots are high (43, 103). *Acidobacteria* show a high level of metabolic versatility that allows them to decompose complex C substrates derived from the recalcitrant SOM pool (69, 101). Recently, subdivision 1 *Acidobacteria* from acidic coniferous forest soil were demonstrated to utilize C from cellulose and to produce high titers of extracellular enzymes (31, 104), indicating their involvement in decomposition in these soils. Unfortunately,

due to their limited culturability, little is known about the ecophysiology of other subdivisions of *Acidobacteria* and the *Planctomycetes*, except that they are common in forest soils (105, 106). *Verrucomicrobia*, which are also abundant in forest soils (56, 107, 108), show an increased abundance with soil depth (109), but it is unclear whether this is due to their preference for the oligotrophic environment or to the occupation of specific microniches. Members of the phylum *Bacteroidetes*, such as the genus *Mucilaginibacter*, which are common in forest soils, have been shown to be potent decomposers of cellulose and other biopolymers (31, 33, 104).

Importantly, some soil bacteria are involved in the weathering of minerals, a process of great importance in nutrient-poor soils, where minerals represent an important pool of inorganic nutrients (37, 110). Members of the *Betaproteobacteria*, such as the genera *Burkholderia* and *Collimonas*, have been recognized as efficient mineral-weathering bacteria. These taxa are common in both deciduous and coniferous forest soils (31, 56, 106, 108, 110–112).

For linking of the presence of bacteria or their activity to soil properties, it is important that soil is a complex of microniches with heterogeneous physicochemical properties on various scales. Because bacteria inhabit small niches, the properties of their immediate environment rather than the mean soil properties affect the local bacterial community. This spatial heterogeneity has been shown to result in the heterogeneity of bacterial communities on small scales of $<$1 cm (113). Furthermore, local dispersal limitations can also remarkably influence the bacterial community composition (93, 114). Considering the high level of spatial variation of forest C stocks on the same scale (115), the occurrence of individual taxa in forest soil may actually be highly variable on a small scale and may differ among activity hot spots, such as the rhizosphere and the bulk soil (49, 50). The transient nature of some physicochemical factors, such as soil moisture, can strongly influence the physical connectivity of the soil matrix, affecting bacterial and nutrient dispersion and, as a consequence, rates of key soil processes (116–118). Our ability to define and identify activity hot spots and to analyze their properties, as well as the abundance, composition, and function of their bacterial inhabitants, will be critical in future analyses to increase our mechanistic understanding of the roles of bacteria in biogeochemical processes.

Rhizosphere Bacterial Communities

In temperate and boreal forests, most C enters the soil food web via the roots in the form of labile C compounds, such as sugars, amino acids, and organic acids (119, 120), with approximately one-third of the plant net primary production (NPP) allocated to roots and soil (121). Indeed, root exudation, water and nutrient uptake by roots, decay, respiration, and physicochemical changes in soil are important factors influencing the composition and function of the microbial community in the rhizosphere, with biogeochemical consequences for the entire soils (46, 122).

The roots and rhizospheres of trees as well as ground vegetation associate with fungi to form mycorrhiza. While the ground vegetation mostly forms a symbiotic relationship with arbuscular mycorrhizal (AM) or ericoid mycorrhizal (ErM) fungi (29), more than 90% of forest trees in temperate and boreal zones participate in ectomycorrhizal (ECM) symbiosis, and only a minority of trees associate with AM (123). Thus, ECM is the quantitatively most prevalent and explored mycorrhizal type in forests (124). ECM fungi form mantels around tree root tips, and their mycelia extend into surrounding soils that are used to provide mineral nutrients to their hosts (62, 124, 125). Fungal associations of AM with trees are much less common and are confined to a few tree species (38). Due to the large absorptive area and exudation of labile compounds by ECM hyphae, the mycorrhizosphere and mycosphere represent important niches with features that differ from the nonmycorrhizal rhizosphere and bulk soil, hosting different bacterial communities (62, 126, 127). The exudation of labile C by tree roots or mycorrhizal hyphae enhances the availability of C in the rhizosphere and, consequently, the microbial abundance and activity of extracellular enzymes in comparison to those in the bulk soil (128–131). The input of labile C compounds into the rhizosphere selects

for bacterial strains with rapid growth and low-affinity substrate enzymes (r-strategists) that are enriched in comparison to the bulk soil profile (73, 132). The quantity and quality of exudates select for specific microbial communities and the expression of specific genes and may prime the decomposition of recalcitrant organic matter (133, 134). Considering the seasonal changes in NPP, seasonality is a major driver of microbial community composition and functioning in the rhizosphere (135).

Despite the importance of the associated ecological processes, bacterial communities inhabiting rhizospheres in forests have been explored much less than those from grasslands or agricultural systems. Recent studies from nonforest environments, such as grasslands (136, 137), croplands (138–140), and other ecosystems (134, 141–143), concluded that the rhizosphere contains a certain subset of the bulk soil microbiome, which is enriched in members of the *Proteobacteria*, *Actinobacteria*, and *Bacteroidetes* (136, 140, 142, 143). The dominance of *Alphaproteobacteria*, *Betaproteobacteria*, *Actinobacteria*, and *Bacteroidetes* was also observed in the rhizospheres of beeches in a mountainous forest (144). These observations suggest the enrichment of copiotrophic bacterial taxa (73, 138, 145).

The microbiomes surrounding the ECM roots and hyphae also differ from those in bulk soil (106, 127, 136). An enrichment of *Proteobacteria* (e.g., *Burkholderia*, *Rhizobium*, and *Pseudomonas*) and *Actinobacteria* (such as *Streptomyces*) in the mycorrhizosphere was reported based on culture-dependent studies (41, 124, 146–148). A recent molecular study of *Pinus sylvestris* mycorrhizospheres indicated that the community composition is much more complex and includes both copiotrophic and oligotrophic bacteria (149).

