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Review

Factors Affecting CO_2, CH_4, and N_2O Fluxes in Temperate Forest Soils

Amna Saher [1], Gaeun Kim [1,2], Jieun Ahn [1,3,4], Namyi Chae [4], Haegeun Chung [5] and Yowhan Son [1,*]

[1] Division of Environmental Science and Ecological Engineering, Korea University, Seoul 02841, Republic of Korea; saheramna@korea.ac.kr (A.S.); gaeun.kim@slu.se (G.K.); ahnjieun24@gmail.com (J.A.)
[2] Department of Forest Ecology and Management, Swedish University of Agricultural Sciences, 901 83 Umeå, Sweden
[3] Food and Agriculture Organization of the United Nations (FAO), Maputo P.O. Box 1928, Mozambique
[4] Institutes of Life Sciences and Natural Resources, Korea University, Seoul 02841, Republic of Korea; cnamyi@korea.ac.kr
[5] Department of Civil and Environmental Engineering, Konkuk University, Seoul 05029, Republic of Korea; hchung@konkuk.ac.kr
* Correspondence: yson@korea.ac.kr; Tel.: +82-2-3290-3015

Abstract

Greenhouse gas (GHG) fluxes from forests, including carbon dioxide (CO_2), methane (CH_4), and nitrous oxide (N_2O), are regulated by complex interactions of abiotic and biotic factors. A better understanding of these interactions involving GHGs can help manage forests and enhance their sequestration potential. This review examines how soil properties (moisture, temperature, and pH) and tree species-specific traits (litter quality, carbon storage, and microbial regulation) interactively control GHG dynamics in temperate forest soils, moving beyond a single-factor perspective. This literature review confirms that temperate forest soils are CH_4 sinks and sources of CO_2 and N_2O; however, flux direction and magnitude differ across spatial and temporal scales. CH_4 fluxes show high spatial variability and are sensitive to biogeochemical conditions. While soil temperature and moisture are well studied, their combined effects with site-specific variables such as substrate availability, soil texture, and canopy structure remain underexplored. Tree litter plays a dual role: chemically influencing microbial physiological/functional traits through priming, thereby affecting CO_2 and N_2O, and physically limiting CH_4 diffusion. These mechanisms collectively determine whether soils act as GHG sources or sinks, and future research should account for how litter priming may override their carbon sink function while integrating site-specific factors to improve GHG predictions and forest management.

Keywords: carbon dioxide; methane; nitrous oxide; greenhouse gas fluxes; temperate forest; litter quality

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1. Introduction

Forests play a significant role in global carbon (C) and nitrogen (N) cycles by acting as both sinks and sources of greenhouse gases (GHGs). Forest soils are major emitters of carbon dioxide (CO_2) and nitrous oxide (N_2O), making them the second-largest source of these gases after wetlands [1], while often acting as net sinks for methane (CH_4), especially in well-aerated temperate forest ecosystems [2]. Temperate forests are distributed between latitudes 30° and 60° across the Southern and Northern hemispheres, with approximately 80% of them located in the Northern Hemisphere.

This latitudinal band typically has a 4- to 6-month growing season, with mean annual temperatures ranging from 5 to 20 °C. It also experiences cold periods at or below 0 °C and receives more precipitation than potential evaporation [3]. Temperate forests are distinguished by massive litter production during autumn [4] and are generally classified into needle-leaf evergreen, needle-leaf deciduous, broadleaf deciduous, and mixed forest stand types [5]. A global analysis showed that annual litterfall ranges from 3 to 11 Mg ha^{-1} and varies significantly by the forest stand types [4]. A meta-analysis study reported that root and leaf litter contribute approximately 48% and 41% of total annual litter, respectively [6]. Moreover, leaves make up over 70% of the above-ground litter [7]. These inputs are important substrates for microbial decomposition, driving soil respiration and influencing GHG fluxes from forest soil. As microbial functional groups break down organic matter and transform inorganic nutrients through their specific metabolic pathways, they release CO_2 [8,9] and N_2O [10,11].

Tree species composition affects soil properties by altering (1) physical processes, including temperature and moisture, (2) chemical aspects such as pH, nutrient availability, and organic matter content, and (3) biological processes like microbial activities of soils through differences in crown structure, leaf quality, litter quality, and root systems [12–14]. Canopy density and light interception level may vary among tree species; this impacts the amount of light reaching the soil and influences soil temperature and water evaporation [15–17]. For example, compared to an evergreen canopy, deciduous plants have greater light penetration, especially in autumn and spring, which can elevate soil temperature and influence soil moisture [18]. These shifts can further impact the activities of the microbial soil community and their processes, ultimately affecting GHG emissions (Figure 1).

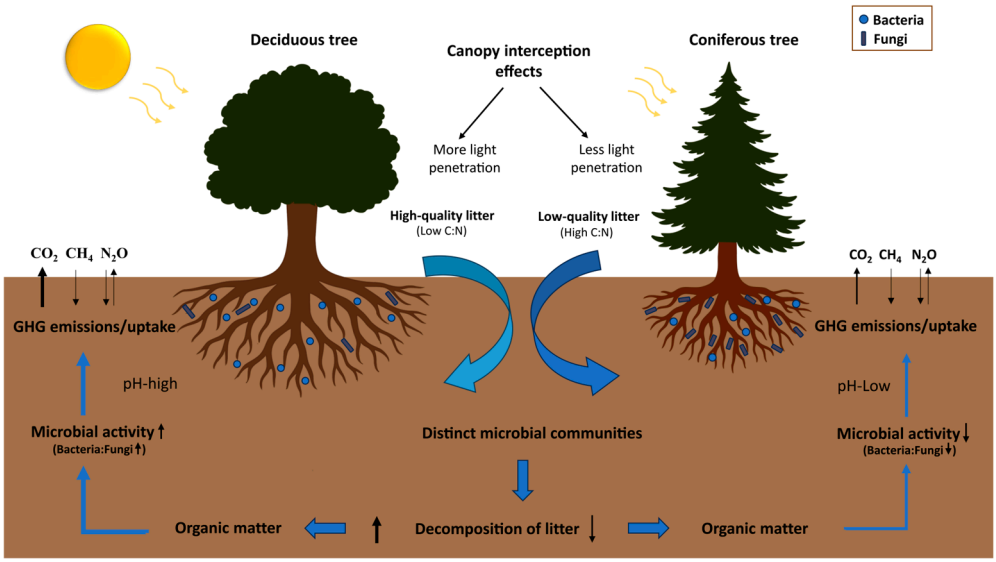

Figure 1. The diagram illustrates key pathways by which tree species affect soil microbial processes and associated GHG fluxes in the forest. The width of the arrows represents the relative strength of each process across different forest types; thicker arrows indicate stronger microbial activity and higher GHG emissions. High-quality litter has a lower C:N ratio, whereas low-quality litter has a higher C:N ratio.

Litter quality determines the litter decomposition rate and especially the lignin content and C–N ratio. For example, soil organic C (SOC) storage is different in deciduous and conifer forests, with more of it in the latter, since coniferous forest litter has a higher C:N ratio and decomposes more slowly than deciduous forest litter [19] due to the presence of higher amounts of lignin compounds. These litter traits not only affect C storage but also influence the structure of soil microbial communities (Figure 1) and their functions [20]; they

also govern the processes of respiration, methanogenesis, denitrification, and nitrification, which result in varying CO_2, CH_4, and N_2O fluxes among tree species.

Given these complex biotic and abiotic interactions, accurately quantifying GHG fluxes requires careful consideration of measurement approaches, each with distinct advantages and limitations. The traditional approaches include laboratory incubation-based and chamber-based methods. While laboratory studies help understand the influence of specific parameters on soil fluxes, they may not reflect field conditions [21]. On the other hand, the chamber method is more cost-effective and can capture soil gas fluxes easily and rapidly from multiple spots within a study area. Another approach, eddy covariance (EC), provides continuous gas exchanges between forest ecosystems and the atmosphere. However, all methods have some methodological limitations and are influenced by environmental variations [22,23]. Moreover, these methods fail to distinguish between root-derived and microbial emissions, whereas stable isotope analysis (e.g., ^{13}C and ^{15}N) can help differentiate microbial and root-derived CO_2 sources [24].

Previous syntheses have shown that soil structure influences microbial activity [25], and that management practices such as thinning can increase GHG emissions [26]. However, the responses of GHG fluxes also depend on climatic factors such as temperature and precipitation [27], as well as soil edaphic properties [28]. The sensitivity of GHG fluxes to these variables varies with biome type. A meta-analysis study by Gatica et al. [28] reported that temperate forest CH_4 fluxes were the most sensitive to climate and soil variables. In contrast, predicting CO_2 emissions from temperate forests heavily depends on other factors, such as SOC and net ecosystem productivity [29]. Despite this growing body of research, a comprehensive synthesis of how abiotic–biotic interactions specifically control GHG dynamics in temperate forest soils is limited, hindering our ability to predict flux direction and magnitude. Understanding how forest vegetation and abiotic factors jointly influence soil biogeochemistry and microbial processes is essential for explaining GHG flux patterns. This review addresses this gap through a qualitative synthesis of how soil physicochemical properties and tree species composition jointly regulate GHG fluxes via their effects on soil C storage, microbial community structure and function, including soil microbial biomass, enzyme activity, and gene regulation. Such understanding is essential for improving biogeochemical models and informing sustainable forest management strategies.

