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Review

How Can Litter Modify the Fluxes of CO₂ and CH₄ from Forest Soils? A Mini-Review

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Abstract: Forests contribute strongly to global carbon (C) sequestration and the exchange of greenhouse gases (GHG) between the soil and the atmosphere. Whilst the microbial activity of forest soils is a major determinant of net GHG exchange, this may be modified by the presence of litter through a range of mechanisms. Litter may act as a physical barrier modifying gas exchange, water movement/retention and temperature/irradiance fluctuations; provide a source of nutrients for microbes; enhance any priming effects, and facilitate macro-aggregate formation. Moreover, any effects are influenced by litter quality and regulated by tree species, climatic conditions (rainfall, temperature), and forest management (clear-cutting, fertilization, extensive deforestation). Based on climate change projections, the importance of the litter layer is likely to increase due to an litter increase and changes in quality. Future studies will therefore have to take into account the effects of litter on soil CO₂ and CH₄ fluxes for various types of forests globally, including the impact of climate change, insect infestation, and shifts in tree species composition, as well as a better understanding of its role in monoterpene production, which requires the integration of microbiological studies conducted on soils in different climatic zones.

Keywords: litter; forest soil; greenhouse gases; CO₂; CH₄; climate change; forest management



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1. Introduction

Forest ecosystems are a critical component of the global carbon (C) budget through their ability to sequester and retain large amounts of CO₂ [1]. An elucidation of the functioning of forest ecosystems, including their contribution to greenhouse gas (GHG) exchange, is crucial for the development of adaptation and mitigation strategies. In Europe, forests cover about 35% of the total land area, corresponding to 227 million ha with a decreasing share of coniferous (46%), broadleaved (37%), and mixed (17%) tree species [2].

Forest soils influence the GHG balance, with carbon dioxide (CO₂) and methane (CH₄) as key elements of the global C cycle. Of the three major GHGs the CO₂ flux is quantitatively often the most important and its concentration has increased by 1.9 ppm yr⁻¹ in the last 10 years [3]. The biogenic sources of CO₂ efflux from soil are root respiration, rhizomicrobial respiration, priming-related effects, and basal respiration associated with the microbial decomposition of organic matter in soils [4]. Forest ecosystems also significantly contribute to the increase in CO₂ emission through forest fires, deforestation [5–7], and CO₂ release by soil microorganisms colonizing dead trees [7]. For many forests, soil CH₄ is another important GHG with a global warming potential (GWP) 28 times greater than that of CO₂ [8]. Soils may be a source or sink for CH₄ depending on the balance between CH₄ production (methanogenesis in an anaerobic environment) and CH₄ oxidation (methanotrophy in aerobic conditions) [9,10]. The process of methanotrophy has significant mitigating potential since methanotrophs can contribute to the reduction in atmospheric CH₄ (high affinity methanotrophy) on the one hand, but, on the other hand, can also

oxidize the higher soil CH₄ concentrations before this reaches the atmosphere (low affinity methanotrophy) [11]. Methanotrophy in forest soils is of particular importance, as these soils show high activity compared to soils from other ecosystems due to the dominance of high affinity methanotrophs [12].

In addition to soil, the surface litter layer can make an important contribution to C and nutrient cycling in forest ecosystems [13], changing the soil microclimate [14,15] and affecting soil microbiota. Forest litter is a layer of dead plant material present on the soil surface [16], which may be a source of nutrients and energy for soil microorganisms [17] but can also act as a bidirectional (from the atmosphere to the soil profile and vice versa) barrier to gas diffusion [3,18,19]. The presence of litter may modify soil–atmosphere fluxes of GHGs through different mechanisms. Due to the predicted increase in both atmospheric CO₂ concentration and litterfall, the importance of the litter layer as a source of C is likely to rise [20,21], as would any indirect effects associated, for instance, with litter acting as a barrier to gas diffusion. Additionally, management practices in forests, e.g., cultivation or extensive deforestation, often result in enhanced litter fall combined with soil mixing, which accelerates its decomposition and may affect CO₂ emission [1,13,22–26]. Thus, the litter layer could be used as an indicator of the likely amount of trace gas emissions, such as CO₂, from the forest soil [18]. In terms of CH₄ oxidation, it has been reported that litter is more important in regulating CH₄ uptake from soil than from roots [27]. The effect of litter on CH₄ consumption by forest soils has been documented to be strongly dependent on hydrologic conditions [18,19,28]. Moreover, the regulation of soil processes and the litter layer itself may be a source or sink of GHGs [29–31], although this has received little attention in studies [32].

Although litter can have a major impact on the C and GHG balance in forest ecosystems, this has not always been fully recognized. In this review we summarize the available information on the effects of litter on CO₂ emission and CH₄ uptake in forest soils, including forest-specific impacts, environmental drivers, quantification, the influence of human activity, and the likely effects of climate change. Based on the recent research, we identify a number of knowledge gaps, and directions for future research are highlighted for a better understanding of the relationship between litter and soil–atmosphere GHG (CO₂, CH₄) exchange, as part of the C cycle.

2. Litter as a Controller of GHG (CO₂, CH₄) Fluxes

Litter can modify GHG fluxes in different gas-specific ways, although there are also common mechanisms of its effect, regulated by climatic conditions, forest management and climate change factors, summarized in Figure 1.

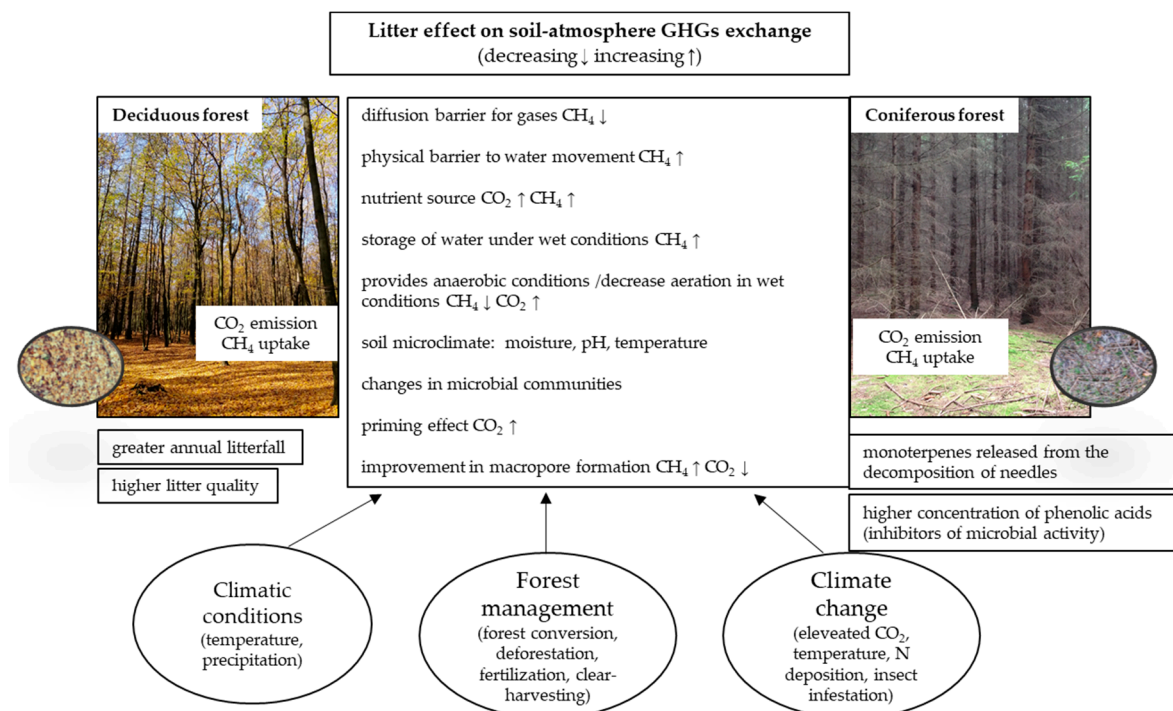


Figure 1. Diagram showing general drivers of litter effects on CO_2 emissions and CH_4 uptake, including regulating factors.

2.1. Carbon Dioxide (CO_2)

There are two essential processes that contribute to the total CO_2 efflux from the soil: production and transport [33]. The processes of autotrophic respiration (related to roots and rhizospheric microorganisms) and heterotrophic respiration (from non-rhizospheric microorganisms, bacteria and fungi, including the litter layer) are the soil sources of CO_2 [34–36]. Respiration is very sensitive to climatic changes and can be influenced by various environmental factors, such as soil moisture and temperature, microbial communities, the type of vegetation, or soil surface litter [13,36–38]. It is documented in many studies that aboveground litter inputs have a significant effect on soil respiration in various types of forests (see [13,39–42]). Moreover, modifications of soil-based CO_2 fluxes and decomposed litter are also important CO_2 sources [32].

Different mechanisms for the effects of litter on soil CO_2 fluxes are presented in the literature. They can generally be classified based on the following impacts (Table 1):

- (i) An alteration in the availability of substrates for soil microbes;
- (ii) modifications in soil microbial communities;
- (iii) a priming effect;
- (iv) the creation of a physical barrier that decreases gas exchange and/or water movement/water retention and acts as an insulating layer that modifies soil temperature.

Table 1. The main drivers underlying the effects of litter on CO₂ emission in different forest soils from different regions based on field studies.

The Main Driver	Forest Type	Dominant Tree Species	Tree Age [Years]	Tree Height [m]	DBH [cm]	Tree Density [Trees/ha]	Litter Input [g/m ² /year]	MAT [°C]	MAP [mm]	Soil Type	Soil Texture (Sand/Silt/Clay [%])	Soil Temperature [°C]	Soil Moisture [%]	Effect of Litter on CO ₂ Fluxes	Landscape Type	Location	Ref.
Litter as a source of nutrient for microbes	Plantation	<i>T. grandis</i> (92%)	~10	n/a	10.72 ± 2.1	429	n/a	n/a	1598	n/a	n/a	28.78 ± 1.75	10.60 ± 2.42	Increased by 14.4% **	n/a	Jharkhand, Eastern India	[40]
	Plantation	<i>Eucalyptus</i> sp.	3	12	n/a	700	n/a	25	1200	Arenosol (FAO)	Sandy	~24–33	n/a	Increased **	coastal	Pointe Noire, Southwestern Congo	[30]
	regrowth forest	<i>L. pubescens</i> , <i>M. sylvatica</i> , <i>V. guianensis</i> , <i>C. scrobiculata</i> (all species represent 71% of all stems in the stand)	12	4.9 ± 0.4	n/a	21,300	n/a	24–27	2539 ± 280	Distrophic Yellow Latosol Stony Phase I (Brazilian Classification), Sombriustox (U.S. Soil Taxonomy)	Sandy clay loam (74/6/20)	n/a	n/a	Increased by 28% **	n/a	Northern Brazil (1° 19' S, 47° 57' W)	[43]
	Plantation	<i>Ac. mangium</i>	8	23.6	22.5	n/a	20–270 (fresh litter); 780–1130 (decayed litter); 1050–1160 (fresh + decayed litter) in wet and dry season	27.3	2750	Acrisols (WRB 1998)	n/a	n/a	55.5–66.3% WFPS	Increased *	Undulating topography (upper and lower plateau, upper and foot slope)	South Sumatra (3° 52' 40" S, 103° 58' 40" E) Indonesia	[44]
	Pine forest	<i>P. massoniana</i>	30	5	n/a	2600	n/a	17.8	1785	Ferric Acrisols (USDA soil taxonomy)	Loamy clay (21/43/36)	24.2	60.3% WFPS	Increased by 24–32% *	Hilly region	Yingtian, Jiangxi Province, Southeastern China (28° 15' N, 116° 55' E)	[3]
	Sclerophyll forest	<i>Cr.alba</i> , <i>Q. saponaria</i> , <i>Pe. boldus</i> , <i>L. caustica</i>	n/a	5.06 ± 0.87	6.51 ± 1.39	2600 ± 978	314 ± 30	n/a	503	Pachic Humixerepts	Sandy (62.4/26.4/11.2)	n/a	n/a	Increased by 21.2–33% **	Top slope (<4% slope)	Central Chile (34° 7' S, 71° 11' 18" W)	[45]
	Mixed pine-broadleaf forest	<i>Cs. chinensis</i> (50.9%), <i>S. superba</i> , <i>P. massoniana</i>	100	n/a	n/a	n/a	861	22.3	1680	Ultisol (USDA soil taxonomy)	Lateritic	17.5–24.0	20.8–27.8	Increased by 33–38% **	n/a	Dinghushan Biosphere Reserver, Southern China (23° 09' 21" N, 112° 30' 39" E, 112° 33' 41" E)	[13]
	Pine forest	<i>P. massoniana</i> Lamb. (90%)	50	n/a	n/a	n/a	356	22.3	1680	Ultisol (USDA soil taxonomy)	Lateritic	18.2–24.8	17.1–20.9	Increased by 37–42% **	n/a		
	Monsoon evergreen broadleaf forest	<i>Cs. chinensis</i> ; <i>Cr. chinensis</i> , <i>S. superba</i> , <i>Cr. concinna</i> , <i>Ap. yunnanensis</i> , <i>Ac. acuminatissima</i> , <i>G. subaequalis</i> (all these species represent >60% of the community biomass)	>400	n/a	n/a	n/a	849	22.3	1680	Ultisol (USDA soil taxonomy)	Lateritic	16.2–23.1	26.4–28.7	Increased by 29–35% **	n/a		

Table 1. Cont.