Various roles, ranging from mycorrhiza helpers to mycophages, have been assigned to the ECM-associated bacteria (124). The mycorrhiza helper bacteria (MHB) isolated from the mycorrhizospheres of different ECM symbionts either enhance the formation of mycorrhiza or support the previously established symbiosis (126, 150, 151). In the mycorrhizosphere, plants, ECM fungi, and bacteria form tripartite associations in which each player critically affects the metabolism of the others. It has been proposed that ECM fungi select for bacterial communities through the exudation of low-molecular-weight compounds, such as organic acids and amino acids (116, 152). Different ECM fungi in a similar environment can host very similar bacterial communities that are suited for this niche (146). MHB influence both ECM fungi and their plant host. For example, MHB from the genera *Pseudomonas* and *Streptomyces* promote mycorrhiza formation by modifying the gene expression of the ECM, leading to accelerated mycelial growth and stimulating the formation of new lateral roots (92, 150, 153). Rhizosphere bacteria also provide additional benefits to plants. For example, *Streptomyces* AcH 505 is an antagonist of plant pathogens and can induce defense mechanisms in *P. abies* and *Quercus robur* (125, 154, 155). Other very-well-known bacteria promoting plant vigor are endophytes, such as the members of the genus *Rhizobium*, which form nodules on the roots of *Alnus* plants, fix gaseous N, and provide it to their host.

BACTERIAL INVOLVEMENT IN ECOSYSTEM PROCESSES

Role of Bacteria in the Carbon Cycle

Forest soils store two-thirds of the terrestrial C (156). The flux of C is initiated by the fixation of atmospheric CO_2 by photosynthesis and mediated by the allocation of recalcitrant and simple organic compounds into the soil (Fig. 3). When plant debris and simple organic compounds are decomposed and used by microorganisms to build their biomass, some C is returned to the atmosphere via respiration. Because root exudates can readily be assimilated by soil microorganisms, decomposition of the dead plant biomass has been highlighted as the key process regulating C flow in soil systems that influences the ratio between C mineralization and immobilization (156).

Recent studies indicated that bacteria play a more important role in the transformation of the dead plant biomass than was previously assumed and significantly contribute to decomposition processes in litter and soil (31–33). The plant biomass is composed largely of lignocellulose, a highly organized and interlinked mix of different polymers that contains various amounts of cellulose, hemicelluloses, and lignin (157).

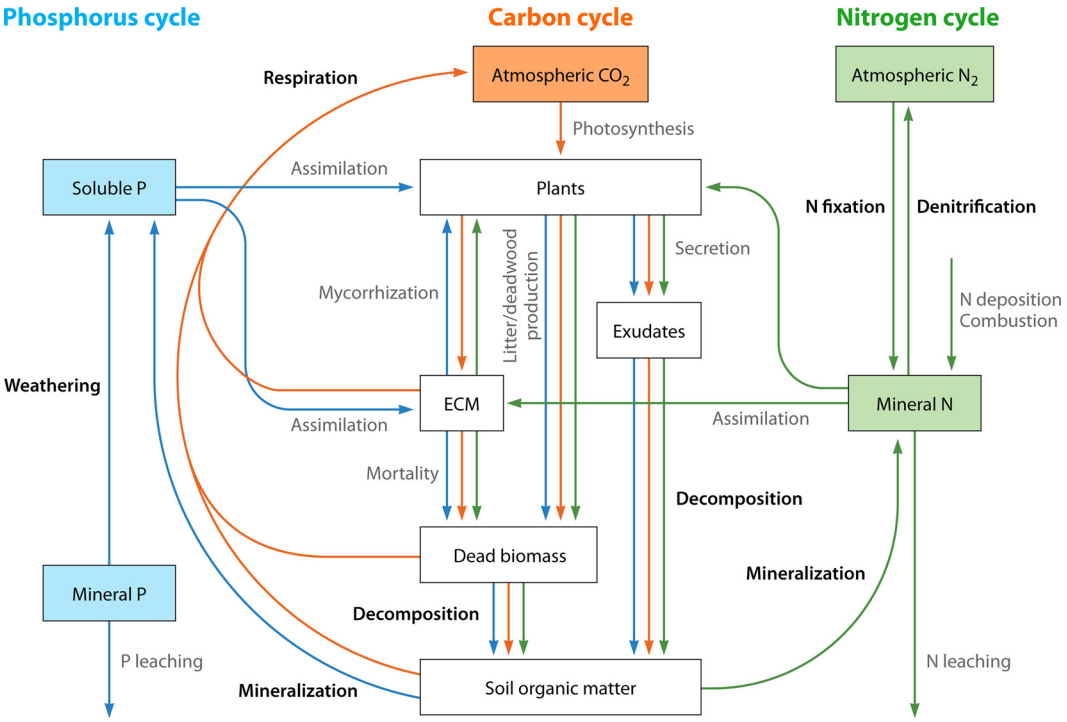

FIG 3 Schematic view of the coupled biogeochemical cycles of carbon, nitrogen, and phosphorus in forest ecosystems. Colored arrows show the transfer of elements (C in orange, N in green, and P in blue) between ecosystem compartments. Ecological processes with the active involvement of bacteria are highlighted in bold.