Specifically, this review addresses three main questions:

1. How do physicochemical factors related to forest soils (e.g., temperature, moisture, pH, and nutrient availability) influence GHG fluxes?
2. How does litter quality, influenced by tree species composition, shape soil C and N dynamics and soil microbial activity, ultimately leading to different GHG flux rates?
3. What are the strengths and limitations of the methodologies used to measure GHG fluxes?

To address these questions, we used a scoping review methodology to compile and analyze peer-reviewed research published through 2025. Studies were collected from databases including Scopus, Google Scholar, Web of Science, and ScienceDirect. Our literature search focused on keywords such as “forest GHG fluxes”, “soil temperature”, “soil moisture”, “soil pH”, “soil C and N”, “tree composition”, “litter quality and decomposition”, and “soil microbial activities in temperate forest soil”.

This review emphasizes spatial patterns of GHG fluxes across different forest types (deciduous, coniferous, and mixed) and examines temporal trends where data are available. We include laboratory studies, chamber-based measurements, and EC studies to provide a comprehensive view of methodological approaches. However, chamber-based approaches are more commonly adopted in the literature, highlighting their widespread use in forest soil GHG research.

2. Soil Properties and GHG Fluxes

Soil properties such as soil moisture and temperature are important in shaping GHG fluxes, as they influence microbial activities and nutrient cycling. Moreover, soil pH, nutrient availability, and organic matter quality directly impact the emissions and uptake of CO_2, N_2O, and CH_4, respectively, in forest soils. We summarize studies exploring the effects of soil variables on GHG fluxes from forests in Table 1.

2.1. Soil Moisture Content

Soil moisture has been found to significantly influence GHG fluxes. For CO_2, moderate soil moisture enhances soil CO_2 emission by promoting microbial respiration and root activity [30–32], while intense soil moisture can limit oxygen availability and suppress soil CO_2 fluxes [33]. Meanwhile, Yoon et al. [34] have reported a negligible effect. This shows that other site-specific variables, such as temperature and organic matter decomposition, may mediate these interactions. Soil compaction can negatively influence moisture retention and reduce pore space and airflow, which can trap CO_2 and lead to higher concentrations within the soil [35]. In addition, tree species-specific traits, such as canopy interception, root structure, and evapotranspiration rate, may influence soil moisture levels, resulting in different CO_2 fluxes. For example, in a common garden study of European deciduous species, Vesterdal et al. [36], observed lower CO_2 fluxes from *Picea abies* associated with lower soil moisture. This highlights the importance of accounting for tree species' ecological traits when estimating GHG fluxes.

CH_4 uptake generally declines with high soil moisture [37] due to methanotrophic bacteria's sensitivity to reduced oxygen availability [38,39] and less pore space, resulting in less soil gas diffusivity [40]. However, a global meta-analysis study reported a positive correlation between CH_4 uptake and increased precipitation [28]. The authors proposed that increased water content alleviates water stress, which overcomes the negative effect of oxygen availability. In addition, several studies [41–44] suggest that increased water-holding capacity enhances methanotrophic activity, except during periods of extreme saturation. CH_4 uptake response to moisture is non-linear and follows a parabolic pattern [45]. It shows that there is likely an optimal moisture range beyond which CH_4 uptake declines. Moreover, hydrological conditions in upland and lowland temperate forests regulate CH_4 uptake and production. Christiansen et al. [46] observed greater CH_4 uptake under drier conditions in upland temperate forest, while soils in lower-lying forests acted as CH_4 sources as the water table rose. Gorgolewski et al. [47] also reported that higher soil moisture in lowland soil turned into a CH_4 source compared to well-drained upland soil. High groundwater level creates anaerobic soil conditions and increases CH_4 emissions in lowland temperate forest [48]. However, optimum soil porosity with little soil moisture positively influences CH_4 consumption [49]. A soil porosity range of 39%–66% enhances soil CH_4 uptake in a lowland mixed deciduous forest [50]. Optimum soil porosity and lowered bulk density enhance CH_4 uptake [51].

Similarly, for N_2O, denitrification becomes more significant at higher water-filled pore space (WFPS) levels, defined as >60% [52], while nitrification occurs below this threshold [53]. On a global scale, a comprehensive study by Liao et al. [54] reported that soil parameters contribute 21.8% to N_2O emissions, whereas other hydroclimate factors account for 78.2%. However, in situ studies rarely observe an interaction between these factors, not only for N_2O but also for other GHGs.

Table 1. Influence of soil properties and environmental variables on GHG fluxes from forest soils.

Gases	Country/Forest Ecosystem/Tree Species	Average Temp (°C)	Annual Pr Range (mm)	Study Period	Method Type	Collar Insertion Depth	Influence of Environmental Parameters/Soil Properties on Fluxes	GHG Flux (Annual Avg.)	Reference
CO_2	South Korea/deciduous/*Alnus hirsuta*	−9.2–29.2	1295	20 months	A chamber equipped with an infrared gas analyzer	<1 cm	ST (+), SM (ns)	150	[55]
	South Korea/deciduous/*Quercus mongolica*	0.4–26.5	1212	N/A	Automated closed dynamic chamber	3 cm	ST (+), SM (+)	549.8–539.5	[56]
	South Korea/coniferous/*Pinus koraiensis*	−18.5–35.2	1358	4 years	Closed dynamic chambers	N/A	ST (+), SM (−)	519.8	[31]
	South Korea/deciduous/*Q. serrata*, *Carpinus laxiflora*, *C. cordata*	−5.2–24.7	N/A	6 years	Automatic open–closed chamber	N/A	ST (ns), Pr (+)	205.3–344.4	[30]
		Same as above	Same as above	1 year	Same as above	N/A	High Pr (−), Moderate Pr (+)	224.5–251.3	[33]
	Poland/coniferous and mixed deciduous/*Luzulo pilosae*, *Cladonio pinetum*, *Vaccinio pinetum*, *Potentillo albae*, *Ficario ulmetum*, *Carpinion betuli*, *Dentario glandulosae*, *L. luzuloides*, *Fraxino alnetum*,	N/A	N/A	N/A	Alkaline absorption method	N/A	pH (+)	1.10–1.40 *	[57]
	United Kingdom/coniferous/ *P. contorta*, *P. sylvestris*	N/A	N/A	2 months	Automatic chambers	N/A	ST (+), SM (+)	39.38	[32]
CH_4	USA/coniferous and deciduous/*Q. rubra*, *P. strobus*, *Acer rubrum*, *Tsuga canadensis*	7.1	1066	2 years	Closed static chamber	7 cm	SM (−)	−68.50	[58]
	Germany/deciduous/*Fagus sylvatica*, *A. campestre*, *Fraxinus excelsior*	7.9	720	N/A	Vented static chambers	N/A	ST (+)	−44.85–83.87	[51]
	Poland/coniferous and deciduous/ *F. excelsior*, *C. betulus*, *Picea abies*, *Populus tremula*, *Larix decidua*, *A. glutinosa*, *P. sylvestris*, *Q. robur*, *Prunus avium*	9.9–10.1	452–630	2 years	Dynamic closed chamber	≈10 cm	ST (+), SM (−)	−30.06	[59]
	South Korea/deciduous/ *A. pseudosieboldianum*, *Q. mongolica*	6.3	1578	2 years	Static chamber	N/A	ST (−)	−61.30	[60]

Table 1. *Cont.*

Gases	Country/Forest Ecosystem/Tree Species	Average Temp (°C)	Annual Pr Range (mm)	Study Period	Method Type	Collar Insertion Depth	Influence of Environmental Parameters/Soil Properties on Fluxes	GHG Flux (Annual Avg.)	Reference
CH_4	Austria/deciduous/*P. alba*, *F. excelsior*	10.3	516	1 year	Closed static chamber	N/A	SM (−)	−9.48–58.3	[61]
	France/deciduous/*Q. petraea*	11	808	1 year	Incubation	N/A	SM (−)	−17.71–28.51	[62]
	Czech Republic/deciduous/*Q. robur*, *F. angustifolia*, *C. betulus*, *Tilia cordata*	9.3	550	Once a season	Closed static chamber	5	ST (−), SM (+)	−34.59–47.92	[50]
	United Kingdom/coniferous/ *P. contorta*, *P. sylvestris*	N/A	N/A	2 months	Automatic chambers	N/A	SM (−)	−25.36–70.35	[32]
N_2O	Poland/coniferous and deciduous/ *P. sylvestris*, *Q. robur*, *F. excelsior*, *C. betulus*, *L. decidua*, *A. glutinosa*, *P. abies*, *P. tremula*, *P. avium*	9.9–10.1	452–630	2 years	Dynamic closed chamber	≈10 cm	ST (+)	6.90	[59]
	Japan/coniferous and deciduous/ *Q. variabilis*, *Chamaecyparis obtusa*, *P. densiflora*, *Q. seratta*, *Cryptomeria japonica*, *Castanopsis cuspidata*	N/A	N/A	Once in a study	Laboratory/Closed container method	N/A	WFPS (+)	5.24	[52]
	Japan/Tama temperate forest	14.4	1600	3 years	Static chamber	≈5 cm	WFPS (+)	10.04	[53]
	Germany/deciduous/*F. sylvatica*, *F. excelsior*, *A. campestre*	7.9	720	N/A	Vented static chambers	N/A	pH (−)	−0.90–5.21	[51]
	China/deciduous/*P. davidiana*, *F. mandshurica*, *Betula platyphylla*, *Phellodendron amurense*, *T. amurensis*	−21.5–32	600–800	2 years	Static chamber	10 cm	pH (−)	4.50–39.5	[63]
	Austria/deciduous/*P. alba*, *F. excelsior*	10.3	516	1 year	Closed static chamber	N/A	SM (+)	3.08–4.45	[61]

Temp = temperature; Pr = precipitation; ST = soil temperature; SM = soil moisture; WFPS = water-filled pore space; N/A = no data. "+" indicates a positive influence, "−" indicates a negative influence, and "ns" indicates a non-significant influence. CO_2, CH_4, and N_2O fluxes are presented in mg C m^{-2} h^{-1}, μg C m^{-2} h^{-1}, and μg N m^{-2} h^{-1}, respectively. Negative values indicate gas uptake by the soil. * Flux calculated as mM CO_2 kg^{-1} SOM 24 h^{-1}.