The Main Driver	Forest Type	Dominant Tree Species	Tree Age [Years]	Tree Height [m]	DBH [cm]	Tree Density [Trees/ha]	Litter Input [g/m ² /year]	MAT [°C]	MAP [mm]	Soil Type	Soil Texture (Sand/Silt/Clay [%])	Soil Temperature [°C]	Soil Moisture [%]	Effect of Litter on CO ₂ Fluxes	Landscape Type	Location	Ref.
Enhancement of anaerobic conditions by litter	Plantation	<i>Pl. orientalis</i>	n/a	n/a	n/a	n/a	n/a	15.7	834	Yellow brown soil	Silty clay (11/41/48)	16.31 ± 1.05	12.34 ± 0.80	Increased by 18.84% *	n/a	Danjiangkou Reservoir, Central China (32°45' N, 111°13' E)	[41]
	Mediterranean oak woodland	<i>Qr. agrifolia</i>	n/a	n/a	n/a	n/a	n/a	19	180	n/a	Gravelly loam	n/a	n/a	Increased by 34.2–44.8% ***	n/a	Santa Monica Mountains, California (34°05'38" N, 118°39'26" W) USA	[46]
	Montane cloud forest	<i>Clusiaceae, Cunoniaceae, Myrsinaceae, Rosaceae, Clethraceae families</i>	n/a	n/a	n/a	n/a	n/a	n/a	12.5	n/a	n/a	Acidic	n/a	n/a	No effect **	n/a	Peruvian Andes (13°11'28" S, 71°35'24" E)
Soil moisture retention by litter	Pine forest	<i>P. massoniana</i>	50	n/a	n/a	n/a	356	22.3	1680	Ultisol (USDA soil taxonomy)	Lateritic	18.2–24.8	17.1–20.9	Increased by 37–42% **	n/a	Dinghushan Biosphere Reserver, Southern China (23°09'21" N–23°11'30" N, 112°30'39" E–112°33'41" E)	[13]
	Mixed deciduous forest	<i>Ar. rubrum, Qr. rubra</i>	n/a	n/a	n/a	n/a	n/a	8.5	1050	Typic Dystrochrept	Fine sandy loam	n/a	n/a	Increased **	n/a	Harvard Forest, Petersham, Massachusetts (42°32' N, 72°11' W) USA	[48]
	Old-growth semideciduous tropical forest	n/a	n/a	n/a	>35	n/a	n/a	n/a	>2000	n/a	n/a	n/a	n/a	Increased **	Flat plateau (the planalto)	Pará, Northern Brazil (3°0'37" S, 54°34'53" W)	[49]
Priming effect	Old-growth moist lowland tropical forest	n/a	n/a	n/a	n/a	n/a	n/a	27	2600	Oxisol	n/a	n/a	n/a	Increased by 20% **	n/a	Gigante Peninsula, central Panama (9°06' N, 79°54' W)	[50]
	Undisturbed old-growth forest	<i>Ts. heterophylla, Ps. menziesii</i>	n/a	n/a	n/a	n/a	n/a	8.7	2370	Typic Hapludands	Coarse loamy	9.5	29	Increased **	n/a	H.J. Andrews Experimental Forest, Oregon (44°13' N, 122°13' W) USA	[23]

Table 1. Cont.

The Main Driver	Forest Type	Dominant Tree Species	Tree Age [Years]	Tree Height [m]	DBH [cm]	Tree Density [Trees/ha]	Litter Input [g/m ² /year]	MAT [°C]	MAP [mm]	Soil Type	Soil Texture (Sand/Silt/Clay [%])	Soil Temperature [°C]	Soil Moisture [%]	Effect of Litter on CO ₂ Fluxes	Landscape Type	Location	Ref.
	Undisturbed old-growth forest	<i>P. menziesii</i> , <i>T. heterophylla</i>	n/a	n/a	n/a	n/a	n/a	8.7	2370	Typic Hapludands	Coarse loamy (13% clay)	9.5	29	Increased by 19% and 58% **	n/a	H.J. Andrews Experimental Forest, Oregon (44°15' N, 122°10' W) USA	[51]
Priming effect	Temperate deciduous forest	<i>Q. petraea</i> (70%), <i>Cp. betulus</i> (30%)	100–150	n/a	n/a	n/a	n/a	10.7	680	Gleyic Luvisol (WRB 2006)	Loam (41.9/38.8/19.3)	2.7 ± 0.5	20.4 ± 0.6	Increased **	n/a	Barbeau National Forest, Northern Central France (48°29' N, 02°47' E)	[20]
	Mixed deciduous temperate woodland	<i>Ar. pseudoplatanus</i> , <i>Fr. excelsior</i>	n/a	n/a	n/a	n/a	n/a	10	714	Stagni-vertic Cambisol (FAO/WRB)	Clay loam	n/a	n/a	Increased by 30% **	n/a	Wytham Woods, Oxfordshire (51°43'42'' N, 1°19'42'' W) UK	[52]
	Semi-deciduous lowland tropical forest	<i>Arecaceae</i> , <i>Burseraceae</i> , <i>Olacaceae</i> families	200	n/a	≥10	n/a	n/a	27	2600	Clay-rich Oxisol	n/a	n/a	n/a	Increased by 10% **	n/a	Gigante Peninsula, central Panama (9°06' N, 79°54' W)	[52]
Litter can act as an insulating layer that also buffers the effects of variations in light, temperature and irradiation	Temperate deciduous forest	<i>Qt. petraeae-cerris</i> community	n/a	n/a	n/a	n/a	2930	10.7	615.6	Brown forest soil, Cambisols (FAO)	n/a	9.94	25.4	Reduction ****	n/a	Bükk Mountains, Northeastern Hungary (47°55' N, 20°26' E)	[21]
	Temperate deciduous forest	<i>Qt. petraeae-cerris</i> community	n/a	n/a	n/a	n/a	2754 ± 206 kg C ha ⁻¹ yr ⁻¹	10.8	599	Cambisol	n/a	11.4 ± 0.93–16.1 ± 0.78	12.8 ± 0.78–28.4 ± 1.39% v/v (soil)	Reduction ****	n/a	Bükk Mountains, Northeastern Hungary (47°55' N, 20°26' E)	[37]

T.—Tectonia; Ac.—Acacia; L.—Lacistema; M.—Myrcia; V.—Vismia; C.—Cupania; P.—Pinus; Pc.—Picea; Cr.—Cryptocarya; Cs.—Castanopsis; Q.—Quillaja; Pe.—Peumus; L.—Lithraea; S.—Schima; Ap.—Aporosa; Ac.—Acmena; G.—Gironniera; Pl.—Plactycladus; Qr.—Quercus; Ar.—Acer; Ts.—Tsuga; Cp.—Carpinus; Fr.—Fraxinus; Qt.—Quercetum; Ps.—Pseudotsuga; DBH—diameter at breast height; n/a—data not available; Methods: * gas chromatography (GC); ** infrared gas analyzer (IRGA); *** quantum cascade laser (QCL) spectrometer **** soda-lime technique.

However, none of these effects are mutually exclusive and a litter-related increase in C substrate availability, for instance, could occur in agreement with an alteration in the microbial communities of the soil and/or a lower soil temperature, as indicated in Table 1.

The litter layer in different forest types can act as a reservoir of organic (e.g., sugars, phenolics, hydrocarbons and glycerides) and inorganic compounds (e.g., N, P, Ca) that can be used as substrates for soil microbes and plants [16,18,41]. Removal of the litter layer in an eastern Amazonian regrowth forest resulted in a significantly lower soil CO₂ efflux due to a decrease in substrate availability [43]. The litter layer which accumulated during the drier season may be a source of C and N for soil microbes through decay in the wetter season. Therefore, the decrease in CO₂ flux was caused by the withdrawal of fresh substrates for heterotrophic respiration associated with the litter decomposition processes [44]. The removal of litter also resulted in a reduction in the dissolved organic carbon (DOC) concentration, one of the easily mineralizable substrates for microorganisms resulting in a decrease in CO₂ emission from subtropical forest soil [3]. The CO₂ fluxes from the soils of an *Acacia mangium* deciduous forest were linked with the amount of litter and the total soil C content both in the dry and wet seasons. It is also known that litter removal can significantly reduce microbial biomass C (MBC), as well as microbial biomass nitrogen (MBN), in (sub-)tropical forests [15]. In turn, it is shown that the addition of litter increases soil microbial biomass in a coniferous forest in China [53]. On the other hand, the depletion of C substrates for microorganisms because of litter removal did not affect the microbial biomass in a sclerophyll forest in Chile, which was explained by topsoil resilience in this type of ecosystem where litter removal is a common practice due to its use in gardens [45].

The structure of soil microorganisms determines the efficiency of C use, since fungi are more effective in assimilating C from litter than bacteria because they can store more C than is necessary for their metabolic processes [54,55]. These microbes can also decompose some recalcitrant compounds like lignin, as well as cellulose and hemicellulose, contained in fallen leaves and/or needles with the use of fungal polymer-degrading enzymes [56,57]. Fungi are more resistant to decomposition processes than bacteria, as their cell walls contain more durable compounds (i.e., carbon polymers such as chitin and melanin) than bacterial cell walls (i.e., phospholipids and peptidoglycan) [55]. The combination of N [58,59] with an increased fungal biomass was found to decrease the soil respiration rate [13,60], since when the litter layer is N-deficient, decomposing microbes are less capable of utilizing the available C [61]. The vegetation type also influences the structure of microbe populations in the litter. Fungi are more tolerant to tannins than bacteria, and it is known that needle litter contains greater amounts of these compounds than leaf litter [62,63]. Fernández-Alonso et al. [64] reported that leaf litter was dominated by Gram-negative bacteria in contrast to needle litter, which was dominated by Gram-positive bacteria and saprophytic fungi, and also had a higher ratio of fungi to bacteria. The community of microorganisms inhabiting beech forest litter was dominated by fungi [56], and litter removal in subtropical pine forest resulted in an increased ratio of fungi to bacteria [13], while the addition of litter in a nutrient-deficient *Pinus sylvestris* var. *mongolica* plantation significantly reduced the ratio of Gram-positive to Gram-negative bacteria [53]. Based on the information presented above, it can be concluded that changes in microbial communities (e.g., the reduction in microbial biomass and activities) caused by litter manipulations are one of the main factors which decreases soil respiration in coniferous forests [13,39,41,65].

Higher CO₂ emissions related to the addition of litter may have been caused by the so-called priming effect, which resulted in an increased mineralization of fresh organic C residues present in the litter [66–70]. During the priming effect, the contribution of fresh organic matter to the soil increased, the decomposition processes were stimulated, and the older stored C was released from the soil as CO₂ [52,71]. This effect occurred when the activity of microorganisms or the community composition was changed due to the impact of litter manipulations on the decomposition processes associated with organic matter in soil [52,64]. Leaf litter chemistry strongly influenced the magnitude of the soil priming

effect, which was positively influenced by the concentrations of several cations (Ca, K, and Mg) in the later stage of litter decomposition [71]. Although the CO₂ emissions were higher in the tropical forest, the addition of litter due to the priming effect had a greater impact on soil respiration in the temperate deciduous forest. In subtropical and tropical forests, priming effects could occur when nutrients were limited and soil microorganisms had a sufficient substrate (C) which was a source of energy [72].

The litter layer acted as a physical barrier for O₂ diffusion and, especially under wet conditions (e.g., after rainfall), could result in an anaerobic environment for GHG production [32,41]. Generally, both very low and very high water contents resulted in lower soil CO₂ emissions by limiting the substrate supply to microorganisms (under conditions which were too dry) and the reduction in O₂ (under conditions which were too wet) [73]. In a study including different initial soil moisture contents, it was shown that, initially, CO₂ emissions were higher in flooded soil compared with wet soil. In contrast, after 5 days of the experiment, CO₂ emissions were lower since flooding conditions restricted microbial growth and activity. However, at day 20, CO₂ emissions from the flooded soil, which had become wet again, increased and then decreased gradually. The higher CO₂ emissions were explained by enhanced activities of microbes due to the higher DOC contents in the flooded, as opposed to, wet soil [74].