Because of the presence of hemicelluloses in a recalcitrant complex with lignin, cellulose represents the most accessible biopolymer, and its degradation is thus a key step in the C cycle. The most important enzymes involved in this process are endocellulases, exocellulases, and β-glucosidases. Together with these enzymes, a diverse set of hemicellulases, such as endoxylanases, xylosidases, xyloglucanases, endomannanases, mannosidases, fucosidases, arabinosidases, pectinases, and lignolytic enzymes, are necessary for the hydrolysis of other polymers that are present in the plant biomass (158). The genes encoding cellulases are present in 24% of all sequenced bacterial genomes (159), and glycosyl hydrolases that degrade other plant structural biopolymers are also common (30). Recently, López-Mondéjar et al. (33) isolated cellulolytic bacteria belonging to a variety of phyla from a deciduous forest topsoil, and they demonstrated, for the first time, the presence of cellulolytic members among some abundant soil genera, e.g., *Mucilaginibacter*, *Luteibacter*, and *Pedobacter*. Other studies highlight the important ecological role of strains of the phyla *Acidobacteria* and *Actinobacteria* as degraders of plant biomass polysaccharides in the acidic soils of temperate forests (31, 104, 160).

Genomes of several forest soil bacteria encode proteins involved in decomposition of dead plant biomass (33, 161–163). In addition to promotion by hydrolytic enzymes, efficient hydrolysis is often promoted by the presence of carbohydrate-binding modules (CBM) that are part of either the enzymes or bacterial cell surfaces (157). Genes coding for proteins that are involved in signal transduction, nutrient binding, and transport are often found in the same operons as hydrolase genes. Some of these proteins, such as the TonB-dependent receptors, have been established as plant carbohydrate scavengers (164). Other auxiliary proteins, such as the substrate-binding proteins (SBPs) from ATP-binding cassette (ABC) transporters, have been shown to be capable of binding a variety of plant cell wall soluble and insoluble saccharides, including microcrystalline or amorphous cellulose, xyloglucan, xylan, and mannan (165). The rich suite of these auxiliary proteins expressed by a *Paenibacillus* sp. strain from a temperate forest soil suggests their important involvement in polysaccharide

decomposition (162). A suite of carbohydrate-binding proteins, such as type IV pili and an atypical oxidative cellulase, in a cellulolytic *Luteibacter* species from temperate forest soil demonstrates the variability among the cellulolytic systems of bacteria, which remain far from being completely described (33, 166, 167). Since plant biomass represents a renewable and abundant resource for the production of environmentally friendly chemicals and biofuels (168), forest topsoils represent a rich potential source of bacterial strains with biotechnological relevance (169, 170).

Soil bacteria are also able to contribute to the breakdown of phenolic compounds, including lignin, although their efficiency is typically much lower than that of fungi (34, 160). Ligninolytic bacteria can be found among the *Proteobacteria* (genera such as *Sphingomonas*, *Burkholderia*, *Enterobacter*, *Ochrobacterium*, and *Pseudomonas*, among others), *Firmicutes* (*Bacillus* and *Paenibacillus*), and *Actinobacteria* (*Rhodococcus*, *Mycobacterium*, *Microbacterium*, and *Streptomyces*) (35, 171), and there is evidence that potentially ligninolytic taxa are common in soils. For example, abundant bacterial laccase genes have been found in temperate hardwood forests (172), and bacterial taxa possessing laccases, such as *Burkholderia*, *Bradyrhizobium*, and *Azospirillum*, are highly active in forest soils (173). However, even if the enzymology of bacterial lignin degradation is poorly understood compared to that for fungi, bacteria may use ligninolytic peroxidases and laccases to reduce the toxicity of phenolic compounds rather than to degrade lignin.

In addition to plant biomass, fungal mycelia represent an important pool of organic matter in forest litter and soil (174). Forest ecosystems are dominated by ectomycorrhizal fungi (ECM), with a biomass of up to 600 kg ha^{-1} (147, 151), and the annual production of fungal mycelia in a spruce forest ranges from 100 to 300 kg ha^{-1} (77). Fungal mycelia represent a large C and N pool that typically contains chitin and other polysaccharides, such as glucans and glucomannans, as well as phenolics, such as melanin (75, 175). Fungal biomass represents a more readily decomposable substrate than lignocellulose, and bacteria have been reported to be more important contributors than fungi to its decomposition (75, 176). The bacteria associated with fungal biomass decomposition represent a specific subset of the litter and soil communities, dominated by *Pseudomonas*, *Ewingella*, *Pedobacter*, *Variovorax*, *Stenotrophomonas*, and *Chitinophaga*, genera that are known to produce chitinolytic enzymes (75). Chitinolytic enzymes, which are represented by chitinases and *N*-acetylglucosaminidases, appear to be widespread in bacterial genomes, especially *Actinobacteria* (30, 177). The members of this phylum often contain several chitinase genes as well as a diverse array of corresponding CBMs, and they often also possess β-1,3-glucanases, thus encompassing a complex set of enzymes that potentially target fungal cell walls (178). Chitinase production by soil bacteria is a complex adaptation that combines a nutritional strategy with potential involvement in the antagonistic interactions with fungi (178, 179). Although the bacterial biomass in forest soils has a size similar to that of fungi (55), the process of bacterial cell wall polymer decomposition is far less understood. The involvement of *Planctomycetes*, *Verrucomicrobia*, *Armatinomonadetes*, or candidate division OD1 in the degradation of bacterial exopolysaccharides produced in soil was recently demonstrated (180).