We found that across forest soils, many studies consistently highlight moisture as a key factor for GHG dynamics, though the magnitude and direction of its effects vary with local conditions and forest types (Figure 2). While small-scale studies have observed a reduction in CH_4 uptake with high soil moisture levels, global patterns point to an optimal moisture range for methanotrophic activity [28,44], suggesting that moderate increases in moisture may enhance methanotrophic activity at broader spatial scales. Likewise, balanced moisture levels facilitate both nitrification and denitrification processes [52,53]. Moreover, N_2O fluxes are not just a soil-driven phenomenon [54]. Broader climatic factors such as mean annual temperature, precipitation, and solar radiation play a dominant role. Therefore, hydroclimate–soil interactions must be incorporated into study designs and models to understand spatiotemporal variation in not only N_2O but also all GHG fluxes.

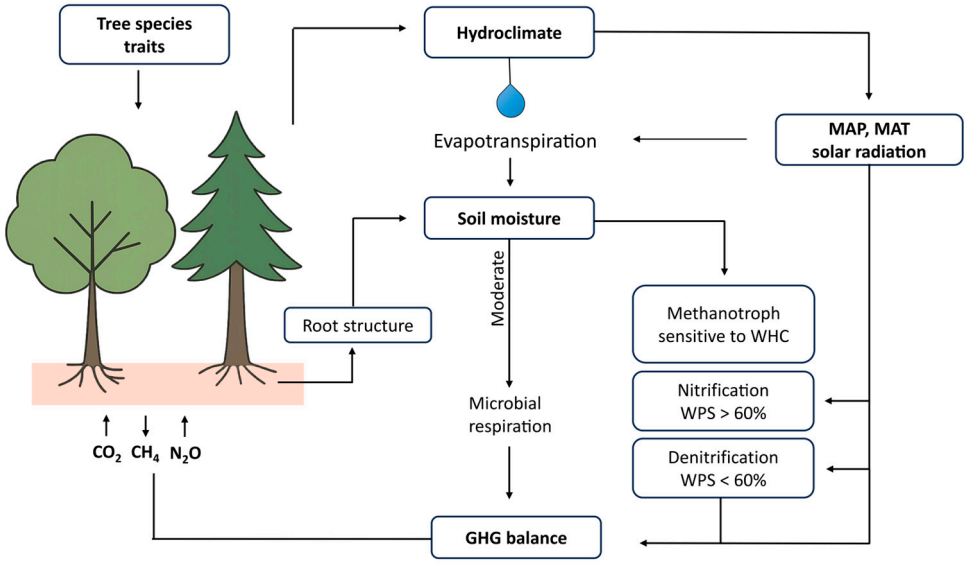

Figure 2. Conceptual illustration of the interactions among tree species traits, hydroclimate variables, and soil properties influencing the GHG balance in forest soils. Hydroclimate factors include mean annual precipitation (MAP), mean annual temperature (MAT), evapotranspiration, and solar radiation. WPS = water-filled pore space; WHC = water-holding capacity.

2.2. Soil Temperature

Soil temperature is a key factor for microbial activity and nutrient cycling. CO_2 emissions consistently increase with rising temperatures [34,55,56,63,64] due to enhanced microbial respiration and organic matter decomposition [65–67]. However, long-term studies indicate that this relationship is moderated by soil moisture availability [30], which can limit respiration despite increasing soil temperature.

In contrast, field studies in temperate forests reported mixed outcomes for CH_4 uptake, ranging from little temperature dependence [68–70] to a negative correlation [60,63] and even a positive correlation [71]. These discrepancies arise due to a limited supply of CH_4 substrate [69], differences in soils with high C and clay content [70], moisture availability [68,71], and reduced the sensitivity of methanotrophs towards temperature [60]. These mixed findings show that temperature alone is not a reliable predictor of CH_4 fluxes in temperate forest soil. The interaction of high temperature and precipitation reduces the temperate forest soil CH_4 uptake capacity [28].

N_2O emissions, on the other hand, show a more sensitive and consistent strong positive correlation with elevated temperatures. Smith et al. [70] found that a 10 °C rise in soil temperature can enhance N_2O emissions by up to tenfold. This response is explained by the fact that at high temperatures, the soil anaerobic zone increases due to high soil microbial activity, creating an environment favorable for denitrification, with ammonia-oxidizing

bacteria (AOB) functioning better than other microbial groups and thereby enhancing N_2O emissions [68]. Supporting this, Ullah et al. [14] reported a significant positive correlation between N_2O and microbial respiration in well-drained *Pinus mariana* forest soil, suggesting microbial processes play an important role in regulating N_2O emissions under aerobic conditions.

Our synthesis indicates that soil temperature is a strong predictor of CO_2 and N_2O fluxes (Figure 3). However, its effects can be mediated by soil moisture, especially in long-term studies. Therefore, more integrated and long-term investigations are needed to better understand how changing climatic variables influence CO_2 fluxes. In contrast, the impact of temperature on CH_4 uptake is less clear and appears to be influenced by multiple factors, including soil texture, moisture, and substrate availability. Future studies should consider multivariate approaches to improve the accuracy of CH_4 flux predictions.

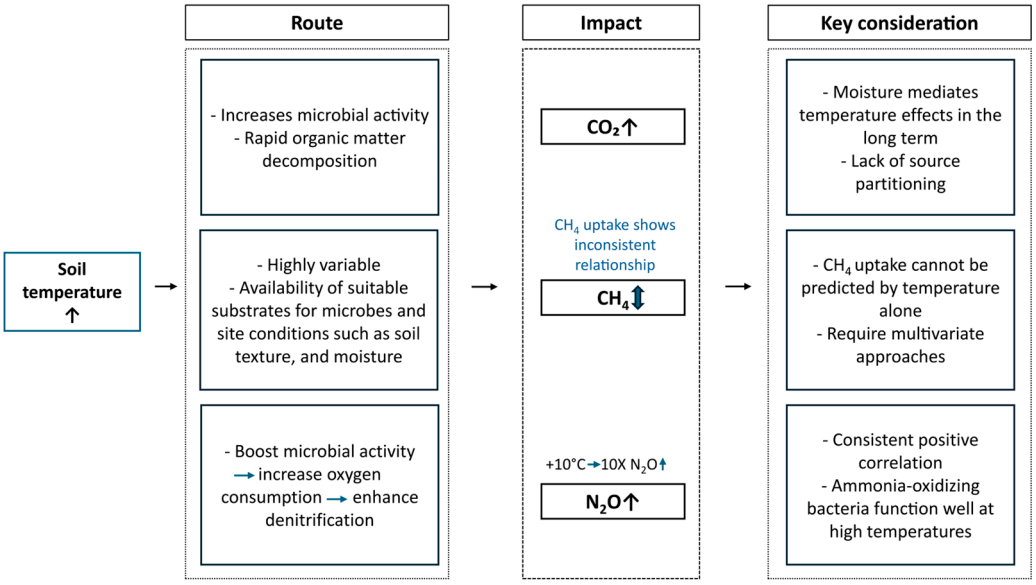

Figure 3. A visual synthesis of the mechanisms and outcomes associated with increased soil temperature in forest GHG dynamics. ↑ indicates an increase in emissions, ↕ while indicates bidirectional change in CH_4 uptake.

2.3. Soil Chemical Properties

Soil chemical properties such as pH and nutrient availability influence GHG fluxes by affecting microbial processes (Table 2).

Table 2. Soil pH and nutrient conditions influence GHG fluxes through the microbial route.

Driver	Microbial Process and Route	GHG Impact and Key Notes
Soil pH	Regulates microbial enzyme activity Affects the methane monooxygenase enzyme Affects nitrification by affecting the equilibrium between NH_4^+ and NO_3^-	CO_2 emissions at neutral pH ↑ CH_4 production at pH 4–7 ↑ CH_4 consumption at pH 6.6–7.5 ↑ Methanotrophs are adaptable across a wide range of pH levels N_2O emissions in acidic soils
Nutrient availability	Increases microbial respiration (CO_2 ↑) Shifts the methanotrophic activity Stimulates nitrification (N_2O ↑)	CO_2 increases if C is not limited CH_4 uptake is reduced when N/SOC is high N_2O is enhanced with increased N inputs

"↑" indicates an increase.