Water fluctuations regulated CH₄ fluxes by affecting soil microorganisms involved in CH₄ balance. CH₄ emissions from soil increased with increased moisture and flood conditions which were preferential for methanogenes producing CH₄, while such conditions limited the process of methanotrophs oxidizing CH₄ under O₂ availability [10]. But methanotrophs needed both O₂ and water, although the optimum moisture for methanotrophy was determined by soil properties [10]. The effect of water on the CH₄ cycle depended on the original soil moisture content. Periodic rainfall events could stimulate methanotrophy (when the soil is dry) and stimulate methanogenes (and CH₄ emission) when the soil was wet.

2.2. Methane (CH₄)

The diffusion of CH₄ from the atmosphere into the soil strongly affects CH₄ consumption, since the upper-most well-aerated mineral soil located immediately underneath the organic layer exhibits the highest methanotrophic activity [28,75]. The mechanisms associated with the effects of litter atmospheric CH₄ uptake by soils are regulated by moisture [19,27,32], as CH₄ diffusion is 10⁴ times slower in water than in air [76].

The litter layer may influence soil CH₄ uptake in opposing ways as summarized in Table 2:

- (i) decrease the uptake by acting as a physical barrier to gas diffusion and reduced aeration due to faster litter decomposition in wet conditions;
- (ii) increase the uptake through the maintenance of soil gas diffusivity under wetter/high rainfall conditions;
- (iii) influence the capability of the soil for oxidizing CH₄;
- (iv) provide a source of nutrients for methanotrophs;
- (v) improve the formation of macro-aggregates, which facilitates CH₄ transport for methanotrophs.

Table 2. The main litter-related drivers of CH₄ uptake in different forest soils from different regions based on field studies (except [77]—laboratory incubations).

The Main Driver	Forest Type	Dominant Tree Species	Tree Age [Years]	Tree Height [m]	DBH [cm]	Tree Density [Trees/ha]	Litter Specification (Thickness/Input)	MAT [°C]	MAP [mm]	Soil Type	Soil Texture (Sand/Silt/Clay [%])	Soil Temperature [°C]	Soil Moisture	Effect of Litter on CH ₄ Uptake	Landscape Type	Location	Ref.	
Litter as a diffusion barrier	Coniferous forest	<i>P. strobus</i> (87–100%)	4–67	n/a	19.3	1265.5 (421–1683)	2.5 cm/ 267–2324 g m ⁻²	7.8	1010	Brunisolic Gray Brown Luvisol and Cleved Brunisolic Gray Brown Luvisol (Canadian System of Classification)	Sand, loamy sand (80–90/8–18/<5)	n/a	n/a	Reduction (in June–September period) *	Lake shore	Southern Ontario, Canada	[78]	
	Boreal coniferous forest	<i>P. sylvestris</i>	27	n/a	n/a	n/a	2–3 cm/n/a	n/a	n/a	Podzol	Coarse sand	n/a	10.9%	Reduction by 50% *	n/a	Central Finland (62°39' N, 27°03' E)	[79]	
	Temperate coniferous forest	<i>Pc. abies</i> , <i>Ab. alba</i> , <i>P. sylvestris</i>	110	n/a	n/a	n/a	n/a	n/a	6	1200	Acid brown	n/a	n/a	n/a *	Reduction by 17%	n/a	Black Forest, Southwestern Germany (48°03' N, 8°22' E)	[80]
	Deciduous forest	<i>Fg. sp.</i> , <i>Qr. sp.</i>	n/a	n/a	n/a	n/a	~600	1–2 cm/ ~570 g dm m ⁻² yr ⁻¹	n/a	n/a	Cambisol	Sandy	n/a	n/a	Reduction by 17%	n/a	South Central Germany, (49°86' N, 8°65' E)	[81]
	Temperate deciduous forest	<i>Fg. sylvatica</i>	n/a	n/a	n/a	n/a	n/a	n/a	6.5	796	Pseudo-gleyic Cambisol	n/a	n/a	n/a	Reduction by 16% *	n/a	Rosalien Mountains, Eastern Austria (47°42'26'' N, 16°17'59'' E)	[32]
	Karst forest	<i>P. massoniana</i>	n/a	n/a	n/a	15	2000	n/a	14.8	1118	Limestone soil	Sand silt	n/a	76.0 ± 7.2% WFPS	Reduction by 24% *	Karst area	Guizhou Province, Southern China (26°32' N, 106°46' E)	[18]
Lower aeration and limited diffusion of atmospheric CH ₄ due to fast litter decomposition	Tropical seasonal rain forest	<i>Pm. tomentosa</i> , <i>Br. macrostachya</i> , <i>G. subaequalis</i> , <i>Tr. myriocarpa</i>	n/a	18.6	≥10	386	n/a	21.7	1557	Oxisol	n/a	n/a	n/a	Reduction by 29% *	Plot located between two hills	Xishuangbanna, Southern China (21°56' N, 101°11' E)	[82]	
Monoterpenes released from needles decomposition	Subtropical pine forest	<i>P. massoniana</i>	30	5	n/a	2600	n/a	17.8	1785	Ferric Acrisols (USDA soil taxonomy)	Loamy clay (21/43/36)	24.2	60.3% WFPS in wet season	Reduction by 55% *	Hilly region	Yingtian, Jiangxi Province, Southeastern China (28°15' N, 116°55' E)	[3]	
	Temperate deciduous and coniferous forests	<i>F. sylvatica</i> <i>Pc. abies</i>	n/a	n/a	n/a	n/a	n/a	n/a	n/a	Haplic Cambisol	n/a	n/a	n/a	Reduction *	n/a	Steigerwald, South Central Germany (49°51' N, 10°27' E, 49°52' N, 10°27' E)	[77]	

Table 2. Cont.

The Main Driver	Forest Type	Dominant Tree Species	Tree Age [Years]	Tree Height [m]	DBH [cm]	Tree Density [Trees/ha]	Litter Specification (Thickness/Input)	MAT [°C]	MAP [mm]	Soil Type	Soil Texture (Sand/Silt/Clay [%])	Soil Temperature [°C]	Soil Moisture	Effect of Litter on CH ₄ Uptake	Landscape Type	Location	Ref.
Mechanism not known	Broad-leaved pine forest	<i>P. koraiensis</i> , <i>Ar. mono</i> , <i>Tl. amurensis</i> , <i>Ul. mongolica</i> , <i>Fr. mandshurica</i> , <i>Qr. mongolica</i>	n/a	25	28.9	560		−7.3–4.9	600–900	Dark brown forest soil	n/a	n/a	n/a	Reduction*	Slope	Changbai Mountain, Antu County, Northeastern China (42°24' N, 128°28' E)	[83]
A soil moisture > 15.8% v/v—dependence on soil water content	Plantation	<i>P. elliotii</i>	20	15	16.1	n/a	n/a	17.9	1469	Typic Dystrudepts (USDA Soil Taxonomy)	Sandy loam (68/17/15)	n/a	n/a	Increased *	n/a	Qianyanzhou Ecological Research Station, Jiangxi Province, Southeastern China (26°44'39" N, 115°03'33" E)	[19]
Litter as a source of labile C compounds and the improve formation of macro-aggregates	Coniferous forest	<i>Pl. orientalis</i>	n/a	n/a	n/a	n/a	1–2 cm/n/a	15.7	749.3	Yellow-brown soil (Chinese soil classification), Haplic Luvisols (USDA Soil Taxonomy)	Sand (Silt and clay: 9.6%)	19.24 ± 2.69	59.02 ± 3.81% WFPS	Increased by 37.7% *	n/a	Wulongchi Experiment Station, Hubei Province, Central China (32°45' N, 111°13' E)	[27]
Improving gas diffusion in soil surface due to water retention by litter	Temperate coniferous forest	<i>Pc. abies</i> (100%)	121	n/a	n/a	317	>8 cm/n/a	7.5	900	Dystric Cambisol (FAO)	Loamy silt	9.8	0.42 cm ³ cm ^{−3}	Increased by 11.5% *	n/a	Solling (51°46' N, 9°35' W) Germany	[28]
	Temperate deciduous forest	<i>Fg. sylvatica</i> (100%)	130	n/a	n/a	342	<3 cm/n/a	7.5	900	Dystric Cambisol (FAO)	Loamy silt	10.0	0.48 cm ³ cm ^{−3}	Increased by 39% *	n/a		
	Temperate mixed forest	<i>Pc. abies</i> (70%), <i>Fg. sylvatica</i> (30%)	121	n/a	n/a	96	n/a	7.5	900	Dystric Cambisol (FAO)	Loamy silt	9.8	0.39 cm ³ cm ^{−3}	Increased by 24.3% *	n/a		
	Temperate mixed forest	<i>Pc. abies</i> (30%), <i>Fg. sylvatica</i> (70%)	129	n/a	n/a	93	n/a	7.5	900	Dystric Cambisol (FAO)	Loamy silt	9.9	0.42 cm ³ cm ^{−3}	Increased by 19.4% *	n/a		
	Plantation	<i>P. massoniana</i>	20		n/a	n/a	3–5 cm/7.30 t h m ^{−2} yr ^{−1}	21.7	1600	Oxisol	Sandy clay loam	7.7–30.1	4.67–36.91 cm ³ H ₂ O cm ^{−3}	No effect *	Hilly area		

Table 2. Cont.

The Main Driver	Forest Type	Dominant Tree Species	Tree Age [Years]	Tree Height [m]	DBH [cm]	Tree Density [Trees/ha]	Litter Specification (Thickness/Input)	MAT [°C]	MAP [mm]	Soil Type	Soil Texture (Sand/Silt/Clay [%])	Soil Temperature [°C]	Soil Moisture	Effect of Litter on CH ₄ Uptake	Landscape Type	Location	Ref.
Improving gas diffusion in soil surface due to water retention by litter	Pine forest	<i>P. massoniana</i>	73	n/a	n/a	n/a	n/a/1.8 mg C ha ⁻² yr ⁻¹	21.4	1927	Lateritic red earth, Oxisol	Loamy	21.8 ± 1.0	12.3 ± 1.9 cm ³ H ₂ O cm ⁻³	No effect *	Hilly land	Guangdong Province, Southern China (112°30′39″E, 23°09′21″N)	[65]
	Conifer and broadleaf mixed forest	<i>P. massoniana</i> ; <i>S. superba</i> , <i>C. chinensis</i> , <i>Cb. kwangtungense</i>	n/a	n/a	n/a	n/a	n/a/4.3 mg C ha ⁻¹ yr ⁻¹	21.4	1927	Lateritic red earth, Oxisol	Loamy	20.1 ± 0.9	23.3 ± 1.5 cm ³ H ₂ O cm ⁻³	No effect *	n/a		
	Evergreen broadleaf forest	<i>C. chinensis</i> , <i>Cs. chinensis</i> , <i>C. concinna</i> , <i>Er. fordii</i> , <i>Cy.podophylla</i>	n/a	n/a	n/a	n/a	n/a/4.2 mg C ha ⁻¹ yr ⁻¹	21.4	1927	Lateritic red earth, Oxisol	Loamy	19.9 ± 0.9	26.1 ± 1.6 cm ³ H ₂ O cm ⁻³	No effect *	n/a		
Water retention by litter	Plantation	<i>Pl. orientalis</i>	n/a	n/a	n/a	n/a	n/a	15.7	834	Yellow brown soil	Silty clay (11/41/48)	16.31 ± 1.05 (soil)	12.34 ± 0.80%	No effect *	n/a	Danjiangkou Reservoir, Central China (32°45′ N, 111°13′ E)	[41]
	Subarctic wet heath ecosystem	<i>B. pubescens</i>	n/a	n/a	n/a	n/a	n/a	0.2	337	Organic soil	n/a	n/a	n/a	Increased	Slightly slopin terrain **	Northern Sweden (68°20′47″ N, 18°49′34″ E)	[84]
Acting as a diffusion barrier for soil moisture < 15.8% v/v	Plantation	<i>P. elliotii</i>	20	15	16.1	n/a	n/a	17.9	1469	Typic Dystrudepts (USDA taxonomy)	Sandy loam	n/a	n/a	Min Increased +0.7%	n/a *	Qianyanzhou Ecological Research Station, Jiangxi Province, Southeastern China (26°44′39″ N, 115°03′33″ E)	[19]

P.—Pinus; Pc.—Picea; Ab.—Abies; Fg.—Fagus; Pm.—Pometia; Br.—Barringtonia; Tr.—Terminalia; Tl.—Tilia; Ul.—Ulmus; Cb.—Craibiodendron; Er.—Erythrophleum; Cy.—Cyathea; B.—Betula; DBH—diameter at breast height; n/a—data not available; Methods: * gas chromatography (GC); ** Ultraportable Greenhouse Gas Analyzer (UGGA).