Finally, a large fraction of C in forest ecosystems is allocated belowground during the vegetation period via tree roots, in the form of root exudates (181, 182). Up to 40% of newly photosynthesized C can be allocated to the soil via roots, where it is rapidly respired or incorporated into the microbial biomass (183, 184). The rhizosphere, including the root-associated mycelia of mycorrhizal fungi, is thus probably the most important C allocation hot spot in forest soils and is strongly influenced by plant activity (185). Because ECM fungi cover most of the fine roots and root tips, the largest fraction of this C is allocated to them (186). The fraction of assimilates that is exuded directly from roots into the rhizosphere is estimated to range from 1 to 5% and is composed mainly of carbohydrates, amino acids, and organic acids (120, 187). The rhizodeposition of C by plants exhibits severalfold seasonal differences that correspond to the intensity of photosynthesis throughout the year (182). While direct evidence of a net C flux from

plants to rhizosphere microbiota has been shown for many crops, little is known about the structure and function of bacterial and fungal communities that are actively involved in the assimilation of root exudates in forest ecosystems (188). Although decomposer fungi can find suitable conditions in the nonmycorrhizal rhizospheres of trees, this niche has traditionally been considered bacterium dominated because their rapid growth favors their utilization of root exudates (185). Recent studies indicated that soil bacteria indeed use root exudates in forest soils (189), and the seasonal production of root exudates leads to an increase in bacterial biomass as well as in the share of the rhizosphere- and mycorrhizosphere-specific bacteria in mineral soil in summer (56, 70). In the same way as that of tree roots, hyphae of ectomycorrhizal fungi exude low-molecular-weight organic compounds that support diverse bacterial communities (78, 190). The rhizosphere of roots colonized by mycorrhizal fungi is specific in that a portion of the plant-derived C is released into the soil through the ECM mycelium (155). As a consequence, ECM fungi constitute a nutrient hot spot for other microorganisms, because the fungal symbionts have a very large surface area and receive a direct supply of photosynthetic C (149). Soil bacteria have been found to grow abundantly and rapidly at the expense of the exudates from *P. sylvestris* roots colonized by *Piloderma*, supporting a role for the bacteria in the metabolism of the organic acids and other compounds produced by the fungus (152). The observation that these bacteria are able to utilize fungal sugars more readily than plant sugars supports the existence of a bacterial guild that is specialized for hyphal exudates (191).

Methane represents a gaseous form of organic C that can be oxidized by certain forest soil bacteria under aerobic conditions (192). These methanotrophic bacteria are the main consumers of atmospheric methane as well as methane generated by methanogenic archaea in waterlogged anaerobic horizons of certain soils (193–196). Due to the presence of methanotrophic bacteria, forest soils (especially those of the boreal forests) may represent a sink of atmospheric methane. Although methanotrophs are phylogenetically located in two bacterial phyla, most of the characterized isolates belong to the *Alphaproteobacteria* and *Gammaproteobacteria* (197). The discovery of new acidophilic methanotrophs related to *Verrucomicrobia* recently revealed a higher level of diversity of methanotrophic bacteria in as yet unexplored acidic environments (198). In addition to using organic C sources, certain soil bacteria are able to fix CO_2. These autotrophic taxa were described for the genus *Bradyrhizobium* (*Betaproteobacteria*), whose members are abundant inhabitants of forest soils (199, 200), and a recent transcriptomic study confirmed the expression of the components of a photosynthetic apparatus in the *Cyanobacteria* and *Proteobacteria*. The input of C into forest soils through fixation is, however, apparently minimal (55).

Role of Bacteria in Nitrogen and Phosphorus Cycles

Nitrogen is the most common limiting nutrient in soils, entering the ecosystem largely through fixation (Fig. 3). This process is dominated by bacteria that are estimated to be responsible for more than 95% of the N input in unmanaged environments (36, 201). The presence of the *nifH* gene of the *Alphaproteobacteria* (*Bradyrhizobium*, *Azospirillum*, *Hyphomicrobium*, and *Gluconacetobacter*) and *Deltaproteobacteria* (*Geobacter* spp.) was observed in different temperate forest soils, demonstrating the ubiquity of some N-fixing bacteria, not only as symbiotic but also as free-living taxa (200). The observed diversity of N-fixing bacteria may rapidly change if there is an exogenous input of N (36). Particularly in temperate forest soils that are strongly affected by anthropogenic N deposition, N input is a good predictor of N fixation activity (202).

Nitrification and denitrification lead to the loss of N from soils through NO, N_2O, and N_2 gas emissions as well as through the leaching of NO_3 if its concentration exceeds the ecosystem retention capacity (203, 204). Among these, nitrous oxide is a particularly powerful greenhouse gas with a potentially warming effect that is almost 300 times larger than that of CO_2 (205). Nitrification is the biological oxidation of ammonia to nitrate via a multienzymatic process. The *amoA* gene, encoding ammonia oxidase, which performs the first step of nitrification, is present in ammonia-oxidizing bacteria