CO_2 emissions increase under neutral conditions, possibly due to optimal microbial respiration and enzymatic activity. In comparison, methanogens and methanotrophs exhibit their highest activity between pH 4 and 7 and between 6.6 and 7.5, respectively [72]. This aligns with the microbial sensitivity of methane monooxygenase (MMO), a key enzyme in CH_4 oxidation.

However, recent studies challenge the previous findings and demonstrate that even in acidic and alkaline environments, methanotrophs act as a CH_4 sink [73]. This adaptability points to the methanotroph's composition shift across the pH gradient. In contrast, acidic soil influences the nitrification process and disturbs the equilibrium between NH_4^+ and NO_3^-, thereby reducing N_2O production [74]. These patterns underline that each GHG pathway has a distinct pH sensitivity, microbial adaptation, and soil chemistry interaction. It suggests that more detailed, microbially informed research is needed to better understand how pH influences GHG fluxes under different soil conditions.

In addition to pH, soil nutrient availability, particularly N, also regulates microbial dynamics and GHG fluxes. An increase in soil N content generally leads to higher CO_2 emissions if soil C is not limited [75], likely by boosting microbial respiration and decomposition activity. Recent studies show that higher microbial biomass, both C (MBC) and N (MBN), increases CO_2 emissions and CH_4 uptake in forest soil [51]. This supports the idea that larger microbial communities play a key role in C cycling and GHG fluxes. Notably, CH_4 uptake was negatively correlated with soil chemical properties (SOC and total N) but positively influenced by physical factors such as soil porosity and lower bulk density, while N_2O emissions were negatively influenced by soil pH and bulk density and positively affected by organic C availability in the NO_3^- rich soil [76]. This suggests that gas diffusivity and soil aeration may override nutrient availability in determining CH_4 fluxes. Similarly, acidic conditions and limited oxygen diffusion may restrict nitrification and denitrification processes but are influenced by C availability in N-enriched soil. Collectively, this pattern suggests coupled interactions between nutrient status, microbial capacity, and soil physical structure. Yet, despite their importance, the relationship between these factors has received limited attention so far.

3. Impact of Tree Litter on GHG Fluxes

This section discusses how the chemical composition of litter affects decomposition rate and SOC stocks, followed by how the litter layer affects GHG fluxes and microbial communities.

3.1. Litter Quality, Litter Decomposition, and SOC Stock

The rate of litter decomposition and release of C and N in forest soils is determined by litter chemical composition [77,78]. It is well known that tree species with slow-decomposing litter have higher C stock accumulated in the forest compared to tree species with faster decomposing litter [79]. For example, coniferous tree species have thick C-rich forest floors due to the presence of lignin-rich needles [80]. However, mineral soils under coniferous species accumulate relatively small amounts of SOC due to reduced microbial activity in the acidic soil [81].

While recalcitrant organic matter is commonly thought to play a key role in C stabilization, some studies suggest that labile organic matter is equally important in stabilizing soil C [82,83]. Fast-decomposing litter enhances plant litter transformation and microbial stabilization, as increased microbial residue production leads to greater SOC accumulation in mineral soils [84,85]. Fast-growing microorganisms use this high-quality litter to produce microbial necromass, which in turn increases the SOC stock in the soil [86,87] (Figure 4).

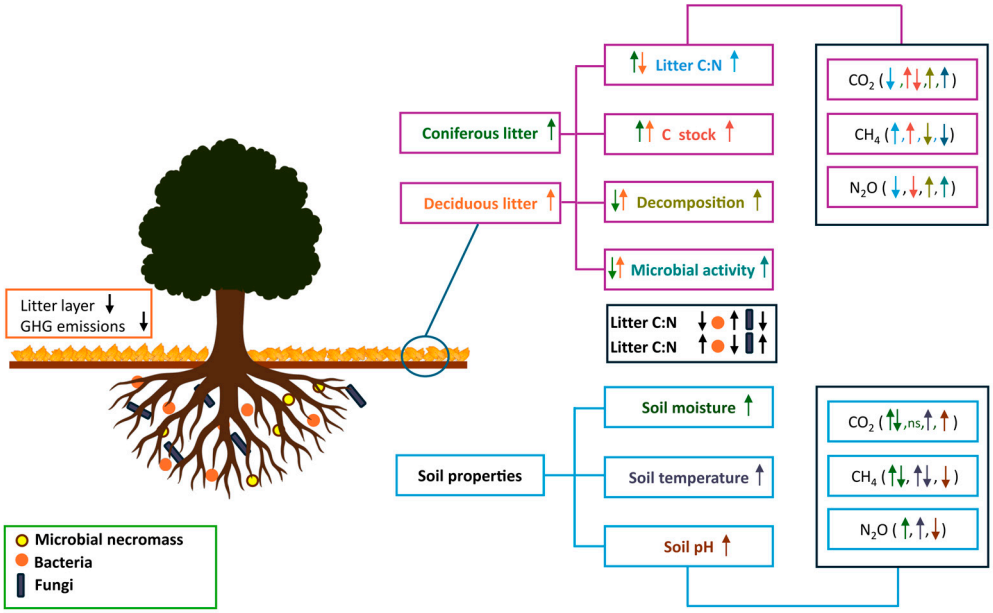

Figure 4. A comparative graphical representation of CO_2, CH_4, and N_2O fluxes under varying litter layer attributes and soil properties across different forest types. Each property, such as litter C:N ratio, is represented by a unique color. Arrows of the same color indicate the direction of that property's influence on GHG: ↑ indicates an increase, ↓ indicates a decrease, and ns indicates no significant change in emissions.

However, this microbially mediated C stabilization process is not always straightforward. By using stable isotopes, Craig et al. [88] found that although the addition of labile litter increases short-term soil C input, it also stimulates microbial growth, which speeds up existing SOC (including necromass) decomposition and offsets the positive effect of litter quality on long-term C retention. The phenomenon is called litter priming [89,90]. Their findings challenge the idea of necromass as the main factor determining SOC persistence in temperate forests. Instead, it suggests other factors, such as litter priming and alternative pathways in SOC formation, can decouple microbial processes from SOC stabilization [88,91].

Supporting this complexity, lab incubation studies by Cai and Feng [92] found that fast-decomposing substrate (^{13}C-labeled glucose) showed a rapid and transient increase in necromass, while lignin-rich substrate supported steady and slow necromass accumulation. They also reported a positive but scattered correlation between substrate input and necromass production, suggesting that soil properties and microbial diversity may affect necromass accumulation efficiency. This indicates that C stabilization by microbes is a complex process and cannot be predicted by substrate type alone. However, lab-prepared soils may not fully represent natural soil conditions, where potential interactions between plant roots and microbes could further modify these processes.

The priming effect itself is influenced not only by litter chemistry [91] but also by the timing of litter input and environmental conditions [93]. Seasonal fluctuations in priming-induced soil C release are mediated by soil moisture and temperature, whereas interannual patterns reflect the cumulative effects of litterfall quantity and timing [94]. Bréchet et al. [94] demonstrated this in a three-year litter manipulation experiment where priming effects on mineral soil C were initially suppressed during winter due to low temperatures that inhibited litter decomposition. Over the subsequent year, accumulated litter inputs and slower C turnover rates maintained a sustained supply of labile substrates, which supported prolonged microbial activity and enhanced soil respiration.

Moreover, an incubation study on broadleaf and mixed Korean pine forest soils showed that, after some time, microbes reach the metabolic saturation point where additional input does not further stimulate the decomposition of existing soil SOC [95]. This indicates that the magnitude of priming is controlled by metabolic capacity and nutrient availability, and that excess labile C input may promote C stabilization rather than loss. These findings suggest that environmental variables such as soil temperature, moisture, and the temporal dynamics of litter inputs play critical roles in regulating microbial activity and, consequently, both SOC turnover and GHG fluxes from soil–aspects that warrant further investigation in natural forest ecosystems.

3.2. Influence of Litter Quality and Litter Layer on GHG Fluxes

The relationship between forest type and GHG fluxes is shaped not only by litter quality but also by nutrient turnover and soil nutrient status. We summarize the tree species-specific influence on GHG fluxes driven by litter traits in Table 3.

Table 3. Species-specific influence on GHG fluxes driven by litter traits.

Factor	Mechanism	Effect on CO_2	Effect on CH_4 Uptake	Effect on N_2O	References
Litter quality	Highly labile C and N in deciduous and mixed forest litter Increases substrate availability	+	+	↔/+	[13,96–98]
Litter removal	Reduces substrate Improves gas exchange Temporary shift in microbial composition	−	+	−	[99–101]
Doubling the litter amount	Increases labile C May trigger priming	+	+	+	[22,90,93]
Species identity	Influences litterfall Shape the soil microbial community	−	+	↔	[58,99,100]
Organic horizon depth	Deep horizons may restrict gas diffusion	N/A	−	N/A	[75]

"+" indicates a positive influence, "−" indicates a negative influence, and "↔" indicates a dependency on soil condition. "N/A" indicates no available data.

Deciduous and mixed forests, particularly those dominated by *Quercus* spp., appear to increase microbial substrate availability and enhance C and N turnover due to rapid decomposition compared to coniferous forests [13,96], resulting in higher CO_2 emissions (+17.5%) and increased CH_4 uptake (+12.4%). However, N_2O emissions are small and not significantly affected by forest types, suggesting that, compared to litter composition, other factors, such as soil nutrient status, may play a more dominant role in the nitrification and denitrification processes. For example, Ambus et al. [97] demonstrated high N_2O emissions in deciduous forest soil, but forest type showed a pronounced effect on these emissions, as the deciduous forest soil in their study was more N-rich compared to the previous study. This aligns with Liu and Greaver [98], who found that soil N level, rather than forest type, is the main factor regulating N_2O emissions. These findings collectively indicate that, in addition to litter source, the soil nutrient profile under different forest types should also be considered in forest type studies.