The role of litter as a physical barrier that restricts the uptake of atmospheric CH₄ is confirmed in studies on forests with different tree species, e.g., pine forests (*P. strobus* L.) [78], Scots pine [79], evergreen slash pine [19], pure and mixed stands of Norway spruce and European beech [28,80], and beech and oak forests [75,81]. Since the litter layer may serve as a moisture-dependent bidirectional buffer for atmospheric CH₄ uptake, various effects of litter on CH₄ uptake by forest soils are observed in different ecoregions of China [19,31]. The increase in CH₄ oxidation after litter removal is the result of an effect on the availability of both CH₄ and O₂ for methanotrophs through an impact on gas diffusion, which may be limited, particularly under wet conditions [3,18,19,75,80–82]. Since O₂ diffusivity in water ($2.1 \times 10^{-5} \text{ cm}^2 \text{ s}^{-1}$) is lower compared to CH₄ ($2.6 \times 10^{-5} \text{ cm}^2 \text{ s}^{-1}$), it is more likely that O₂ availability is the major factor influencing soil microbiological processes in wet soil. The diffusivity of O₂ in air is also lower than CH₄, corresponding to $0.205 \text{ cm}^2 \text{ s}^{-1}$ and $0.250 \text{ cm}^2 \text{ s}^{-1}$, respectively. The diffusion of CH₄ into soil was facilitated by litter removal, especially under the higher soil moisture contents found in autumn and winter in pure mature beech forests [32]. With a higher water content, litter may impede CH₄ and O₂ permeation into the soil [81]. Therefore, CH₄ oxidation can be independent of the presence of litter in the dry season, as reported by Wu et al. [27] and Yan et al. [82]. Furthermore, in its role as a physical barrier, the litter layer may facilitate gas diffusion in soil by increasing the formation of macropores [27] since the transformation of litter into organic matter affects soil porosity [85,86]. However, under higher moisture levels, particularly during rainfall events, the presence of litter may increase CH₄ uptake by storing water, which cannot penetrate into the soil profile, as suggested by Boroken and Beese [28] in a study on loamy silt soil (under mixed and pure beech stands) and Wang et al. [19] in a study on sandy loam (under evergreen slash pine). The lower CH₄ oxidation in the wet season is a consequence of the lower aeration and the limited diffusion of atmospheric CH₄ due to the reduced diffusion of gases through the litter layer [82] as a consequence of the lower diffusivity of O₂ than CH₄. On the other hand, there are reports showing an increased CH₄ uptake in litter-covered soils. A few studies demonstrate that the litter layer may show a substantial high affinity of CH₄ oxidation that occurs in the deepest organic layer overlying the mineral soil [87], which is partly supported by the results of Wu et al. [27]. In contrast, a study on the effect of litter from deciduous and coniferous forests shows that the litter itself is not a significant sink or source of CH₄ [88] but may be a source of labile C compounds that can be used by methanotrophs [27,89–91].

Despite the suggested mechanisms for litter-related regulation of GHG exchange, there are also studies that show a litter-induced reduction in CH₄ uptake from the atmosphere, but they do not explain the mechanisms involved in this process [83,92], which underlines the need for further research in this area.

It is difficult to quantify the effects of litter or litter quality on GHG emissions because of the paucity of reliable data. Two examples (the Figure A1 in Appendix A) indicate that the effects of litter can vary depending on the GHG under consideration, with a positive effect of litter amount on CO₂ fluxes but a negative effect on CH₄ fluxes, assuming that litter thickness reflects the amount of litter present. The correlations are significant but could be influenced by all the other factors, e.g., variation in soil conditions, tree species, and climate zones.

3. Tree Species-Specific Mechanisms of the Litter Effect on GHG Fluxes

Tree species and age may also influence the effect of litter on GHG fluxes through differences in litter quality [42,93] that may modify both the soil characteristics and microbial activity. In tropical forests, the C/N ratio in leaf litter differed significantly among four sites with dominant *Leuceana leucocephala*, *Acacia*, *Cereus*, and *Pilosocereus* species varying among different forests [94]. In contrast, a study on litter from tree species common in temperate forests (Norway spruce, Sitka spruce, Douglas-fir, European beech, and common oak) reveals that the total litterfall and nutrient concentrations does not differ significantly among the tree species but is affected by site characteristics [95]. The production of leaf

litter of a forest predominance of beech (*Fagus sylvatica* L.), with three deciduous-tree species (beech, ash (*Fraxinus excelsior* L.), and lime (*Tilia cordata* Mill. and/or *T. platyphyllos* Scop.) was also similar to which dominated by five deciduous-tree species (beech, ash, lime, hornbeam *Carpinus betulus* L.), and maple (*Acer pseudoplatanus* L. and/or *A. platanoides* L.). The increasing tree-species diversity (and decreasing the abundance of beech) is accompanied by an increase in the total quantity of Ca and Mg deposited on the soil surface by leaf litter [96]. The increased base status influences microbial populations, biomass and activity through changes in pH. The interpretation of the effect of litter on GHG exchange is improved when studies include accurate and detailed information on ground vegetation. Although studies to date focus mainly on dominant tree species, a few studies also report ground cover, e.g., natural growths and shrubs (*Lantana camara*, *Eupatorium odoratum*, *Hyptis suaveolens*) [40], herbs, grasses, scattered patches of mosses [78] and vegetation (*Camellia oleifera*, *Itea yunnanensis*), and some low-rise herbs (*Artemisia* sp.) [18].

3.1. Carbon Dioxide (CO₂)

The contribution of the litter layer to respiration ranged from 5% to 45% of the total CO₂ emissions from temperate forests soils [3]. The emissions of CO₂ were confirmed to be often lower in coniferous forest soils than in deciduous forests [97]. A meta-analysis revealed that natural and doubled litter inputs increased soil respiration in forest ecosystems by 36% and 55%, respectively. The effect of litter inputs on the increase in soil respiration in different types of forests assumed the following order: coniferous forests (50.7%) > broad-leaved forests (41.3%) > mixed forests (31.9%) [89]. In coniferous forests, the removal of litter caused a reduction in CO₂ emissions, ranging from 2.61% in a fir forest in Poland to 68% in a *Pinus caribaeae* plantation in Puerto Rico [39]. After the litter layer removal in a pine forest, CO₂ emissions were reduced by 43%, while CH₄ uptake increased more than twofold under dry and warm soil conditions [78].

These differences may result from the characteristics of the litter layer. Coniferous litter often contains more phenolic acids (e.g., ferulic and p-coumaric acids) than deciduous litter, which can only be used in small concentrations by microbes as substrates for metabolism. At higher concentrations, phenolic acids may inhibit bacterial and fungal activity [62]. Monoterpenes are biogenic volatile organic compounds produced especially by coniferous trees and released through root and litter [98]. Moreover, monoterpenes as well as phenolic compounds belong to secondary plant metabolites [99]. The presence of monoterpenes may increase CO₂ production due to their microbial mineralization, as reported in a Norway spruce site, in contrast to European beech samples [77].

The effect of litter on CO₂ fluxes can also be influenced by tree age. The removal of litter in deciduous forests lowered CO₂ emissions by 5% and 16% in old-growth and 85-year-old forests, respectively [100]. The CO₂ fluxes were found to be higher in a newly established (one-year-old) and a mature (38-years-old) stand, than in young (12-years-old), *P. radiata* plantations. The new and mature stands had more ground vegetation cover (80–90%) than the young radiata pine stands (30%). Together with a lower soil ammonium content (and lower mineralization rate) in the young stand, poor vegetation coverage may have resulted in lower CO₂ emissions [25]. The newly established pine stand also showed significantly higher CO₂ emissions than the mature stand, due to clear-cut harvesting practices, which result in a lower C/N ratio in the top 10 cm of the soil and lower organic matter quantity. It is known that the maximum CO₂ flux occurs in the top 15 cm of soil depth [40]. A reduced amount of litter and a lower C/N ratio cause rapid C mineralization, which results in increased litter respiration [101].

Broadleaf forests were found to have a relatively higher mean annual litterfall and a higher litter quality compared to mixed or pine forests [102,103]. The removal of litter reduced CO₂ emissions, to varying extents, depended on the type of deciduous tree species. In hornbeam oak forests, soil respiration decreased only slightly: from 2.88 kg CO₂ m⁻² year⁻¹ (research point with litter) to 2.78 kg CO₂ m⁻² year⁻¹ (litter-free research point), but in the acidophilous beech forest, CO₂ emissions decreased from

2.18 kg CO₂ m⁻² year⁻¹ to 1.32 kg CO₂ m⁻² year⁻¹ after excluding litter. The amount of CO₂ emitted from forest soils also depended on the speed of litter decomposition, which differed in different types of forests [42]. A beech stand was found to have the slowest litter decomposition, and its accumulation was approximately two to three times higher than in mixed stands of deciduous tree species [104]. Similarly, in a hornbeam oak forest litter decomposition, processes were faster and CO₂ was released more rapidly than in a beech forest. It was estimated that the average decrease in soil respiration globally after litter removal was 27% for different types of forests. The litter decomposition rate, along with soil respiration decreased after litter removal, in a seasonally flooded gallery forest and an upland forest where litter removal resulted in a 10–20% reduction in soil respiration [105]. Therefore, it can be concluded that the rate of litter decomposition had a significant impact on many differences in soil CO₂ emissions between various ecosystems. Tropical forests were very important in this context [50], as may have contributed about 67% to the total annual global CO₂ efflux [105]. These forests could react differently to litter manipulations, since they differed from temperate forests in terms of soil age, biotic composition, erosion, and/or uplift rates [106,107]. Tropical and subtropical forests may also have varied significantly in soil abiotic (e.g., soil moisture and temperature) and biotic (e.g., litter quantity and quality, tree species) factors, which also influenced the impact of litter inputs on CO₂ emissions [39,106,108,109].

3.2. Methane (CH₄)

Similar to CO₂ emission, forest types differ in soil CH₄ uptake ability. The high consumption of atmospheric CH₄ by forest soils confirms the involvement of high affinity methanotrophs [12] and the process is carried out by different groups of methanotrophs [110]. Among the most abundant methanotrophs, *Methylocystis* spp. and *Methylococcus* more often populate deciduous forest soils than mixed and coniferous forest soils [111]. A number of studies conducted under the same climatic conditions also indicate that tree species affect CH₄ uptake in forest soils, with deciduous forests consuming more CH₄ than coniferous forests [28,48,112,113]. One of the explanations for this is that it is due to vegetation and soil-related differences in the structure and activity of methanotroph communities [111,114]. Of the factors that could be important, litter and soils from coniferous forests have a lower pH than deciduous stands, typically ranging between 3 and 4 in pine-dominated forests [115–118]. Such conditions are below the optimum typical level for methanotrophs [119] and may result in a lower CH₄ uptake; however, some methanotrophs have adapted to such conditions in forest soils [120]. A study on different temperate tree species shows that soil under beech trees is more acidic and has lower inputs of Ca and Mg via litter in comparison with mixed stands of deciduous tree species [96,104].

The properties of the litter itself are also an important element. Litter in deciduous forests is characterized by a higher degradability than in coniferous forests, which results in higher soil N turnover rates [121]. Strong interactions between CH₄ oxidation and soil N have also been reported [122–124]. In temperate forests, N fertilization is reported to reduce the CH₄ sink [125] due to a salt effect [126] or a higher nitrification rate [127]. In subtropical forests, N deposition can suppress CH₄ uptake by altering methanotroph and methanogen abundance, diversity, and community structure [128].