(AOB) as well as ammonia-oxidizing archaea (AOA), but AOB rather than AOA seem to dominate in soils (206, 207). The reaction catalyzed by this enzyme is often limiting in temperate and boreal forest soils (208). All known AOB belong to the *Betaproteobacteria* and *Gammaproteobacteria*, and they are mostly represented by the genera *Nitrosomonas*, *Nitrosococcus*, and *Nitrosospira*. *Nitrosomonas* and *Nitrosospira* are further subdivided into clusters with different responses to environmental drivers, such as acidity, pH, and ammonia availability, and due to that, changes in soil N availability can result in dramatic shifts in the composition of the AOB community (206, 208, 209). *Nitrosospira* seems to be the most abundant AOB in acidic forest soils with low NH_4^+ contents (206, 210, 211). The *amoA* gene content, however, appears to vary across forest soils (212). Nitrification rates seem to be correlated with the AOB abundance in soil (209, 213). AOB are also involved in N losses from soil by producing N_2O during denitrification (214). Denitrification is essential for the global N cycle, maintaining the reduction of nitrate or nitrite to gaseous nitrogen compounds, such as N_2 and nitrous oxide. The denitrification pathway is known as dissimilatory nitrate reduction because nitrate or nitrogen oxides are the final electron acceptors, allowing bacteria to produce energy at the expense of reduced electron donors in the absence of oxygen. Denitrifying bacteria are not always able to perform all the steps of the dissimilatory pathway, and incomplete denitrification is the major source of N_2O emissions from soils (215). Denitrification can be addressed by studying marker genes involved in the individual enzymatic steps, such as the reduction of nitrate (*narG*), nitrite (*nirK*/*nirS*), nitric oxide (*norB*), and nitrous oxide (*nosZ*) (205). Denitrifying bacteria are abundant and widespread in forest soils, and denitrification genes have been found in bacterial strains belonging to the *Acidobacteria*, *Proteobacteria*, and *Firmicutes*, as well as in other bacterial phyla (216–218). A significant correlation was described among gene abundances, denitrification rates, and NO and N_2O fluxes, confirming the importance of their carriers for the environmental processes that occur in forest soils (69, 203, 219). In addition to mineral N forms, bacteria may obtain N from a range of organic compounds present in forest soils, namely, the chitin present in the polysaccharides of fungal mycelia and the amino acids and proteins in dead organic matter. The utilization of these compounds is expected to be subject to intensive competition among ectomycorrhizal fungi, saprotrophic fungi, and bacteria (146).

While the potential source of N—the atmosphere—is theoretically unlimited, this is not the case for phosphorus (P), which is supplied mostly by weathering of minerals; P thus represents the limiting nutrient in many soils (Fig. 3). Bacteria are important mediators of the P cycle because some are able to solubilize mineral P while others may immobilize it in their biomass. Unfortunately, the involvement of bacteria in the P cycle has received far less attention than that in the N and C cycles. The main mechanism responsible for P uptake by bacteria is through the solubilization and uptake of inorganic P, its most abundant source. The ability to solubilize inorganic P has been described for different bacteria and ectomycorrhizal fungi present in the rhizosphere and soil. This ability is related to the release of organic anions, such as citrate, gluconate, oxalate, and succinate, into the soil (220). Phosphatase enzymes release phosphate from organic phosphate esters during organic matter decay (221). In a recent metagenomic analysis of temperate forest soils, it was highlighted that members of the *Alphaproteobacteria*, *Betaproteobacteria*, *Actinobacteria*, and *Acidobacteria* dominated the processes related to P turnover (222, 223). While genes related to P solubilization are more abundant in P-rich soil, those that play a role in P uptake systems are more abundant in P-limited soil (222).

EFFECTS OF GLOBAL CHANGE ON BACTERIAL COMMUNITIES IN FOREST ECOSYSTEMS

Bacteria strongly contribute to key ecological processes that are important for society in light of the ongoing global change (114). The determination of how relationships between site factors and bacterial communities affect the equilibrium between soil organic matter decomposition and C sequestration in forests is of para-

mount importance for prediction of the responses of terrestrial ecosystems to climate change (224). Future climatic conditions are predicted to produce tree species migration (225, 226), an increase in extreme events, such as droughts and wildfires, and an increase in vegetation productivity due to longer growth seasons (13, 227, 228). These effects in combination with other phenomena, such as increased N deposition, may cause dramatic shifts in global C fluxes, in particular affecting the boreal and temperate forests of the northern continental regions (229–231). The high diversity of C compounds released into the soils and the complex structures of bacterial and fungal communities, with their overlapping functions, create a very complex system that is difficult to incorporate into predictive models (16). The complex nonlinear interactions between forest and atmosphere have the capacity to constrain or amplify climate change-associated processes, depending on the activity of soil bacteria and fungi (232–234). Recent studies investigating the effects of global change on ecosystem properties offer the first clues to the prediction of future developments (Table 1).

Carbon Dioxide

Increasing CO_2 concentrations are predicted to boost NPP in boreal and temperate forests (235); however, their capacity to maintain such high levels of NPP will strongly depend on their ability to overcome nutrient limitations (236). Unfortunately, the degree to which forests will persist as C sinks remains uncertain (237); in particular, the rhizosphere priming effect may be reduced, and the increased NPP may increase soil C storage (238, 239). It is clear that the degree to which rising CO_2 levels will be offset by C sequestration in forest ecosystems will strongly depend on the adaptation of both trees and soil microorganisms to the altered environmental conditions.

Thus, how do CO_2 levels affect bacterial populations in forest topsoils? And is it possible to generalize the observations obtained across ecosystems for different soils with various vegetations? The effects of elevated CO_2 levels do not directly affect soil bacterial populations: CO_2 concentrations in soil pores are normally higher than those in the atmosphere, and the response of bacteria to small CO_2 changes is thus negligible (240). As a result, the observed effects are mostly indirectly driven by altered plant production and root exudation, which are both tree species specific. In addition, changes in organic acid exudation by mycorrhizal fungi as a result of the presence of CO_2 will affect the bacterial community composition (152), and this process also depends on the vegetation properties. It is difficult to determine whether the functional responses of bacterial communities to CO_2 will be similar across forests or will depend on soil and vegetation characteristics. The expected increase in root exudation should generally favor the development of soil copiotrophic bacteria over specialized oligotrophs. A good example of this response is the decrease in abundance of oligotrophic *Acidobacteria* in various soils following an increase in CO_2 (144, 152, 238, 240). Such a general response is rather exceptional considering that different members of the same phylum often respond differently to the same disturbance (241). The increased abundance of certain bacterial taxa will have functional consequences only if their functional traits do not change in response to the treatment, which may explain the sometimes controversial results obtained for responses to CO_2 in different forest soils, despite the fairly consistent response of bacterial abundance after an increase in CO_2 (238, 240, 242). For example, while some studies have indicated that an elevated CO_2 level does not affect the AOB abundance or nitrifying activity (207), others have described an increase in nitrification or nitrifying taxa (240, 243), even in an unaltered bacterial community. Thus, it is unclear whether the effects of increased CO_2 levels on bacterial biomass, richness, community composition, and functionality will be consistent across different forest ecosystems.