In addition to differences in litter quality and nutrient cycling between forest types, the presence of the litter layer on the forest floor itself also plays a significant role in GHG fluxes by regulating gas diffusion and soil microclimate. For example, a thick litter in coniferous forests can decrease the soil water content by acting as a barrier to rainfall infiltration and can also limit CH_4 uptake by limiting gas diffusion in coniferous soil compared to broadleaf forest [99]. In a short-term field experiment, Leitner et al. [100] demonstrated that litter

layer removal reduced CO_2 emissions by 30%, produced a seasonal (autumn and winter) increase in CH_4 uptake by 16%, and led to a turning of soil from a net N_2O source to a slight N_2O sink. Microbial composition was temporarily affected one week after litter removal, but this effect did not last for a long time.

Similarly, Cui et al. [101] revealed that litter removal enhanced CH_4 and N_2O uptake by 9% and 16%, respectively, in temperate forests, which could be attributed to the removal of physical barriers and an increase in atmospheric CH_4 diffusion [100]. The absence of surface litter may accelerate evaporation, resulting in lower soil moisture and a more favorable aerobic environment for methanotrophic CH_4 oxidation [101]. However, soil structure, including the proportion of sand, silt, and clay, may mediate CH_4 uptake rather than litter removal.

This finding implies that the litter layer restricts CH_4 diffusion, and forests with dense layers may have a lower potential for CH_4 uptake. Moreover, microbes are more resilient to litter disturbance and may buffer the long-term impact of litter removal on GHG, but seasonal variations must be considered [100].

The impact of litter layer removal can vary between forest types, especially in deciduous forests, where labile litter serves as a key source of substrate for microbial activity. A recent meta-analysis study by Fan et al. [22] reported a decrease in soil GHG emissions after the removal of the litter layer by reducing soil MBC, TC, TN, SOC, and dissolved organic C concentration in forest soil, as well as an increase in emissions after doubling the litter amount due to enhanced labile C in soil. Moreover, doubling the litter amount shows a priming effect on the existing litter and enhances the litter decomposition rate, increasing CO_2 emissions [90]. However, litter priming effects depend on litter quality, soil fertility, and potentially the duration of observation [93]. This underscores the need to partition the impact of the litter layer on soil nutrient profiles and gas exchange across different forest types to improve the predictability of GHG fluxes.

In the case of CH_4, the influence of the litter layer as a physical barrier can be offset by ecosystem productivity. Jevon et al. [58] found that CH_4 uptake was positively correlated with the amount of litter input, contradicting previous studies on CH_4 uptake under thinner litter layers. The authors suspected that CH_4 uptake responded to greater overall productivity rather than litter layer depth, especially in areas with higher litterfall. Compared to a thicker litter layer, a deep organic horizon may serve as a posing barrier to CH_4 transport in forest soil. It was observed under *Q. rubra* species. These findings emphasize the need to assess how litter layers, driven by tree species identity, contribute to soil nutrient status, GHG diffusion, and microclimate regulation across forest types (deciduous, coniferous, mixed), particularly under varying climatic conditions.

3.3. Tree-Microbe Interactions as Drivers of Soil GHG

Tree species shape microbial communities through their litter chemistry, as microbial communities can change and adapt according to the type of plant litter in specific environments [102]. Early decomposition is mostly controlled by litter chemistry, as shown by Bray et al. [103], where variables like litter N% and C:N ratio explained 60%–72% of the variation in decomposition rates at 1, 2, and 8 months. However, in the later stages of decomposition, microbial community composition explained 67% of the variation, highlighting a temporal shift from litter chemistry to microbial function. This shift was supported by Fernández-Alonso et al. [104], who observed changes in microbial populations over time, with fungi favored in high C:N environments. Notably, conifer *Tsuga canadensis* litter supports the fungal-dominated microbial community compared to other conifer species, possibly due to its high hydrolysable tannin content [105]. These findings indicate that the tree species not only influence microbial composition but also the succession of microbial communities

over time. In addition to litter C:N, other substrate qualities, such as lignin and tannins, can enhance predictions of species-specific microbial response.

The soil microbial communities are strongly influenced by soil horizon and seasonal variations, mainly due to differences in temperature, moisture, and the supply of nutrients [106]. López-Mondéjar et al. [106] observed a high abundance of *Proteobacteria* and *Bacteroidetes* in the litter horizon of deciduous *Q. petraea*. These bacterial phyla thrive in a labile organic environment and are associated with rapid decomposition and CO_2 production. In contrast, organic and mineral horizons were dominated by *Acidobacteria*, *Actinobacteria*, and *Firmicutes*, which are adapted to low-nutrient environments and specialized in degrading recalcitrant organic compounds.

Seasonal dynamics further shape these communities. The summer and winter communities in the litter layer showed increased abundance of *Gp1* and *Gp2 Acidobacteria* and *Ferruginibacter,* whereas *Luteibacter* was more abundant in spring. Mineral soil bacteria exhibited the most pronounced seasonal variation in summer, when *Rhodanobacter*, *Acidobacterium*, *Ferruginibacter*, *Bradyrhizobium*, *Burkholderia*, and *Mucilaginibacter* were more abundant. This summer peak coincided with higher extracellular enzyme activity, soil N content, and pH, conditions that favor both decomposition and denitrification processes [106]. Notably, several of these summer-abundant genera (*Rhodanobacter*, *Burkholderia*, *Bradyrhizobium*) are known denitrifiers capable of producing N_2O [107–109], suggesting that seasonal warming may enhance N_2O emissions from temperate deciduous forests.

In coniferous forests, seasonal variation is less pronounced, as litter input is not seasonally restricted [110]. Regarding fungi, litter layers experience large shifts in fungal composition because litter chemistry changes with decomposition and the timing of input. Meanwhile, root-associated fungi in the deeper horizon show minor seasonal variation, as they rely on relatively stable root exudates rather than variable litter inputs [111]. This spatial and temporal partitioning of microbial communities suggests that different soil depths contribute to GHG fluxes through distinct microbial pathways, with litter horizons showing high seasonal variability in CO_2 and potentially N_2O emissions, while deeper horizons maintain more stable but lower levels of microbial activity.

The composition of soil microbial communities shapes microbial physiological traits, specifically microbial C use efficiency (CUE) [112] and N use efficiency (NUE) [113,114]. These microbial physiological traits play an important role in GHG fluxes [115]. A high CUE allows more C to be incorporated in microbial necromass, resulting in less CO_2 loss, while a low CUE results in more CO_2 being released through cellular respiration [8,116]. These efficiencies are controlled by the level of soil C and N. Low soil C and high N lead to higher CUE and C retention, while excess C and low N suppress CUE and lead to more CO_2 release from the soil [117]. Through litter composition, tree species influence how efficiently soil microbes use C and store it in their biomass. A few studies show that tree species with fast-decomposing litter enhance microbial growth and CUE, as well as increasing mineral SOC [88,118,119]. However, Craig et al. [89] also reported that the effect was pronounced during the intermediate stages of decomposition. This could be due to the strongest effect of litter quality on microbial physiological traits and production of microbial extracellular products. The author suggested that high-quality litter addition enhances CUE and microbial biomass production, which enhances SOC decomposition rather than soil necromass. The higher microbial growth and efficiency may elevate the decomposition of new or old SOC. The accurate assessment of soil nutrient availability, substrate quality, and microbial community—physiological activities that influence CUE—is essential for making more reliable predictions of long-term soil C storage [120].

Similarly, NUE indicates N retention, with high NUE suggesting that most of the immobilized N is retained in microbial biomass under N-limited conditions [114], while low NUE shows more N is transferred to the atmosphere in the form of N_2O [121].

Therefore, the interaction between tree litter input and microbial functional traits, together with soil physicochemical conditions, determines whether soils act as a source or sink of CO_2 and N_2O. Moreover, soil N availability, both from litter and soil, appears to be a stronger regulator of microbial activity and GHG emissions than C alone (Figure 5).