The presence of monoterpenes may be a largely conifer-specific mechanism responsible for the negative effect of the litter layer on methanotroph activity [3,77]. The concentrations of monoterpenes are negligible in European beech leaves (as well as the roots and soil samples) compared with samples from Norway spruce [77]. Monoterpenes are highly volatile but are initially present at relatively high concentrations in recently fallen litter [99,129,130]. They are released during the long-term decomposition of needle litter (or released by roots), and involve rapid changes in their composition [99,129]. Although the rates of monoterpene loss from needle litter are found to vary initially between conifers, most of the monoterpene content is lost after 4–6 months [99] and decreases sharply by 40–85.4% after 90–120 days [129]. Some compounds are also detected in soils and may

interact with soil microorganisms, inhibiting methanotrophs, and decreasing soil CH₄ oxidation [3,77,131,132]. Methanotrophs may differ in their response to monoterpenes at the same concentration [133]. Among the most abundant monoterpenes, α -pinene is the major inhibitor of CH₄ oxidation in soils from a pine, aspen, and mixed stand in Canada [131], while β -pinene has the greatest inhibitory effect on the process in Norway spruce soil [77]. Among conifers, different monoterpene compounds may dominate. For example, α -pinene is found to be the dominant form in needles of *Pinus densiflora*, *Pinus rigida*, and *Pinus sylvestris*, while β -pinene is dominant in needles of *Pinus thunbergii*, *Picea sitchensis*, and *Picea abies* [129]. The removal of the organic layer in a German coniferous mixed forest causes a significant increase in CH₄ oxidation rates by a factor of 1.4–2.5 [80]. In Chinese pine stands, the removal of the litter layer reduces soil CO₂ emission by 17% and increases CH₄ uptake by 24% [18]. This is even higher in a study reported by Fan et al. [3] where the CO₂ emissions decrease by 24–32%, while CH₄ uptake increases by 55%. Although the litter layer reduces the atmospheric CH₄ uptake by dry soil, the removal of the layer has a minimal effect (+0.7%) on the annual CH₄ budget, through compensating effects during the wet and dry seasons [19].

4. Environmental Controllers of the Impact of Litter on GHG Fluxes

Consideration of the litter effect on soil GHG fluxes should include the role of climatic conditions, mostly temperature and precipitation. Due to the dynamics of these parameters, the litter effect on GHG fluxes may show significant seasonal variability.

Rainfall in an oak forest is reported to increase CO₂ emissions, which results in the rapid reactivation of litter-associated microorganisms [46]. On the other hand, in a tropical montane cloud forest in Peru, lower moisture levels do not change the soil respiration after litter removal, which is explained by the fact that the litter and organic matter are decomposed by microorganisms with different moisture sensitivities [47]. Litter respiration also depends largely on moisture content, and the contribution of litter to soil respiration is influenced by the frequency and amount of precipitation [46,48,134,135]. Warm and humid climatic conditions accelerate organic matter decomposition, resulting in increased rates of soil respiration [100]. Changes in the water content of the litter layer are often transient, since litter is directly exposed to wind and solar radiation [136]; nevertheless, they can influence CO₂ emissions, and therefore the overall forest CO₂ budget [137]. Continuous cycles of wetting and drying of the litter layer led to transient CO₂ emission [136,138]. An increase in CO₂ emissions followed by an increase in the litter moisture content due to rainfall was also reported in a semi-deciduous old-growth tropical forest (with mostly evergreen species) [49] and in a forest dominated by *Quercus serrata* Thunb. [136]. Studies carried out in coniferous and deciduous forests in different locations in Europe (Italy, the Netherlands, and Finland) show that leaf litter is the main source of CO₂ and the emissions peak at the higher moisture contents for all types of litter, temperatures, or sites, while the optimum soil CO₂ emissions are achieved at intermediate moisture contents (40–70% WFPS) [88]. Litter removal causes a decrease in soil moisture [15] (compared to soil with litter) and when soil moisture is low, both the transport of nutrients and the metabolism of decomposing microbes are reduced [139,140].

Hydrological conditions are a strong regulator of the CH₄ cycle since saturated (flooded) soil can be a source of methane, while well-aerated soil can be a sink of this gas [10]. After a high rainfall in the temperate zone or during the wet season in a tropical climate, soil may also emit CH₄, although the net exchange between soils and the atmosphere depends on how this impacts the balance between CH₄ production and consumption [19]. The strong dependence of CH₄ oxidation on water content is confirmed as litter addition during the dry season, as this does not significantly affect CH₄ uptake, while it decreases by $47.1 \pm 4.9\%$ during the wet season after doubling the litter level [27]. The litter effect may result from enhanced microbial activity and/or from changes in litter quality and decomposition rate [16]. It is reported that litter may store water during rainfall events. Since water cannot penetrate the mineral soil, a high soil diffusivity is main-

tained [28]. However, a study on different types of needleleaf and broadleaf litters revealed that the rainfall interception storage capacity of the litter layer varied with physical features and rainfall characteristics [93]. The interception-related storage capacity of needle litters varied significantly with the litter type, while there were no significant differences in water storage across the broadleaf litter types. It was reported that a higher intensity or longer duration of rainfall events could increase the interception storage capacity in all broadleaf and needleleaf litters [93].

The litter layer was an effective insulator, isolating the soil from the effects of variations in irradiance, consequently lowering soil temperature [21]. In a deciduous forest, litter and soil temperatures were responsible for 68% to 81% of the variability in CO₂ emissions, respectively [100]. When there was no litter on the soil surface, the influence of temperature on soil respiration was higher, the activity of soil microbes and their enzymes increased, and the degradation of organic matter was greater. Thus, under these conditions, an increase in soil CO₂ emission could often be observed [21,141–143]. After the removal of litter in a *Quercetum petraeae-cerris* forest in northeastern Hungary, the soil was found to reach higher temperatures in summer and lower temperatures in winter [37]. The greatest reductions in CO₂ emissions after litter exclusion were observed in a *Cinnamomum camphora* forest in China (39.2%) [144], in a beech (*Fagus sylvatica*) forest in Poland (about 39.45%) [42], and in a wet tropical forest dominated by *Tabebuia heterophylla* in Puerto Rico (54%) [39].

5. Forest Management

In addition to environmental regulators, forest management can also control the contribution of litter to GHG emissions, via their effect on litter inputs through management practices involving tree removal, grazing, extensive deforestation, or fertilization [13,22–24]. Soil disturbance, as well as the mixing and movement of litter and organic material deeper into the mineral soil layer during the mechanical site preparation in clear-cut sites results in a decrease or no increase in CO₂ emissions, although litter decomposition accelerates [1,25,26]. It is reported that clear-cut harvesting results in an up to 50% decrease in soil C [1,25], but a low or insignificant impact on C stocks is also reported [145,146]. In spruce forests after clear-cutting, soil respiration is higher in undisturbed plots than in plots with a disturbed upper soil layer and this is influenced by the thickness of the litter layer, the degree of upper soil damage, and the presence of logging residues on the soil surface [147]. Different management practices modify the soil conditions for methanotrophic bacteria and may differently affect CH₄ uptake in forest soils. Clear-cutting is found to weaken the capability of methanotrophs to oxidize CH₄ through alterations in soil temperature, water content, and C decomposition, while selective cutting stimulates, suppresses, or has no effect on CH₄ uptake [148]. Similar to agricultural soils, fertilization inhibited soil CH₄ uptake in N-rich forest soils but promoted consumption in N-deficient forest soils [148]. Forest conversion, which has an important effect on all GHG fluxes, significantly affects CH₄ absorption capacity through plant allelopathy (including the release of monoterpenes from litter and roots), changes in soil properties (e.g., temperature, moisture, pH, C and N availability), and has an effect on soil microorganisms [132]. The conversion of a naturally grown beech forest into a pure spruce and a mixed stand in Germany reduces the mean CH₄ uptake rates by 58% and 22% during the growing season and by 54% and 20% during the dormant season. This is associated with the formation of a distinct O horizon during the succession and changes in the population density or activity of methanotrophs [28].

6. Effect of Climate Change

Climate change influences CH₄ and CO₂ fluxes and the net ecosystem C balance through its effect on abiotic and biotic drivers [149,150]. The predicted increases in CO₂, N deposition, temperature, elevated ozone concentrations, drought, and acid deposition will have an impact on net primary production (NPP), which in turn will affect both the quality and quantity of aboveground litter [15]. An increase in atmospheric CO₂ concentration may stimulate plant growth and thus increase litterfall [20,21,51,144]. The

increased litter input will influence soil nutrient content and substrate availability, thereby impacting on microbial community structure and activity with associated increases in CO₂ efflux [14,52,105,151–156]. Natural and doubled litter inputs tend to increase soil microbial biomass C and soil DOC by 21.0–33.6% and 60.3–87.7%, respectively. Litter inputs also increase the total phospholipid fatty acid (PLFA) content, which are linearly related to soil respiration, whilst decreasing the fungal/bacterial PLFA ratio, which decreases soil respiration [89]. A doubling of needle litter input in old-growth western hemlock (*Tsuga heterophylla* (Rafinesque) and Douglas fir (*Pseudotsua menziessi* Mirb.) forests results in increased soil respiration [23] while it does not increase CO₂ emissions in a European deciduous forest due to low soil moisture contents, which impede the litter decomposition processes [37]. Higher litter amounts can promote soil C release through the priming effect [70]. It is found that litter addition has a stronger effect on soil respiration in subtropical broadleaf forests than in pine and mixed forests, which is a result of the quantity and quality of the litterfall [13] reflected in the foliar N content, soil C:N ratio, lignin:N ratio, and phenolic content [157]. Climatic factors can also change the chemistry of the litter and affect its susceptibility to decomposition. Elevated CO₂ levels decrease the quality of *Populus tremuloides* leaf litter by increasing the C:N ratio, the phenolic, and the lignin content [158]. In a study on *Molinia caerulea* litter, N fertilization increases the N and decreases the C concentration, whereas elevated CO₂ decreases litter quality (increases C:N) and increases the lignin and saturated fatty acid content [159]. As a consequence, CH₄ production in laboratory incubation experiments decreases when litter from N-fertilized plants is used, whereas the litter from elevated CO₂ treatments has no effect [159]. Litter addition, in combination with warming, significantly increases CH₄ uptake rates due to a soil drying effect and increases the availability of DOC [159]. In turn, the repeated addition of beech litter impedes the diffusion of CH₄ and significantly reduces the annual uptake rate; due to their shape, broad beech leaves reduce CH₄ uptake more efficiently than spruce needles [160]. Future increases in N deposition may modify monoterpene fluxes in subtropical forests, as demonstrated in a study on a Masson pine forest and a monsoon evergreen broad-leaved forest, where long-term N addition results in an increased monoterpene release from litter [98]. Higher monoterpene contents in the future may reduce methanotrophic activity, as reported previously [3,77].

An increase in the range and impact of alien pests, particularly in Northern and Eastern Europe, is another likely consequence of climate change that may decrease C sequestration in forests, reduce forest structural and functional redundancy, and affect their resilience to future climate change [161,162]. Insect defoliation increases the organic inputs into the soil in the form of insect feces, cadavers, litter (changed in quality), and other plant material, and may result in an increase in soil CO₂ emission via a transformation of tree biomass into fast decomposable organic matter [163]. Aside from defoliators, wood-boring infestations can shift forests from C sinks to sources [162].

7. Future Research

The complex and multi-level influences of litter on the soil-atmosphere GHG exchange in forests shows a strong relationship between above- and below-ground processes. Given the important contribution of forest ecosystems to climate change mitigation, an understanding of the interactions between litter production, CO₂ emissions and CH₄ uptake, is essential for a more complete understanding of the underlying controls and drivers of the GHG budget in these ecosystems. In turn, this will provide information on how best to utilize forest ecosystems to sequester carbon and reduce GHG emissions. This approach also needs to consider the effects of human activity and associated management interventions and how these are impacted by climate change. Based on this review, we propose that future research should focus on the following areas:

- (i) Due to the sensitivity of soil CO₂ efflux to climatic factors, it is important to focus on the multiple effects of climate change (e.g., increased CO₂ and CH₄ concentrations, increased temperature, drought, extreme precipitation events) on GHG exchange

between the atmosphere and the litter-covered soil (or soil without litter) in various types of forests, globally. The litter may have direct or indirect effects on GHG emissions and decomposition processes [144], and even small changes can alter the global C balance, and atmospheric CO₂ concentrations, or nutrient cycling, with the potential to exacerbate the effects of climate change [21,105].