Global Warming

The rise in temperature is intimately linked to the increased CO_2 concentration in the atmosphere, because the latter largely causes the former. Although both processes appear globally, the extent of the rise in temperature is predicted to be pronounced in

TABLE 1 Effects of carbon dioxide, temperature, and nitrogen increases on bacterial communities and biogeochemistry in northern forests in manipulative experiments[a]

Manipulation	Habitat	Vegetation	Effects on biogeochemistry	Effects on bacterial populations	Effects on bacterial taxa	Selected reference(s)
[CO_2]	Temperate forest	*Pinus taeda*, *Populus tremuloides*, *Populus alba*, *Pinus nigra*, *Acer saccharum*, *Betula papyrifera*	↑ NPP, ↑ efficiency of C-fixing enzymes, ↑ N sequestration	= bacterial biomass, = AOB biomass, ↑ bacterial diversity	= *Proteobacteria* (↓ *Bradyrhizobium*, ↑ *Rhodoplanes*, ↑ *Pseudomonas*, ↑ *Nitrosospira*), ↑ *Actinobacteria*, ↑ *Bacteroidetes*, ↓ *Acidobacteria* (except Gp4 and Gp6)	207, 235, 236, 241, 271
	Temperate forest	*Pinus taeda*	↑ dichotomous branching index, ↑ root soil exploration, ↑ exudation (growing season), ↑ NAGase activity, ↑ phenol oxidase, ↑ NH_4 turnover	↑ microbial biomass (growing season)		120, 121
	Temperate forest	*Populus tremuloides*, *Betula papyrifera*, *Acer saccharum*, *Pinus sylvestris*	↑ SOM decomposition, ↑ decomposition of low-molecular-weight organic acids	= bacterial abundance, ↑ bacterial diversity	↓ *Acidobacteria*, ↓ *Bacteroidetes*, ↑ *Burkholderia*, ↑ *Nitrosospira*	152, 240
	Temperate forest	*Fagus sylvatica*	= NPP, ↑ SOM decomposition, ↑ genes for decomposition of labile C, = NH_4, ↑ NO_3 depletion, ↑ exudation	↓ bacterial diversity	↑ *Pseudomonas*, ↑ *Actinobacteria*, ↑ *Planctomycetes*, ↑ *Firmicutes*, ↓ *Acidobacteria* (except Gp5, Gp6, and Gp7)	144
	Temperate forest	*Fagus sylvatica*, *Quercus robur*, *Quercus petraea*, *Carpinus betulus*	= NPP, = NH_4, ↑ NO_3 accumulation, = C/N ratio for trees			243
Temp	Boreal forest	*Abies balsanea*, *Pinus sylvestris*, *Picea abies*	↑ soil respiration, ↑ enzyme activities on labile C, = SOM decomposition	= microbial biomass, ≠ microbial community composition		231, 272
	Temperate forest	*Picea asperata*	↑ root exudation rates, ↑ C/N ratio for exudates, ↑ SOM decomposition			273
	Temperate forest	*Picea rubens*, *Abies balsamea*, *Fagus grandifolia*, *Acer saccharum*, *Acer rubrum*, *Betula lenta*, *Prunus serotine*, *Quercus rubra*	↑ soil respiration, ↑ SOM decomposition, ↑ V_{max} of enzymes			274, 275
	Temperate forest	*Betula papyrifera*, *Betula lenta*, *Acer rubrum*, *Quercus velutina*, *Quercus rubra*, *Fagus grandifolia*, *Picea abies*, *Fagus sylvatica*, *Abies alba*	↑ soil respiration, ↑ extracellular enzyme activity, = C, = N	= bacterial biomass, ≠ bacterial community composition	↓ Gram-negative bacteria, ↑ *Acidobacteria*, ↑ *Alphaproteobacteria*	16, 246, 276
	Temperate forest	*Acer rubrum*, *Betula papyrifera*, *Quercus velutina*, *Acer pensylvanicum*	↑ oxidative activity	↑ bacterial diversity	↑ *Acidobacteria*, ↑ *Actinobacteria*	234
N	Boreal forest	*Picea abies*	↑ soil C (high N deposition), ↓ soil respiration (high N deposition)	↓ bacterial biomass, = *amoA* gene abundance, ≠ AOB community composition		263, 267
	Temperate forest	*Acer saccharum*	↓ SOM decomposition, ↓ soil respiration, = NPP, ↑ OM in forest floor, ↓ extracellular enzyme activity, ↑ N in soil organic matter, ↑ NO_3 leaching	↓ bacterial diversity (site specific), ↑ carbohydrate metabolism genes, ↑ aromatic metabolism genes, ↑ respiration metabolism genes, ↓ chitin decomposition genes (site specific), ↓ lignocellulose decomposition genes (site specific), ↓ N cycle genes (site specific)	↓ *Bacteroidetes*, ↓ *Gammaproteobacteria*, ↑ *Firmicutes*, ↑ *Actinobacteria*, ↓ *Acidobacteria*, ↓ *Verrucomicrobia*	213, 260–262, 264
	Temperate forest	*Fagus grandifolia*, *Acer saccharum*, *Acer rubrum*, *Picea rubens*	↓ soil respiration (*P. rubens* site)	↓ microbial biomass (*P. rubens* site)		257