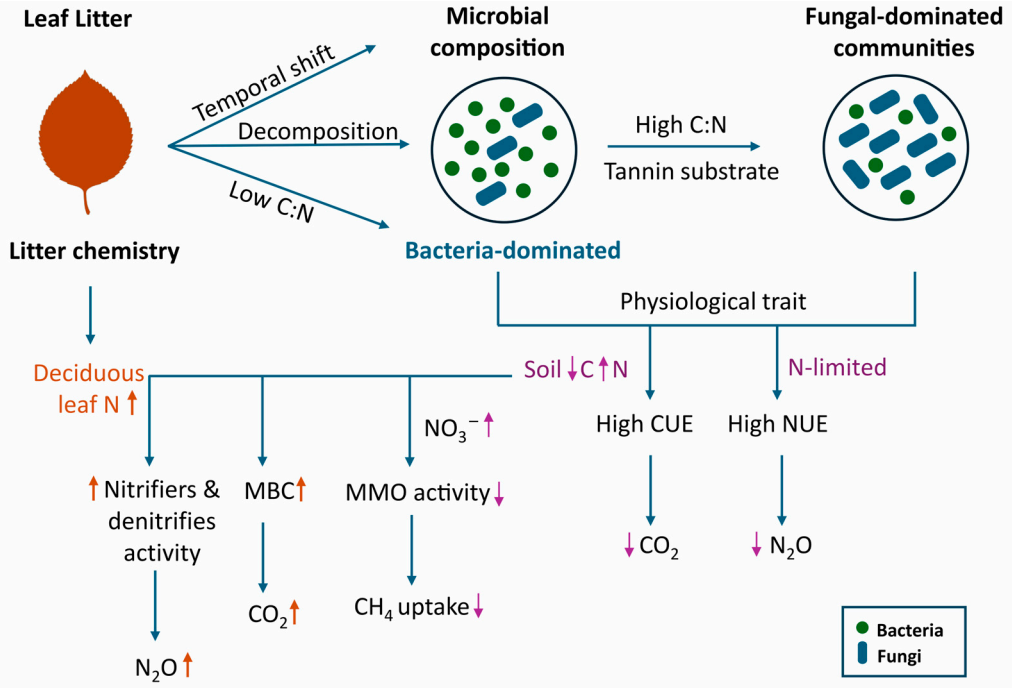

Figure 5. Chemical composition of tree leaf litter, particularly N content, along with soil N availability, shapes soil microbial composition and activity, thereby influencing GHG fluxes. Arrow colors correspond to specific properties (e.g., orange = deciduous leaf N). CUE = microbial C use efficiency; NUE = microbial N use efficiency; MMO = methane monooxygenase.

Soil microbial biomass reflects the size of the living soil microbial community [122], and MBC and MBN are reliable indicators of microbial activity that influence nutrient cycling and GHG fluxes [51]. Soil nutrient status determines the MBC and MBN pattern [123,124]. For example, Kumar et al. [125] reported higher CO_2 emissions from *Q. leucotrichophora* forests than from *P. roxburghii* forests, where total N and MBC enhanced the microbial activity in a favorable soil structure (i.e., lower bulk density). Similarly, Rubaiyat et al. [51] observed a significant positive correlation between CO_2 emission from deciduous forest and soil MBC and MBN, indicating that greater microbial biomass led to greater CO_2 emissions, while CH_4 uptake was positively correlated with MBC only. Likewise, in a deciduous *Camellia oleifera* forest, Qin et al. [126] observed higher N_2O flux than in coniferous *P. elliottii* forests; it is likely that high leaf litter N content stimulated nitrifiers and denitrifiers. These patterns suggest that N-rich environments in deciduous forests promote microbial growth and activity, enhancing both CO_2 and N_2O fluxes.

In addition, the availability of C and N supports microbial enzyme activity and leads to increased CO_2 emissions from forest soil [127,128]. The activities of the C-acquiring enzyme are determined by the composition and quantity of soil organic matter (SOM), mean annual temperature, and the site's precipitation [129]. The presence or addition of N increases the microbial production of C and N-acquiring enzymes, β-glucosidase, cellobiohydrolase, β-xylosidase, and N-acetyl-β-glucosaminidase, leading to more litter

decomposition under high temperatures and, subsequently, more CO_2 emissions from forest soil [130–132]. Tian et al. [132] reported that 14 years of long-term warming enhances the activities of β-glucosidase, N-acetylglucosaminidase, and leucine aminopeptidase by 31%, 106% and 46%, respectively, and increases CO_2 emissions by 39%. This can be explained by the reduced incorporation of C and N into microbial biomass, with decreases of 15% and 17% in CUE and NUE, respectively, along with greater fine root biomass, leading to the release of more CO_2 and inorganic N into the environment.

Moreover, studies have reported that the abundance of C degradation genes, such as *SGA1*, *amyA*, *TYR*, *chitinase*, and *pectinesterase*—which are involved in the breakdown of starch, lignin, chitin, and pectin—dominates and can be used to predict enzyme activities and CO_2 emissions from forest soil [133,134]. The functional diversity of C and N cycling-related genes is an important contributor to GHG fluxes [135], with their abundance shaped by soil physicochemical properties and climate (Table 3). Wang et al. [134] demonstrated this through metagenomic analysis of *Robinia pseudoacacia* forests of China, where regional differences in C-cycling gene abundances exceeded local variations. Northern forests showed significantly higher abundances of genes encoding starch-degrading (*amyA*, *SGA1*), cell wall-degrading (*pectinesterase*, *chitinase*), and formaldehyde assimilation (*glyA*, *ppc*) enzymes, corresponding with elevated CO_2 emissions. Conversely, southern forests exhibited higher CH_4 emissions. These regional patterns were primarily driven by soil pH, temperature regimes, and moisture gradients, which shaped distinct microbial functional communities and their associated C flux profiles.

In the case of CH_4, methanotrophs use different biological cycles to consume CH_4 by oxidizing it into CO_2 and H_2O. Type II methanotrophs, such as *Methylocystis* spp., *Methylosinus* spp., are more commonly found in forest soil [136] and consume CH_4 through the Serine cycle [137]. CH_4 oxidation is primarily mediated by the particulate MMO (pMMO) enzyme, which is present in almost all methanotroph classes, including Methylocystaceae, Methylococcaceae, Verrucomicrobia methanotrophs, and NC10 phylum bacteria [138]. A key subunit of pMMO is encoded by the *pmoA* gene, which serves as a widely used biomarker for identifying and quantifying methanotrophs in soil [139].

Climatic conditions and soil properties shape the abundance of *pmoA* genes in the forest ecosystem. A study by Heděnec et al. [139] showed that *pmoA* abundance was positively correlated with the mean annual temperature and precipitation but negatively correlated with the total organic C in temperate regions. These patterns suggest that methanotrophic communities respond dynamically to both climate drivers and substrate availability.

The abundance of Upland soil cluster alpha (USC-α) methanotrophs, another dominant group in temperate forest soil, is positively correlated with CH_4 uptake [136], and is influenced by tree species composition. Täumer et al. [140] observed a higher abundance of the USC-α gene in soil under *Quercus* spp. and *Pinus* spp. compared to *P. abies* and *Fagus sylvatica* forests in Germany. Tree species appear to influence methanotrophs through their chemical exudates. Maurer et al. [141] reported that monoterpenes released from the litter and root of *F. sylvatica* and *P. abies* inhibited CH_4 oxidation by 90% in laboratory incubations, suggesting that secondary metabolites from these species may substantially reduce the CH_4 sink capacity of forest soils, though the magnitude of this effect under field conditions remains to be quantified.

Conversely, tree–methanotroph interactions are not limited to chemical inhibition. A study shows that the presence of fine roots and ectomycorrhizal hyphae of *P. contorta* and *P. sylvestris* significantly enhances CH_4 uptake [32] by providing labile C compounds (methanol and formate) that support active methanotroph communities [142–144]. These contrasting effects exemplify how chemical inhibition by monoterpenes and nutritional support through root exudates can operate simultaneously with opposing outcomes.

Alongside tree species composition, soil properties also regulate USC-α abundance; for example, organic C, NH_4^+, and soil pH negatively influence the USC-α gene abundance [140]. The role of N, particularly NO_3^-, in regulating methanotrophic activity remains complex and site-dependent. Jang et al. [60] highlighted that NO_3^- can suppress CH_4 uptake in a Korean temperate forest by inhibiting MMO activity. However, earlier studies reported no inhibitory effect of inorganic N on CH_4 uptake [145–147]. These contradictory findings point to the potential influence of site-specific factors, such as methanotroph community composition, N form and concentration, soil pH, and moisture levels, which may mediate the N–CH_4 interaction. Table 4 summarizes the main microbial taxa, key functional genes, and environmental drivers regulating CO_2, CH_4, and N_2O fluxes in forest ecosystems.

Table 4. Summary of specific microbial taxa or functional gene pathways involved in GHG emissions.

GHG	Main Microbial Taxa	Key Functional Genes	Environmental Drivers	References
CO_2	*Actinobacteria*, *Proteobacteria*, *Acidobacteria*, *Chloroflexi*, *Bacteroidetes*, *Phanerochaete chrysosporium* *Ascomycota*, *Basidiomycota*, *Piloderma*, *Tylospora fibrillose*, *Cortinarius biformis*	*SGA1*, *TYR*, *chitinase amyA*, *pectinesterase*, *glx*, *cbhI*	Soil pH positively correlates with CO_2-cycling gene abundance, while soil moisture, organic C, and N show negative relationships.	[111,133,134,148,149]
CH_4	*Methylocella*, *Methylcystis*, *Methylosinus*, *Methaothermobacter*, *Methanoculieus*, *Methanospirillum*, *Metanoregula*, Upland soil cluster alpha methanotrophs	*ppc*, *glyA*, *pmoB*, *mttB*, *mch*, *pmoA*	Gene abundance is positively influenced by mean annual temperature and precipitation but negatively affected by soil organic C, moisture, NH_4^+, and pH.	[68,134,136,140,150]
N_2O	Nitrifiers: *Crenarchaeota*, *Nitrospira*, *Nitrobacter*, *Nitrococcus*, *Nitrosococcus*, Denitrifiers: *Cyanobacteria*, *Acidobacteria*, and *Planctomycetes*	*amoA*, *amoB*, *hao*, *nosZ*, *nirK*, *nirS gdh*	Nitrification gene abundance (*amoA*, *hao*) is negatively correlated with NH_4^+, while denitrification gene abundance (*nirS*, *nirK*) shows negative correlations with NO_3^-. Overall, N_2O-related gene abundances are positively influenced by temperature and moisture and negatively affected by NH_4^+, NO_3^-, SOC, and C:N ratio.	[68,148,150–152]

Given these complexities, future research should adopt long-term, integrative studies that simultaneously track microbial succession, functional gene dynamics, and substrate quality across contrasting forest types and climatic gradients. Two priorities are particularly critical: first, resolving the mechanisms underlying site-dependent N effects on methanotrophs, and second, quantifying the relative importance of different tree-mediated pathways (litter chemistry, root exudates, secondary metabolites) under field conditions. Improving our understanding of microbial C and N use efficiency in response to tree species composition will be essential for predicting whether forest soils act as net GHG sources or sinks under changing environmental conditions.