- (ii) Equally noteworthy is the need to have a better understanding of global change-driven forest succession, where broad-leaved trees have begun to appear in needle-leaved ecosystems. Due to the shifts in tree composition, a number of ecosystem (e.g., litterfall rates, litter quality and soil-related processes, soil organic matter decomposition, and GHGs production) are changing [64].
- (iii) Climate change affects the primary productivity of forests, and elevated CO₂ concentrations in the atmosphere may result in increased litterfall and increased organic matter inputs into the soil, resulting in increased C sequestration [52,144]. Large amounts of aboveground litter can also lead to a priming effect—a complex but not fully understood (especially in situ) soil–plant interaction [68]. As a result of the increased contribution of fresh organic matter to the soil, the decomposition processes are stimulated and the older stored C is released from the soil as CO₂ [52]. A better understanding of this phenomenon is important in the context of future climatic scenarios, according to which litter inputs will be increased [52] and the occurrence of priming effects may intensify.
- (iv) The effect of monoterpenes on CH₄ uptake is a largely uninvestigated topic and we propose several research areas that require attention: (a) the better recognition and identification of monoterpenes dominant in litter from different tree species, combined with the recognition of methanotroph responses; (b) understanding the longevity of any effects of monoterpenes in litter since recently fallen litter has a higher content of monoterpenes [129,130,164]; (c) finding out whether there are inhibitors that reduce the emissions of terpenes from litter, since monoterpenes can decrease the activity of methanotrophs; (d) the verification of whether methanotrophs produce monoterpenes [165] would be worthwhile with the objective of stimulating CH₄ uptake in coniferous forests, as terpenes are generally widespread in both plant and bacterial metabolism [166]; (e) further work is also required on the effect of increasing the N deposition on monoterpene fluxes [98] in all climatic zones.
- (v) The effect of forest pests on GHG emissions, including their impact on litter quality and quantity, is poorly understood [162,163] and requires further investigation.
- (vi) The identification of the underlying processes through which litter influences soil processes requires research into the species composition of microbial consortia occurring in different forest types in a range of climatic zones.
- (vii) Finally, the characteristics of the investigated litter needs to be specified in more detail, including the thickness of the litter, its morphology, temperature, number of layers and the degree of decomposition.

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Appendix A

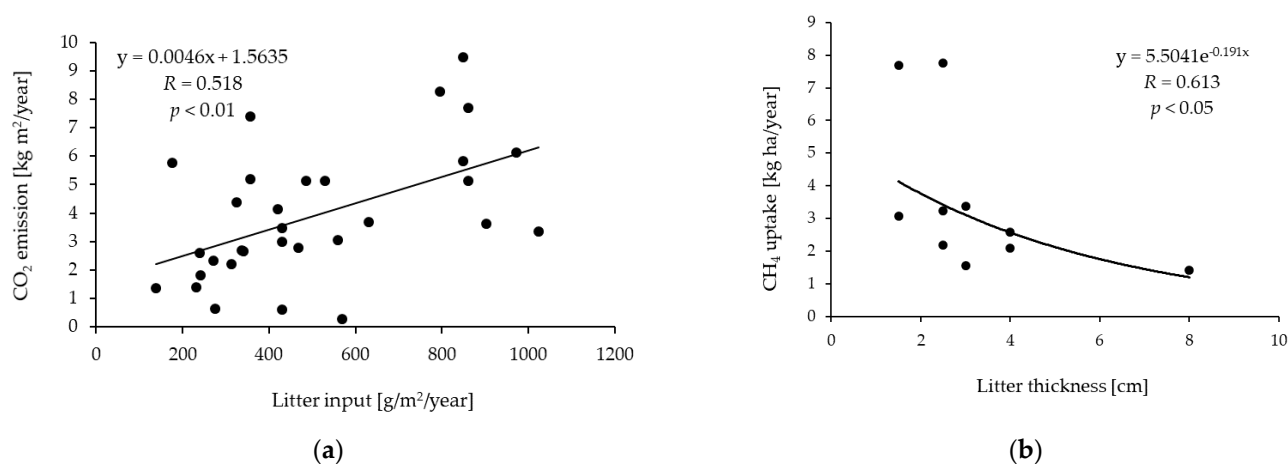


Figure A1. Relationship between (a) annual CO₂ emission and litter input (based on: [27,28,33,78,81,86,167,168]); (b) annual CH₄ uptake rates and thickness of litter layer (based on: [13,18,20,21,37,44,53,65,74,143,169–174]) from different forests.

References

- Lal, R. Forest soils and carbon sequestration. *For. Ecol. Manag.* **2005**, *220*, 242–258. [CrossRef]
- Forest Europe. *State of Europe's Forests 2020*; Forest Europe: Bonn, Germany, 2020.
- Fan, J.; Luo, R.; McConkey, B.G.; Ziadi, N. Effects of nitrogen deposition and litter layer management on soil CO₂, N₂O, and CH₄ emissions in a subtropical pine forestland. *Nat. Sci. Rep.* **2020**, *10*, 8959. [CrossRef]
- Kuzyakov, Y. Sources of CO₂ efflux from soil and review of partitioning methods. *Soil Biol. Biochem.* **2006**, *38*, 425–448. [CrossRef]
- Baccini, A.; Goetz, S.J.; Walker, W.S.; Laporte, N.T.; Sun, M.; Sulla-Menashe, D.; Hackler, J.; Beck, P.S.A.; Dubayah, R.; Friedl, M.A.; et al. Estimated carbon dioxide emissions from tropical deforestation improved by carbon-density maps. *Nat. Clim.* **2012**, *2*, 182–185. [CrossRef]
- Carvalho, J.A., Jr.; Amaral, S.S.; Costa, M.A.M.; Soares Neto, T.G.; Veras, C.A.G.; Costa, F.S.; Van Leeuwen, T.T.; Krieger Filho, G.C.; Tourigny, E.; Forti, M.C.; et al. CO₂ and CO emission rates from three forest fire controlled experiments in Western Amazonia. *Atmos. Environ.* **2016**, *135*, 73–83. [CrossRef]
- Waheed, R.; Chang, D.; Sarwar, S.; Chen, W. Forest, agriculture, renewable energy, and CO₂ emission. *J. Clean. Prod.* **2018**, *172*, 4231–4238. [CrossRef]
- IPCC. *Climate Change 2014: Synthesis Report. Contribution of Working Groups I, II and III to the Fifth Assessment Report of the Intergovernmental Panel on Climate Change*; IPCC: Geneva, Switzerland, 2014.
- Le Mer, J.; Roger, P. Production, oxidation, emission and consumption of methane by soils: A review. *Eur. J. Soil Biol.* **2001**, *37*, 25–50. [CrossRef]
- Wnuk, E.; Walkiewicz, A.; Bieganski, A. Methanogenesis and aerobic methanotrophy in arable soils contaminated with cadmium. *Catena* **2020**, *189*, 104480. [CrossRef]
- Reay, D.S.; Nadwell, D.B. Methane oxidation in temperate soils: Effects of inorganic N. *Soil Biol. Biochem.* **2004**, *36*, 2059–2065. [CrossRef]
- Nazaries, L.; Murrell, J.C.; Millard, P.; Baggs, L.; Singh, B.K. Methane, microbes implication for landscape-integrated CH₄ budget. *Glob. Change Biol.* **2013**, *23*, 966–976.
- Han, T.; Huang, W.; Liu, J.; Zhou, G.; Xiao, Y. Different soil respiration responses to litter manipulation in three subtropical successional forests. *Sci. Rep.* **2015**, *5*, 18166. [CrossRef]
- Sayer, E.J. Using experimental manipulation to assess the roles of leaf litter in the function of forest ecosystems. *Biol. Rev.* **2006**, *81*, 1–31. [CrossRef]
- Xu, S.; Liu, L.L.L.; Sayer, E.J. Variability of above-ground litter inputs alters soil physicochemical and biological processes: A meta-analysis of litterfall-manipulation. *Biogeosciences* **2013**, *10*, 7423–7433. [CrossRef]
- Krishna, M.P.; Mohan, M. Litter decomposition in forest ecosystems: A review. *Energ. Ecol. Environ.* **2017**, *2*, 236–249. [CrossRef]
- Thoms, C.; Gleixner, G. Seasonal differences in tree species' influence on soil microbial communities. *Soil Biol. Biochem.* **2013**, *66*, 239–248. [CrossRef]

18. Cheng, J.; Lee, X.; Zhou, Z.; Wang, B.; Xing, Y.; Cheng, H.; Tang, Y. The effects of litter layer and soil properties on the soil-atmosphere fluxes of greenhouse gases in karst forest, southwest China. *Pol. J. Ecol.* **2013**, *61*, 79–92.
19. Wang, Y.; Wang, H.; Ma, Z.; Dai, X.; Wen, X.; Liu, Y.; Wang, Z.L. The litter layer acts a moisture-induced bidirectional buffers for atmospheric methane uptake by soil of a subtropical pine plantation. *Soil Biol. Biochem.* **2013**, *66*, 45–50. [[CrossRef](#)]
20. Prévost-Bouré, N.C.; Soudani, K.; Damesin, C.; Berveiller, D.; Lata, J.C.; Dufrêne, E. Increase in aboveground fresh litter quantity over-stimulates soil respiration in a temperate deciduous forest. *Appl. Soil Ecol.* **2010**, *46*, 26–34. [[CrossRef](#)]
21. Kotroczó, Z.; Veres, Z.; Biró, B.; Tóth, J.A.; Fekete, I. Influence of temperature and organic matter content on soil respiration in a deciduous oak forest. *Eurasian, J. Soil Sci.* **2014**, *3*, 303–310. [[CrossRef](#)]
22. Holmes, K.W.; Chadwick, O.A.; Kyriakidis, P.C.; Silva de Filho, E.P.; Soares, J.V.; Roberts, D.A. Large-area spatially explicit estimates of tropical soil carbon stocks and response to land-cover change. *Glob. Biogeochem. Cycles* **2006**, *20*, GB3004. [[CrossRef](#)]
23. Crow, S.E.; Lajtha, K.; Bowden, R.D.; Yano, Y.; Brant, J.B.; Caldwell, B.A.; Sulzman, E.W. Increased coniferous needle inputs accelerate decomposition of soil carbon in an old-growth forest. *For. Ecol. Manag.* **2009**, *258*, 2224–2232. [[CrossRef](#)]
24. Huang, W.; Spohn, M. Effects of long-term litter manipulation on soil carbon, nitrogen, and phosphorus in a temperate deciduous forest. *Soil Biol. Biochem.* **2015**, *83*, 12–18. [[CrossRef](#)]
25. Barrena, I.; Menéndez, S.; Duñabeitia, M.; Merino, P.; Stange, C.F.; Spott, O.; González-Muria, C.; Estavillo, J.M. Greenhouse gas fluxes (CO₂, N₂O and CH₄) from forest soils in the Basque Country: Comparison of different tree species and growth stages. *For. Ecol. Manag.* **2013**, *310*, 600–611. [[CrossRef](#)]
26. Mjöfors, K.; Strömberg, M.; Nohrstedt, H.Ö.; Gärdenäs, A.I. Impact of site-preparation on soil-surface CO₂ fluxes and litter decomposition in a clear-cut in Sweden. *Silva Fenn.* **2015**, *49*, 1–20. [[CrossRef](#)]
27. Wu, J.; Lu, M.; Feng, J.; Zhang, D.; Chen, Q.; Li, Q.; Long, C.; Zhang, Q.; Cheng, X. Soil net methane uptake rates in response to short-term litter input change in a coniferous forest ecosystem of central China. *Agric. For. Meteorol.* **2019**, *271*, 307–315. [[CrossRef](#)]
28. Borken, W.; Beese, F. Methane and nitrous oxide fluxes of soils in pure and mixed stands of European beech and Norway spruce. *Eur. J. Soil Sci.* **2006**, *57*, 617–625. [[CrossRef](#)]
29. Eickenscheidt, N.; Brumme, R. Regulation of N₂O and NO_x emission patterns in six acid temperate beech forest soils by soil gas diffusivity, N turnover, and atmospheric NO_x concentrations. *Plant Soil* **2013**, *369*, 515–529. [[CrossRef](#)]
30. Epron, D.; Nouvellon, Y.; Rouspard, O.; Mouvondy, W.; Mabiala, A.; Saint-André, L.; Joffre, R.; Jourdan, C.; Bonnefond, J.; Berbigier, P.; et al. Spatial and temporal variations of soil respiration in a *Eucalyptus* plantation in Congo. *For. Ecol. Manag.* **2004**, *202*, 149–160. [[CrossRef](#)]
31. Wang, Y.; Chen, H.; Zhu, Q.; Peng, C.; Wu, N.; Yang, G.; Zhu, D.; Tian, J.; Tian, L.; Kang, X.; et al. Soil methane uptake by grasslands and forests in China. *Soil Biol. Biochem.* **2014**, *74*, 70–81. [[CrossRef](#)]
32. Leitner, S.; Sae-Tun, O.; Kranzinger, L.; Zechmeister-Boltenstern, S.; Zimmermann, M. Contribution of litter layer to soil greenhouse gas emissions in a temperate beech forest. *Plant Soil* **2016**, *403*, 455–469. [[CrossRef](#)]
33. Liu, H.; Zhao, P.; Lu, P.; Wang, Y.S.; Lin, Y.B.; Rao, X.Q. Greenhouse gas fluxes from soils of different land-use types in a hilly area of South China. *Agric. Ecosyst. Environ.* **2008**, *124*, 125–135. [[CrossRef](#)]
34. Andersson, M.; Kjoller, A.; Struwe, S. Microbial enzyme activities in leaf litter, humus and mineral soil layers of European forests. *Soil Biol. Biochem.* **2004**, *36*, 1527–1537. [[CrossRef](#)]
35. Bond-Lamberty, B.; Wang, C.; Gower, S.T. A global relationship between the heterotrophic and autotrophic components of soil respiration? *Glob. Change Biol.* **2004**, *10*, 1756–1766. [[CrossRef](#)]
36. Hanson, P.J.; Edwards, N.T.; Garten, C.T.; Andrews, J.A. Separating root and soil microbial contributions to soil respiration: A review of methods and observations. *Biogeochemistry* **2000**, *48*, 115–146. [[CrossRef](#)]
37. Fekete, I.; Kotroczó, Z.; Varga, C.; Nagy, P.T.; Várbíró, G.; Bowden, R.D.; Tóth, J.A.; Lajtha, K. Alterations in forest detritus inputs influence soil carbon concentration and soil respiration in a Central-European deciduous forest. *Soil Biol. Biochem.* **2014**, *74*, 106–114. [[CrossRef](#)]
38. Ivanov, A.V.; Braun, M.; Zamolodchikov, D.G.; Lynov, D.V.; Panfilova, E.V. Forest litters as a link in the carbon cycle in coniferous-broadleaved forests of southern far east of Russia. *Eurasian Soil Sci.* **2018**, *51*, 1164–1171. [[CrossRef](#)]
39. Li, Y.; Xu, M.; Sun, O.J.; Cui, W. Effects of root and litter exclusion on soil CO₂ efflux and microbial biomass in wet tropical forests. *Soil Biol. Biochem.* **2004**, *36*, 2111–2114. [[CrossRef](#)]
40. Mukhopadhyay, S.; Maiti, S.K. Soil CO₂ flux in grasslands, afforested land and reclaimed coalmine overburden dumps: A case study. *Land Degrad. Develop.* **2014**, *25*, 216–227. [[CrossRef](#)]
41. Dou, X.; Zhou, W.; Zhang, Q.; Cheng, X. Greenhouse gas (CO₂, CH₄, N₂O) emissions from soils following afforestation in central China. *Atmos. Environ.* **2016**, *126*, 98–106. [[CrossRef](#)]
42. Wroński, K.T. Spatial variability of CO₂ fluxes from meadow and forest soils in western part of Wzniesienia Łódzkie (Łódź Hills). *For. Res. Pap.* **2018**, *79*, 45–58. [[CrossRef](#)]
43. Vasconcelos, S.S.; Zarin, D.J.; Capanu, M.; Littell, R.; Davidson, E.A.; Ishida, F.Y.; Santos, E.B.; Araújo, M.M.; Aragão, D.V.; Rangel-Vasconcelos, L.G.T.; et al. Moisture and substrate availability constrain soil trace gas fluxes in an eastern Amazonian regrowth forest. *Glob. Biogeochem. Cycle* **2004**, *18*, GB2009. [[CrossRef](#)]
44. Konda, R.; Ohta, S.; Ishizuka, S.; Heriyanto, J.; Wicaksono, A. Seasonal changes in the spatial structures of N₂O, CO₂, and CH₄ fluxes from *Acacia mangium* plantation soils in Indonesia. *Soil Biol. Biochem.* **2010**, *42*, 1512–1522. [[CrossRef](#)]