(Continued on following page)

TABLE 1 (Continued)

Manipulation	Habitat	Vegetation	Effects on biogeochemistry	Effects on bacterial populations	Effects on bacterial taxa	Selected reference(s)
	Temperate forest	*Pinus resinosa*, *Quercus velutina*, *Quercus rubra*, *Betula lenta*, *Acer rubrum*, *Fagus grandifolia*	↓ soil respiration, ↓ SOM decomposition, ↑ C stocks (except at *Pinus* site), ↑ tree biomass, ↓ extracellular enzyme activity, ↑ lignin recalcitrant C, ↑ NO_3, ↑ nitrification, = litter fall (except ↑ at *Pinus* site), = root biomass (except ↓ at *Pinus* site), = root productivity	↓ microbial biomass, ↑ bacterial richness, ↑ specific operational taxonomic units	↑ *Proteobacteria*, = *Acidobacteria*	257, 266, 268
	Temperate and boreal forests		↑ aboveground NPP, ↑ belowground C, ↑ tree growth, ↑ litter fall, = litter decomposition, = soil respiration, ↑ C sink	↓ microbial biomass		277

[a]Arrows indicate increases and decreases of the listed parameters. =, no significant change in the parameter; ≠, significant change in the parameter.

the Northern Hemisphere, where temperate and boreal forest ecosystems dominate. The long-term scenarios are, however, not clear because multiple long-term events, such as the depletion of labile C limiting bacterial growth, thermal adaptation of microbial processes, and shifts in microbial communities or in the expression of their metabolic potential, may attenuate positive feedbacks of warming (244). The C balance after warming will largely depend on the efficiency of soil microbes in accessing and using C in response to the altered environmental conditions (12). A very recent work showed that an increase in temperatures can increase tree exudation rates (229). As a consequence, warming can alter soil drivers through exudation, which in turn might produce different responses of soil rhizosphere bacterial communities, affecting SOM decomposition differently in different environments, depending on the tree-specific exudation (229).

After years of experimentally increased warming in boreal and temperate forest soils, bacterial biomass values are usually not significantly different from those of nonwarmed controls, suggesting an attenuation effect (234, 245–248). However, it has been demonstrated that warming affects bacterial diversity and that these changes reflect the magnitude of the temperature change (249). These shifts in bacterial communities may affect the C cycling processes that involve bacteria. Multiple studies have shown that short- and long-term warming can affect the composition of the soil bacterial community toward populations that are more adapted to the use of complex sources of C (234, 250). Members of the *Alphaproteobacteria* and *Acidobacteria* display increased abundances after simulated warming, suggesting a change in soil bacterial lifestyle from copiotrophy to oligotrophy, which coincides with the depletion of labile C while maintaining high levels of respiration (16, 234). This finding is contradictory to the aforementioned effect of increased atmospheric CO_2, which should boost copiotrophic bacterial populations, highlighting the necessity of studies that combine the manipulation of both variables. However, other studies have documented no shifts in bacterial communities after years of warming (90, 246).

Considering the warming effects on N cycle processes, we may rely only upon a few contradictory works examining that topic. An increase in temperature was observed to accelerate nitrification and denitrification processes, affecting the N cycle in soils (229, 251). The warming effect may be offset by other factors, such as N deposition, which can increase the temperature sensitivity of the enzymes involved in SOM decomposition or suppress the decomposition process, counterbalancing the priming effects (245, 252).

Nitrogen Deposition

Global anthropogenic N inputs are estimated to be 30% to 50% higher than those from natural sources. They have increased 10-fold in the past 150 years and are projected to double during the next century (253, 254). In contrast to global warming and increased levels of CO_2, however, their effects are largely local. Since N is a limiting nutrient in most terrestrial ecosystems, including boreal and temperate forests (255), anthropogenic N deposition may strongly influence NPP in these environments by reducing this limitation (256). N deposition also has a range of additional consequences that range from shifts in the soil C/N ratio, soil acidification, and root exudation to changes in the vegetation and microbiota (257). Bacterial soil communities are clearly sensitive to increased levels of N itself as well as to all the associated soil physicochemical changes (213, 258, 259).

There appears to be a general consensus that N deposition increases soil C sequestration due to the decline in SOM decomposition via the reduction of biomass and activity of soil microbial populations in many different soil environments, including temperate and boreal forests (258, 260–264). The most probable reason for C sequestration is the observed reduction of tree root exudation (256), although direct effects of a pH decrease induced by N deposition were proposed as an alternative explanation (265). Although the reduction of biomass following N input was mostly observed in fungi (256, 266), it was recently noted that the biomass of soil bacteria can be reduced

as well, by up to 50% (258, 263, 267). Reduction of the bacterial biomass, however, depends on the level of N input. At chronically low levels of N, which are typical of boreal and temperate forest soils, the bacterial biomass may remain stable while the fungal biomass markedly drops. This decrease in the fungal/bacterial biomass ratio due to N addition is consistently found across forest soils, where it ranges from 25% to 70% (256, 257, 263, 266).

N deposition also changes the composition of bacterial communities in forest soils. The abundances of *Acidobacteria* and *Verrucomicrobia* decrease, while those of *Actinobacteria* and *Firmicutes* increase, following the addition of N to a variety of soils (264). In a report on a temperate forest, the share of *Acidobacteria* did not respond to N addition, but some groups within the phylum were significantly affected, suggesting that the response of the bacterial community may be complex (268). Also, in other cases, the deposition of N significantly affected relative abundances of core bacterial phyla, but it reduced bacterial diversity and altered the bacterial composition at lower taxonomic levels (258, 261).