4. GHG Measuring Approaches and Their Limitations

Many studies have demonstrated how biotic and abiotic factors influence GHG fluxes, but synthesizing these results is often challenging due to differences in measurement methods. Techniques vary in temporal and spatial scale and in sensitivity, which can lead

to contrasting interpretations of the same factors. Therefore, it is important to consider measurement approaches alongside GHG regulators and the establishment of unified protocols to improve comparability across studies. To better understand these methodological differences, it is useful to summarize the main approaches used to quantify GHG fluxes in forests. GHG fluxes from forests are quantified using chamber-based methods [153,154], laboratory experiments [155], the EC method [156], the root exclusion method [157], and the less commonly applied isotopic techniques. In Table 5 we summarize the strengths, limitations, and suggestions for each method.

Table 5. Comparison of methods for measuring and partitioning soil GHG fluxes in forest ecosystems.

Method	Strengths	Limitations	Suggestions
Chamber-based (static/dynamic)	Widely used and accessible Suitable for multiple gases Measures GHG at multiple points simultaneously	Long-term collar use alters soil conditions Manual disturbance Limited spatial integration Temperature, pressure, and humidity artifacts No standardization between systems	Regularly monitor collar effects Standardize chamber design and protocols Increase the number of replicates for spatial coverage Use automated chambers
Open dynamic chambers	Continuous gas flow prevents accumulation bias Real-time data Less pressure/temperature influence	Technically complex and expensive Limited portability Requires constant power and calibration	Develop cost-effective portable systems Combine with automated data logging Combine with closed chambers for comparison
Laboratory	Controls for specific factors (litter, moisture) High repeatability	Transport and storage Poor field representation Homogenization alters soil structure	Avoid excessive sieving Integrate with in situ measurement to enhance reliability
Eddy covariance	Continuous high-frequency flux data Captures seasonal/annual trends Large spatial scale ~1 km^2	Underestimates during low turbulence and in dense forest Unable to partition the CO_2 sources	Use with chambers for validation Apply machine learning for bias correction Combine stable isotopes to partition the CO_2 sources
Remote sensing (satellite-based)	Large-scale/global coverage High temporal and spatial resolution Continuous temporal monitoring	Limited accuracy for near-surface emissions Poor performance in cloudy regions Cannot directly quantify soil fluxes Dependence on atmospheric correction models	Integrate satellite data with ground-based chambers Develop algorithms to separate soil vs. vegetation signals
Open-path Fourier transform infrared spectroscopy (FTIR)	Near-ground micrometeorological method Multiple-gas detection Continuous monitoring Non-destructive	Short path range (less than 500) Sensitive to weather (temperature, humidity, and turbulence) Scaling results from the site to the regional level is difficult	Combine with flux towers or chamber data for validation Improve correction Develop low-cost, portable FTIR systems for broader field use
Modeling (e.g., forest-DNDC)	Simulates multiple processes (decomposition, nitrification, etc.) Covers local to global scales Useful for scenario testing and upscaling	Dependent on input data quality May deviate up to 1 order of magnitude Limited by sparse validation data Regional bias toward temperate zones	Use high-quality, site-specific input data Validate models with chamber and EC data Include long-term monitoring data for model refinement
CO_2 partitioning root exclusion	Simple and cost-effective	Soil disturbance from trenching Residual roots decomposition biases the data	Combine with isotopic labeling
Isotopic labeling (^{13}C, ^{15}N)	Accurately partitions sources (plants, SOM, microbes) Tracks priming and N cycling Enables source tracking (e.g., denitrification via $\delta^{15}N$)	Expensive, complex logistics Difficult to apply in situ Short ^{13}C signal persistence Difficult in low-flux forest soils, low fluxes reduce signal strength	Combine with EC or chamber data Target plots with high activity Comparative studies across forest types

Among these, the flux chamber-based method is most widely used [44,153,158]. The chamber collar is inserted a few centimeters deep [159] and left in place for 24 h to several months [160]. However, it is reported that long-term collar deployment increases the soil bulk density, reduces microbial biomass, lowers roots inside the collar, and causes a reduction in CO_2 emissions and the SOC decomposition rate [23]. Therefore, regular

monitoring is required to assess the changes in soil properties so that adjustments can be made early to avoid possible disparities in data. Additionally, automated chambers can be used to minimize manual disturbance and enhance the temporal resolution of GHG measurements [161].

Laboratory approaches are useful for isolating the effects of specific parameters, such as soil temperature and litter effect, on emissions [155]. However, maintaining consistent soil conditions during sampling and transport is challenging [1]. While homogenized samples are better for elucidating the parameter observation [155,162,163], lab processing techniques, like sieving and air-drying, significantly alter soil structure and microbial activity [1]. The EC method directly analyzes the turbulent heat and gas exchange between forest ecosystems and the atmosphere [164,165]. This approach is sensitive to nighttime [166,167], weather conditions, and fluctuations in solar radiation, which can introduce uncertainties in measuring the annual C balance [168]. The studies can include integrating the EC method with chamber-based techniques to validate flux estimates [167,169], applying machine learning models to correct biases caused by low turbulence, and using alternative methods, such as flux partitioning models and stable isotopes, to partition the CO_2 sources to enhance data accuracy.

Remote sensing offers large-scale, high-resolution, and continuous monitoring, but has limited accuracy for near-surface emissions and cannot directly quantify soil fluxes [170]. Integrating satellite data with ground-based chambers and developing algorithms to separate soil and vegetation signals can improve reliability [171,172].

Open-path FTIR enables simultaneous, non-destructive measurement of CO_2, CH_4, and N_2O. While its short detection range and weather sensitivity pose challenges, combining it with flux-tower systems and improved correction algorithms enhances field applicability [173,174].

Modeling tools (e.g., Forest-DNDC) simulate multiple biogeochemical processes across scales and are valuable for scenario testing and upscaling [175]. However, they rely heavily on input data quality and validation; using site-specific data, chamber and EC validation, and long-term monitoring can improve model accuracy [176,177].

The root exclusion method is widely used to differentiate between CO_2 emissions from plant roots and microbial respiration due to its low cost and ease of applicability [157]. However, it disturbs the soil and the remains of dead roots in the soil after trenching biases the fluxes [178].

Isotopic labeling with ^{13}C–CO_2 and ^{18}O–CO_2 allows us to distinguish between these sources. Variations in stable isotope ratios help clarify the relative contributions of microorganisms, SOM, and roots to rhizosphere priming effects [179]. However, this method is mainly suitable for short-term studies because ^{13}C can deplete quickly, causing the isotope signatures of organic matter to become like those of labeled plants over time [180]. As a result, repeating stable isotope labeling of both soil and plants is necessary over a longer period to accurately track CO_2 fluxes.

This approach, however, faces challenges in forest ecosystems due to its high cost and logistical difficulties, complex plant—soil interactions, and slower C cycling than other terrestrial ecosystems. Future studies can target specific plots within the forest ecosystem representing key components, such as areas with high root biomass or microbial activity. By combining isotopic measurements with methods like EC, we can better partition and more accurately assess the contributions of plants and soil to overall ecological respiration [181] and reduce the frequency of isotope application.

Moreover, each ecosystem has its unique isotopic signature based on vegetation type, SOM signature, climatic conditions, and disturbance history [182–184]. For example, isotopic signatures are usually influenced by temperature, soil moisture, and precipitation.

By comparing forests in different climate zones, we can trace variation in isotopic values and reduce the cost and logistical complexity of isotope labeling.

As we discussed earlier, microbial activities are responsible for N_2O and CH_4 fluxes and are affected by nutrient availability. Changes in the $\delta^{15}N$ ratio predict plant root microbial N fixation capacity [185] and the consumption and production of CH_4 and N_2O. Forest soils typically have smaller N_2O and CH_4 fluxes than agricultural soils, making it difficult to detect isotopic signals. However, Snider et al. [186] conducted a soil incubation experiment on upland and wetland temperate forest soil, manipulated temperature and moisture levels, measured how much N_2O was produced, and analyzed ^{15}N and oxygen ^{18}O in the N_2O. The ^{15}N isotope effect ranged from -20% to -29%, confirming that denitrification leads to measurable N fractionation, which can be used to track N_2O sources. The application of this in real field conditions is still challenging.

There is no single best technique for measuring soil GHG fluxes. However, a combination of methods, such as chamber systems and the EC method, allows researchers to gain a detailed understanding of processes and sources of gas fluxes [167,169].