45. Fuentes, J.P.; Bown, H.E.; Perez-Quezada, J.F.; Franck, N. Litter removal in a sclerophyll forest: Short- and medium-term consequences for soil properties. *Soil Sci. Soc. Am. J.* **2014**, *78*, 634–644. [[CrossRef](#)]
46. Sun, W.; Maseyk, K.; Lett, C.; Seibt, U. Litter dominates surface fluxes of carbonyl sulfide in a Californian oak woodland. *J. Geophys. Res. Biogeo.* **2016**, *121*, 438–450. [[CrossRef](#)]
47. Zimmermann, M.; Meir, P.; Bird, M.; Malhi, Y.; Ccahuana, A. Litter contribution to diurnal and annual soil respiration in a tropical montane cloud forest. *Soil Biol. Biochem.* **2009**, *41*, 1338–1340. [[CrossRef](#)]
48. Borcken, W.; Davidson, E.A.; Savage, K.; Gaudinski, J.; Trumbore, S.E. Drying and wetting effects on carbon dioxide release from organic horizons. *Soil Sci. Soc. Am. J.* **2003**, *67*, 1888–1896. [[CrossRef](#)]
49. Goulden, M.L.; Miller, S.C.; Da Rocha, H.R.; Menton, M.C.; De Freitas, H.C.; Silva Figueira, M.; Dias de Sousa, C.A. Diel and seasonal patterns of tropical forest CO₂ exchange. *Ecol. Appl.* **2004**, *14*, S42–S54. [[CrossRef](#)]
50. Sayer, E.J.; Powers, J.S.; Tanner, E.V.J. Increased litterfall in tropical forests Boosts the transfer of soil CO₂ to the atmosphere. *PLoS ONE* **2007**, *2*, e1299. [[CrossRef](#)]
51. Sulzman, E.W.; Brant, J.B.; Bowden, R.D.; Lajtha, K. Contribution of aboveground litter, belowground litter, and rhizosphere respiration to total soil CO₂ efflux in an old growth coniferous forest. *Biogeochemistry* **2005**, *73*, 231–256. [[CrossRef](#)]
52. Bréchet, L.M.; Lopez-Sangil, L.; George, C.; Birkett, A.J.; Baxendale, C.; Castro Trujillo, B.; Sayer, E.J. Distinct responses of soil respiration to experimental litter manipulation in temperate woodland and tropical forest. *Ecol. Evol.* **2018**, *8*, 3787–3796. [[CrossRef](#)]
53. Zhao, Q.; Classen, A.T.; Wang, W.W.; Zhao, X.R.; Mao, B.; Zeng, D.H. Asymmetric effects of litter removal and litter addition on the structure and function of soil microbial communities in a managed pine forest. *Plant Soil* **2017**, *414*, 81–93. [[CrossRef](#)]
54. Keiblinger, K.M.; Hall, E.K.; Wanek, W.; Szukics, U.; Hämmerle, I.; Ellersdorfer, G.; Böck, S.; Strauss, J.; Sterflinger, K.; Richter, A.; et al. The effect of resource quantity and the resource stoichiometry on microbial carbon-use-efficiency. *FEMS Microbiol. Ecol.* **2010**, *73*, 430–440. [[CrossRef](#)]
55. Singh, B.K.; Bardgett, R.D.; Smith, P.; Reay, D.S. Microorganisms and climate change: Terrestrial feedbacks and mitigation options. *Nat. Rev. Microbiol.* **2010**, *8*, 779–790. [[CrossRef](#)] [[PubMed](#)]
56. Schneider, T.; Keiblinger, K.M.; Schmid, E.; Sterflinger-Gleixner, K.; Ellersdorfer, G.; Roschitzki, B.; Richter, A.; Eberl, L.; Zechmeister-Boltenstern, S.; Riedel, K. Who is who in litter decomposition? Metaproteomics reveals major microbial players and their biogeochemical functions. *ISME J.* **2012**, *6*, 1749–1762. [[CrossRef](#)]
57. Bonanomi, G.; De Filippis, F.; Cesarano, G.; La Stora, A.; Zotti, M.; Mazzoleni, S.; Incerti, G. Linking bacterial and eukaryotic microbiota to litter chemistry: Combining next generation sequencing with ¹³C CPMAS NMR spectroscopy. *Soil Biol. Biochem.* **2019**, *129*, 110–121. [[CrossRef](#)]
58. Janssens, I.A.; Luysaert, S. Nitrogen's carbon bonus. *Nat. Geosci.* **2009**, *2*, 318–319. [[CrossRef](#)]
59. Reay, D.; Sabine, C.; Smith, P.; Hymus, G. Spring-time for sinks. *Nature* **2007**, *446*, 727–728. [[CrossRef](#)]
60. Mo, J.; Zhang, W.; Zhu, W.; Fang, Y.; Li, D.; Zhao, P. Response of soil respiration to stimulated N deposition in a disturbed and rehabilitated tropical forest in southern China. *Plant Soil* **2007**, *296*, 125–135. [[CrossRef](#)]
61. Manzoni, S.; Jackson, R.B.; Trofymow, J.A.; Porporato, A. The global stoichiometry of litter nitrogen mineralization. *Science* **2008**, *321*, 684–686. [[CrossRef](#)]
62. Smolander, A.; Loponen, J.; Suominen, K.; Kitunen, V. Organic matter characteristics and C and N transformations in the humus layer under two tree species, *Betula pendula* and *Picea abies*. *Soil Biol. Biochem.* **2005**, *37*, 1309–1318. [[CrossRef](#)]
63. Ushio, M.; Balsler, T.C.; Kitayama, K. Effects of condensed tannins in conifer leaves on the composition and activity of the soil microbial community in a tropical montane forest. *Plant Soil* **2013**, *365*, 157–170. [[CrossRef](#)]
64. Fernández-Alonso, M.; Curriel Yuste, J.; Kitzler, B.; Oritz, C.; Rubio, A. Changes in litter chemistry associated with global change-driven forests succession resulted in time-decoupled responses of soil carbon and nitrogen cycles. *Soil Biol. Biochem.* **2018**, *120*, 200–211. [[CrossRef](#)]
65. Tang, X.; Liu, S.; Zhou, G.; Zhang, D.; Zhou, C. Soil-atmospheric exchange of CO₂, CH₄, and N₂O in three subtropical forest ecosystems in southern China. *Glob. Chang. Biol.* **2006**, *12*, 546–560. [[CrossRef](#)]
66. Kuzyakov, Y.; Friedel, J.K.; Stahr, K. Review of mechanisms and quantification of priming effects. *Soil Biol. Biochem.* **2000**, *32*, 1485–1498. [[CrossRef](#)]
67. Nottingham, A.T.; Griffiths, H.; Chamberlain, P.M.; Stott, A.W.; Tanner, E.V.J. Soil priming by sugar and leaf-litter substrates: A link to microbial groups. *Appl. Soil Ecol.* **2009**, *42*, 183–190. [[CrossRef](#)]
68. Kuzyakov, Y. Priming effects: Interactions between living and dead organic matter. *Soil Biol. Biochem.* **2010**, *42*, 1363–1371. [[CrossRef](#)]
69. Lyu, M.; Nie, Y.; Giardina, C.P.; Vadeboncoeur, M.A.; Ren, Y.; Fu, Z.; Wang, M.; Jin, C.; Liu, X.; Xie, J. Litter quality and site characteristics interact to affect the response of priming effect to temperature in subtropical forests. *Funct. Ecol.* **2019**, *33*, 2226–2238. [[CrossRef](#)]
70. Naldini, M.B.; Harguindéguy, N.P.; Kowaljow, E. Soil carbon release enhanced by increased litter input in a degraded semi-arid forest soil. *J. Arid Environ.* **2021**, *186*, 104400. [[CrossRef](#)]
71. Chao, L.; Liu, Y.; Freschet, G.T.; Zhang, W.; Yu, X.; Zheng, W.; Guan, X.; Yang, Q.; Chen, L.; Dijkstra, F.A. Litter carbon and nutrient chemistry control the magnitude of soil priming effect. *Funct. Ecol.* **2019**, *33*, 876–888. [[CrossRef](#)]