A decrease in oligotrophic bacteria is often found concomitantly with a decrease in the activity of enzymes related to cellulose breakdown, again supporting the hypothesis that the addition of N negatively affects microbial SOM decomposition (262, 264). When genes of the N cycle (fixation, nitrification, and denitrification) were assessed in N deposition experiments, the metabolic potential of the bacterial community remained stable or even decreased in terms of gene abundance (213, 267). However, in studies assessing the effects of N addition on N cycle processes in forest soils, it was reported that after N saturation of the environment, bacterial and archaeal nitrification and denitrification gain importance, initiating the cycle, and result in the efflux of N compounds, such as nitrate, N_2, or nitrous oxide gas, from the soil ecosystem (150, 269, 270). This phenomenon suggests that the abundances of particular genes, in this case, are not correlated with the rates of ecological processes. In this sense, it was recently proposed that even in forest soil environments where the addition of N highly increases nitrification, it is possible that bacteria with more efficient nitrification pathways are selected and that this leads to higher rates of nitrification despite the reduced abundance of nitrifiers and genes related to N cycle processes (213). Clearly, metatranscriptomic or metaproteomic studies are needed to gain insight into the regulation of the N cycle by N availability.

CONCLUSIONS

Undoubtedly, boreal and temperate forests will be important for the global C balance considering the global change. The role of bacteria in these ecosystems has been understudied, and it will be important to clarify whether these biomes will continue to be a large C sink for anthropogenic emissions. Here we show that despite the important role of fungi in forest soils, bacteria fulfill multiple important ecosystem roles in the forest environment, including organic matter decomposition, regulation of mycorrhizal symbiosis, and involvement in N cycle processes. More complex and comparable studies to assess the variables affected by global change in a wide range of ecosystems will be required to predict the future of these environments. The effects produced by greenhouse gas emissions and anthropogenic deposition of chemical compounds may provide a counterbalancing effect in some ecosystems, while the changes may be dangerous in others due to positive feedback. Although our knowledge is still very limited, we stress that the scientific data collected over the past years and even decades is never contradictory with regard to the need for boreal and temperate forest ecosystem protection by strict policies. A greater decrease in global forest area will be particularly detrimental because it will prevent other climate change mitigation efforts, such as the reduction of greenhouse emissions.

Considering the importance of the transfer of C from the roots of primary producers to soil, the rhizosphere is likely the most important hot spot of bacterial activity in soils. The available nutrients provided by plants and mycorrhizal fungi lead to the formation of an interactive network of different soil microbes (not only bacteria) that makes the

rhizosphere a fascinating and very complex system in which conditions are far from those in individual pores of the bulk soil. The number of drivers to consider, including the specificities of compounds and microbial diversity depending on the type of tree or plant and a large influence of seasonal effects (among others), hampers the accessibility to microbial ecologists of the processes that occur in the rhizosphere. However, the function of this niche very likely offers the key to understanding the biogeochemistry of forest soils. Studies combining the assessment of metabolites present in the rhizosphere at different times, their turnovers and transformations, and the effects and implications of bacterial taxa in terms of fluxes are the next step toward elucidating the effects of forest trees on the rhizospheres and how they relate to the cycling of C and other nutrients.

The large number of studies examining the bacterial communities in forest ecosystems that were published in recent years are shedding light on the high diversity and complex structure of these communities. However, to provide insights into the ecological roles and contributions of individual bacterial taxa to biogeochemical processes, it is necessary to link the community composition to specific functions. Although DNA-based analyses aid in unraveling community dynamics and changes in microbial activity, RNA-based studies offer important information about the active bacterial community and the processes that occur in ecosystems. RNA-based studies of forests confirm how thousands of microbial taxa are transcriptionally active in forest litter and soil, underscoring the involvement of many players in important processes that occur in soil and the importance of taxa with a low abundance of DNA.

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We declare that we have no conflicts of interest.

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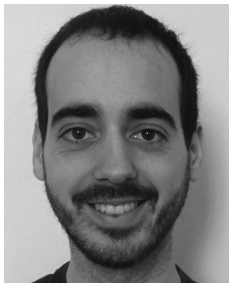
Salvador Lladó is a researcher whose main career focus is to relate bacterial identity to functionality related to the C cycle in temperate forest soils. During his Ph.D. research in the Department of Microbiology of the University of Barcelona, he worked on characterizing bacterial populations involved in the decomposition of hydrocarbon pollutants in contaminated soils. After he obtained his Ph.D., in December 2013, he moved to the laboratory of Petr Baldrian in the Laboratory of Environmental Microbiology of the Czech Academy of Sciences, where he is applying DNA and RNA high-throughput sequencing and metabolomics, combined with classical microbiological methods of isolation and physiological characterization, to obtain a better understanding of the roles of the most abundant bacteria in the C and N cycles in forest soils. His broader interest is to be able to relate bacterial community structure and functionalities in soils with the changing C fluxes due to climate change.



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Petr Baldrian received his Ph.D. in microbiology at the Charles University in Prague, Czech Republic, based on work describing the effects of metals on wood-rotting fungi. He later changed his topic to environmental microbiology, focusing on enzyme activities and the fungal contribution to decomposition of litter and soil organic matter as well as the characterization of enzymatic systems of microorganisms and their biotechnological potential. He is now Head of the Laboratory of Environmental Microbiology of the Institute of Microbiology of the Czech Academy of Sciences in Prague. Recently, he contributed to the identification of the active fraction of the soil microbiome and the analysis of the relative contributions of bacteria and fungi to ecosystem processes. His work is mostly focused on the functioning of forest soils, the seasonality of microbial processes, and the drivers of community assembly of soil bacteria and fungi.