5. Future Direction

While significant progress has been made in understanding the factors driving soil GHG fluxes, key research gaps remain that limit our ability to predict and manage these fluxes under changing environmental and soil conditions. Future research should focus on the following directions:

Current research often relies on soil properties such as temperature and moisture; however, our synthesis reveals that site-specific factors, including soil texture, substrate availability, and hydroclimatic conditions, strongly influence these properties. This is especially critical for CH_4 and N_2O fluxes, which exhibit distinct moisture thresholds, CH_4 peaking at 60%–80% WFPS and N_2O at approximately 60% WFPS [21,187]. Additionally, soil moisture mediates the temperature sensitivity of soil respiration over long timescales [30,187]. Therefore, considering the interactions between soil properties and hydroclimatic drivers is important in field studies to improve the accuracy of GHG flux modeling under both variable and similar environmental conditions.

Tree species can influence soil microclimate through their canopy structure and physiological traits, such as root-mediated water consumption, which differs among tree types and may affect microbial processes and GHG fluxes. Studies on this aspect remain rare in temperate forest ecosystems. Our review demonstrates that these tree-mediated effects directly regulate GHG-producing microbial processes: monoterpenes from *F. sylvatica* and *P. abies* inhibit CH_4 oxidation by up to 90% [141], while ectomycorrhizal hyphae in *Pinus* spp. enhance CH_4 uptake through labile compounds [32,140–142]. Deciduous species with N-rich litter simultaneously stimulate both CO_2 emissions through enhanced microbial biomass [51,125] and N_2O production through denitrifier activity [126]. Despite these mechanistic insights, the net global warming potential when integrating all three GHGs across different tree species compositions remains unquantified. This knowledge gap limits our ability to predict how changes in forest composition, disturbance, or management practices will alter ecosystem C and N fluxes and hinders optimization of forest management for climate mitigation rather than single-gas fluxes.

In forest ecosystems, the soil substrate is complex and depends on both tree species litter and root exudates.

Soil substrate complexity depends on tree species' litter chemistry and root exudates, ranging from simple labile compounds to complex molecules like hydrolysable tannins and recalcitrant lignin. These species-specific traits shape microbial diversity, functional gene abundances (*pmoA*, *nirK*, *nirS*, *nosZ*, *amoA* [68,148,150–152] and GHG flux balances.

Thus, examining the variation in substrate complexity and microbial response, especially in chemically diverse forest rhizospheres, is crucial because it influences microbial diversity, GHG flux balance, microbial CUE, and SOC formation through necromass production. These processes are not straightforward. Labile litter can enhance short-term soil C storage but also stimulates microbial activity, potentially counteracting positive effects through priming-induced decomposition of both new and old SOC [88,94]. Understanding how litter priming decouples microbial activity from net SOC accumulation and quantifying the balance between decomposer-derived contributions to long-term C storage versus priming-induced short-term losses are crucial for developing effective forest soil C sequestration strategies. Moreover, most priming studies span less than one year [88,94], leaving unresolved the question of whether priming effects remain stable across seasons and years or whether microbial communities adapt through shifts in C and N use efficiency that either intensify or diminish priming over time.

This temporal dimension extends to broader microbial–GHG relationships. In the early stages of litter decomposition, microbial decomposition mainly depends on litter chemistry (e.g., C:N ratio, leaf N). However, as decomposition progresses, microbial community composition transitions from summer *Proteobacteria* and *Bacteroidetes* to winter *Acidobacteria* and *Actinobacteria* [106] playing a more dominant role. Short-term experiments often overlook this seasonal shift, potentially underestimating long-term microbial contributions to GHG fluxes and SOC dynamics. Therefore, long-term studies integrating microbial community composition and functional gene expression are crucial to understand how microbial communities adapt or recover from litter addition or disturbances over time, especially across seasons and years, when environmental conditions and substrate inputs vary. This will provide a more precise understanding of microbial resilience and its role in controlling forest soil C and N fluxes.

Forest soil GHG fluxes are strongly influenced by microbial enzyme activities and C-degrading genes [133,134]. Establishing stronger quantitative relationships between the abundance and expression of C degradation genes (e.g., *SGA1*, *amyA*, *TYR*, *chitinase*, *pectinesterase*) and the activities of their corresponding enzymes, as well as the resulting CO_2 fluxes, will improve our understanding of soil C dynamics under changing environmental conditions. Furthermore, it is important to investigate how shifts in SOM quality, temperature regimes, and N availability alter both enzyme activity and functional gene expression across different timescales and forest types.

Incorporating these mechanistic insights, specifically how the moisture–temperature relationship and tree traits control microbial processes through threshold-dependent responses, will enable models to credibly project GHG fluxes under novel climate conditions. However, developing such models requires a structured empirical foundation: (1) in situ monitoring campaigns with seasonal and interannual measurements can establish multivariate relationships and quantify the relative contribution of each driver; (2) meta-analyses leveraging climate gradients (MAT/MAP) across continental or global scales can quantify how tree composition interacts with climate to regulate GHG fluxes; and (3) manipulative experiments with factorial designs (temperature × moisture × tree species) under both ambient and extreme conditions can reveal mechanistic thresholds and non-linear responses.

These empirical frameworks will provide the data needed to parameterize models that (1) link measurable tree functional traits to microbial outcomes; (2) incorporate functional gene abundances (*pmoA*, *nirK/nirS*, *nosZ*, *amoA*) as dynamic state variables; (3) implement gas-specific moisture thresholds, with CO_2 peaking at approximately 40% WFPS, CH_4 at 60%–80%, and N_2O at approximately 60% [21,52,187], modulated by litter-driven CUE/NUE [88,141]; (4) represent moisture-dependent temperature sensitivity rather than additive effects [30,185]; (5) incorporate interannual adaptation of microbial traits;

and (6) employ hybrid frameworks combining process-based and machine learning approaches [185]. Such integrated model–experiment frameworks will bridge empirical observations with mechanistic understanding, enabling both near-term statistical predictions and long-term process-based projections under novel climate conditions.

Standardizing experimental methodologies, such as different approaches to measure GHG fluxes, such as chamber type, frequency, and collar depth, makes cross-study comparisons challenging. Standardized protocols are important to ensure comparability, build robust datasets, and support the development of global GHG flux databases for forest ecosystems.

6. Conclusions

The regulation of GHG fluxes in forest ecosystems involves complex interactions between abiotic and biotic factors, particularly for CH_4. This review indicates that temperate forests generally act as sources of CO_2 and N_2O under favorable conditions (high temperature and moderate moisture levels), while functioning as sinks for CH_4. Still, the magnitude and direction of each gas flux vary and depend on multiple factors. Soil temperature and moisture have been studied extensively, but additional research is needed on their interactions and on other drivers that contribute to spatial and temporal variability in GHG fluxes, such as site-specific characteristics (e.g., soil texture, pH) and tree species traits (e.g., canopy structure). The contrasting responses of these gases depend on local conditions and site-specific characteristics, such as organic matter decomposition, microbial sensitivity to soil moisture and temperature, and substrate availability. Understanding how one factor modulates the effects of others—for instance, the role of soil moisture in mediating long-term temperature effects—is critical. This moisture-mediated temperature sensitivity represents a key mechanistic insight that challenges the additive environmental response functions used in current ecosystem models and explains why simple temperature-based projections fail: high temperature accelerates decomposition only under adequate moisture, while moisture limitation decouples the temperature–respiration relationship even under elevated temperatures.

Compared to other gases, CH_4 flux appears most biogeochemically complex. Further studies are required to determine the relative role of environmental factors and methanotrophs' sensitivity in the spatial variability of CH_4 fluxes. Tree litter chemistry also influences C and N sequestration: while litter can act as a diffusion barrier for CH_4, fresh litter input may enhance CO_2 and N_2O emissions. It is necessary to investigate how priming effects, driven by microbial activity and litter quality, may further accelerate the decomposition of both fresh and existing SOC, potentially converting soils into a net GHG source.

Understanding these mechanisms can help guide afforestation projects aimed at maximizing soil nutrient sequestration. Forest managers can optimize C sequestration by strategically combining species with contrasting litter qualities, using fast-decomposing broadleaf species to enhance microbial necromass production in mineral soils while incorporating slow-decomposing conifers to build forest floor C stocks, thereby maximizing C storage across different soil horizons. However, to minimize priming-induced SOC losses, thinning operations and residue management should be scheduled during periods of lower microbial activity (e.g., late autumn/winter) and distributed gradually rather than creating concentrated litter pulses that exceed microbial metabolic capacity [95]. Site-specific calibration is essential, as soil properties, pH, and existing microbial community composition influence necromass accumulation efficiency [94], meaning that high-quality litter inputs may be counterproductive on acidic, nutrient-poor soils or sites already experiencing metabolic saturation. Adaptive management intensity should account for temporal

dynamics, with moderate thinning interventions that prevent overwhelming microbial processing capacity while maintaining sustained labile substrate supply over extended periods [95]. Climate-responsive planning must also consider how projected changes in temperature and moisture will affect both priming intensity and overall microbial C stabilization pathways, potentially requiring shifts toward more recalcitrant litter species in warming regions. Ultimately, effective forest management for C sequestration requires moving beyond simple species selection toward integrated strategies that synchronize litter quality, input timing, and management intensity with site-specific microbial capacities and environmental conditions, transforming complex litter–microbe–soil interactions into actionable, climate-adaptive silvicultural practices.

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