72. Nottingham, A.T.; Turner, B.L.; Chamberlain, P.M.; Stott, A.W.; Tanner, E.V.J. Priming and microbial nutrient limitation in lowland tropical forest soils of contrasting fertility. *Biogeochemistry* **2012**, *111*, 219–237. [[CrossRef](#)]
73. Luo, Y.; Zhou, X. *Soil Respiration and the Environment*; Academic Press: London, UK, 2006; p. 328.
74. Khalid, M.S.; Shaaban, M.; Hu, R. N₂O, CH₄, and CO₂ emissions from continuous flooded, wet, and flooded converted to wet soils. *J. Plant Nutr. Soil Sci.* **2019**, *19*, 342–351. [[CrossRef](#)]
75. Price, S.J.; Sherlock, R.R.; Kelliher, F.M.; Mcseveny, T.M.; Tate, K.R.; Condon, L.M. Pristine New Zealand forest soil is a strong methane sink. *Glob. Chang. Biol.* **2004**, *10*, 16–26. [[CrossRef](#)]
76. Marrero, T.R.; Mason, E.A. Gaseous diffusion coefficients. *J. Phys. Chem. Ref.* **1972**, *1*, 3–118. [[CrossRef](#)]
77. Maurer, D.; Kolb, S.; Haumaier, L.; Borken, W. Inhibition of atmospheric methane oxidation by monoterpenes in Norway spruce and European beech soils. *Soil Biol. Biochem.* **2008**, *40*, 3014–3020. [[CrossRef](#)]
78. Peichl, M.; Arain, M.A.; Ullah, S.; Moore, T.R. Carbon dioxide, methane, and nitrous oxide exchanges in an age-sequence of temperate pine forests. *Glob. Change Biol.* **2010**, *16*, 2198–2212. [[CrossRef](#)]
79. Saari, A.; Heiskanen, J.; Martikainen, P.J. Effect of the organic horizon on methane oxidation and uptake in soil of a boreal Scots pine forest. *FEMS Microbiol. Ecol.* **1998**, *26*, 245–255. [[CrossRef](#)]
80. Steinkamp, R.; Butterbach-Bahl, K.; Papen, H. Methane oxidation by soils of an N limited and N fertilized spruce forest in the Black Forest, Germany. *Soil Biol. Biochem.* **2001**, *33*, 145–153. [[CrossRef](#)]
81. Dong, Y.; Scharffe, D.; Lobert, J.M.; Crutzen, P.J.; Sanhueza, E. Fluxes of CO₂, CH₄ and N₂O from temperate forest soil: The effects of leaves and humus layers. *Tellus B Chem. Phys. Meteorol.* **1998**, *50*, 243–252. [[CrossRef](#)]
82. Yan, Y.; Sha, L.; Cao, M.; Zheng, Z.; Tang, J.; Wang, Y.; Zhang, Y.; Wang, R.; Liu, G.; Wang, Y.; et al. Fluxes of CH₄ and N₂O from soil under a tropical seasonal rain forest in Xishuangbanna, Southwest China. *J. Environ. Sci.* **2008**, *20*, 207–215. [[CrossRef](#)]
83. Xiao, D.M.; Wang, M.; Wang, Y.S.; Ji, L.Z.; Han, S.J. Fluxes of soil carbon dioxide, nitrous oxide and firedamp in broadleaved/Korean pine forest. *J. For. Res.* **2004**, *15*, 107–112.
84. Pedersen, E.P.; Elberling, B.; Michelsen, A. Seasonal variations in methane fluxes in response to summer warming and leaf litter addition in a subarctic heath ecosystem. *J. Geophys. Res. Biogeosci.* **2017**, *122*, 2137–2153. [[CrossRef](#)]
85. Liu, Y.; Cui, Z.; Huang, Z.; Miao, H.T.; Wu, G.L. The influence of litter crusts on soil properties and hydrological processes in a sandy ecosystem. *Hydrol. Earth Syst. Sci.* **2019**, *23*, 2481–2490. [[CrossRef](#)]
86. Zhao, S.W.; Zhao, Y.G.; Wu, J.S. Quantitative analysis of soil pores under natural vegetation successions on the Loess Plateau. *Sci. China Earth Sci.* **2010**, *53*, 617–625. [[CrossRef](#)]
87. Wolf, K.; Flessa, H.; Veldkamp, E. Atmospheric methane uptake by tropical montane forest soils and the contribution of organic layers. *Biogeochemistry* **2012**, *111*, 469–483. [[CrossRef](#)]
88. Gritsch, C.; Egger, F.; Zehetner, F.; Zechmeister-Boltenstern, S. The effect of temperature and moisture on trace gas emissions from deciduous and coniferous leaf litter. *Biogeosciences* **2016**, *121*, 1339–1351. [[CrossRef](#)]
89. Zhang, Y.; Zou, J.; Meng, D.; Dang, S.; Zhou, J.; Osborne, B.; Ren, Y.; Liang, T.; Yu, K. Effect of soil microorganisms and labile C availability on soil respiration in response to litter inputs in forest ecosystems: A meta-analysis. *Ecol. Evol.* **2020**, *10*, 13602–13612. [[CrossRef](#)]
90. Sullivan, B.W.; Selmants, P.C.; Hart, S.C. What is the relationship between soil methane oxidation and other C compounds? *Glob. Change Biol.* **2014**, *20*, 2381–2382. [[CrossRef](#)]
91. Hensgens, G.; Lechtenfeld, O.J.; Guillemette, F.; Laudon, H.; Berggren, M. Impacts of litter decay on organic leachate composition and reactivity. *Biogeochemistry* **2021**, *154*, 99–117. [[CrossRef](#)]
92. Liu, X.P.; Zhang, W.J.; Hu, C.S.; Tang, X.G. Soil greenhouse gas fluxes from different tree species on Taihang Mountain, North China. *Biogeosciences* **2014**, *11*, 1649–1666. [[CrossRef](#)]
93. Li, Q.; Lee, Y.E.; Im, S. Characterizing the interception capacity of floor litter with rainfall simulation experiments. *Water* **2020**, *12*, 3145. [[CrossRef](#)]
94. Erickson, H.; Davidson, E.A.; Keller, M. Former land-use and tree species affect nitrogen oxide emissions from a tropical dry forest. *Oecologia* **2002**, *130*, 297–308. [[CrossRef](#)]
95. Hansen, K.; Vesterdal, L.; Schmidt, I.K.; Gundersen, P.; Sevel, L.; Bastrup-Birk, A.; Pedersen, L.B.; Bille-Hansen, J. Litter fall and nutrient return in five tree species in a common garden experiment. *For. Ecol. Manag.* **2009**, *257*, 2133–2144. [[CrossRef](#)]
96. Guckland, A.; Brauns, M.; Flessa, H.; Thomas, F.; Leuschner, C. Acidity, nutrient stocks and organic matter content in soils of a temperate deciduous forest with different abundance of European beech (*Fagus sylvatica* L.). *J. Plant Nutr. Soil Sci.* **2009**, *172*, 500–511. [[CrossRef](#)]
97. Longdoz, B.; Yernaux, M.; Aubinet, M. Soil CO₂ efflux measurements in a mixed forest: Impact of chamber disturbances, spatial variability and seasonal evolution. *Glob. Change Biol.* **2000**, *6*, 907–917. [[CrossRef](#)]
98. Huang, X.; Zheng, L.; Guo, P.; Yi, Z. Nitrogen addition inhibits total monoterpene emissions in subtropical forest floor of South China. *Soil Ecol. Lett.* **2021**, *3*, 63–72. [[CrossRef](#)]
99. Huang, J.; Hammerbacher, A.; Weinhold, A.; Reichelt, M.; Gleixner, G.; Behrendt, T.; van Dam, N.M.; Sala, A.; Gershenson, J.; Trumbore, S.E.; et al. Eyes on the future—Evidence for trade-offs between growth, storage and defense in Norway spruce. *N. Phytol.* **2019**, *222*, 144–158. [[CrossRef](#)] [[PubMed](#)]
100. Vose, J.M.; Bolstad, P.V. Biotic and abiotic factors regulating forest floor CO₂ flux across a range of forest age classes in the southern Appalachians. *Pedobiologia* **2007**, *50*, 577–587. [[CrossRef](#)]

101. Parfitt, R.L.; Salt, G.J.; Saggarr, S. Post-harvest residue decomposition and nitrogen dynamics in *Pinus radiata* plantations of different N status. *For. Ecol. Manag.* **2001**, *154*, 55–67. [[CrossRef](#)]
102. Zhou, G.; Guan, L.; Wei, X.; Zhang, D.; Zhang, Q.; Yan, J.; Wen, D.; Liu, J.; Liu, S.; Huang, Z.; et al. Litterfall production along successional and altitudinal gradients of subtropical monsoon evergreen broadleaved forests in Guangdong, China. *Plant Ecol.* **2007**, *188*, 77–89. [[CrossRef](#)]
103. Chen, H.; Gurmesa, G.A.; Liu, L.; Zhang, T.; Fu, S.; Liu, Z.; Dong, S.; Ma, C.; Mo, J. Effects of litter manipulation on litter decomposition in a successional gradients of tropical forests in southern China. *PLoS ONE* **2014**, *9*, e99018. [[CrossRef](#)] [[PubMed](#)]
104. Guckland, A.; Flessa, H.; Prenzel, J. Controls of temporal and spatial variability of methane uptake in soils of a temperate deciduous forest with different abundance of European beech (*Fagus sylvatica* L.). *Soil Biol. Biochem.* **2009**, *41*, 1659–1667. [[CrossRef](#)]
105. Borges Pinto, O., Jr.; Vourlitis, G.L.; De Souza Carneiro, E.M.; De França Dias, M.; Hentz, C.; De Souza Nogueira, J. Interactions between vegetation, hydrology, and litter inputs on decomposition and soil CO₂ efflux of tropical forests in the Brazilian Pantanal. *Forests* **2018**, *9*, 281. [[CrossRef](#)]
106. Townsend, A.R.; Asner, G.P.; Cleveland, C.C. The biogeochemical heterogeneity of tropical forests. *Trends Ecol. Evol.* **2008**, *23*, 424–431. [[CrossRef](#)]
107. Leff, J.W.; Wieder, W.R.; Taylor, P.G.; Townsend, A.R.; Nemergut, D.R.; Grandy, A.S.; Cleveland, C.C. Experimental litterfall manipulation drives large and rapid changes in soil carbon cycling in a wet tropical forest. *Glob. Change Biol.* **2012**, *18*, 2969–2979. [[CrossRef](#)] [[PubMed](#)]
108. Binkley, D.; Giardina, C. Why do tree species affect soils? The Warp and Woof of tree-soil interactions. *Biogeochemistry* **1998**, *42*, 89–106. [[CrossRef](#)]
109. Hasselquist, N.J.; Allen, M.F.; Santiago, L.S. Water relations of evergreen and drought-deciduous trees along a seasonally dry tropical forest chronosequence. *Oecologia* **2010**, *164*, 881–890. [[CrossRef](#)] [[PubMed](#)]
110. Kolb, S.; Knief, C.; Dunfield, P.F.; Conrad, R. Abundance and activity of uncultured methanotrophic bacteria involved in the consumption of atmospheric methane in two forest soils. *Environ. Microbiol.* **2005**, *7*, 1150–1161. [[CrossRef](#)] [[PubMed](#)]
111. Kolb, S. The quest for atmospheric methane oxidizers in forest soils. *Environ. Microbiol. Rep.* **2009**, *1*, 336–346. [[CrossRef](#)] [[PubMed](#)]
112. Menyailo, O.V.; Hungate, B.A. Interactive effects of tree species and soil moisture on methane consumption. *Soil Biol. Biochem.* **2003**, *35*, 625–628. [[CrossRef](#)]
113. Degelmann, D.M.; Kolb, S.; Borcken, W. Methane oxidation kinetics differ in European beech and Norway spruce soils. *Eur. J. Soil Sci.* **2009**, *60*, 499–506. [[CrossRef](#)]
114. Zeng, L.; Tian, J.; Chen, H.; Wu, N.; Yan, Z.; Du, L.; Shen, Y.; Wang, X. Changes in methane oxidation ability and methanotrophic community composition across different climatic zones. *J. Soils Sediments* **2019**, *19*, 533–543. [[CrossRef](#)]
115. Burgess-Conforti, J.R.; Moore, P.A., Jr.; Owens, P.R.; Miller, D.M.; Ashworth, A.J.; Hays, P.D.; Evans-White, M.A.; Anderson, K.R. Are soils beneath coniferous tree stands more acidic than soils beneath deciduous tree stands? *Environ. Sci. Pollut. Res. Int.* **2019**, *15*, 14920–14929. [[CrossRef](#)]
116. Lau, E.; Ahmad, A.; Steudler, P.A.; Cavanaugh, C.M. Molecular characterization of methanotrophic communities in forest soils that consume atmospheric methane. *FEMS Microbiol. Ecol.* **2007**, *60*, 490–500. [[CrossRef](#)]
117. Megonigal, J.P.; Guenther, A.B. Methane emissions from upland forest soils and vegetation. *Tree Physiol.* **2008**, *28*, 491–498. [[CrossRef](#)]
118. Machacova, K.; Bäck, J.; Vanhatalo, A.; Halmeenmäki, E.; Kolari, P.; Mammarella, I.; Pumpanen, J.; Acosta, M.; Urban, O.; Pihlatie, M. *Pinus sylvestris* as a missing source of nitrous oxide and methane in boreal forest. *Sci. Rep.* **2016**, *6*, 23410. [[CrossRef](#)] [[PubMed](#)]
119. Hanson, R.S.; Hanson, T.E. Methanotrophic bacteria. *Microbiol. Rev.* **1996**, *60*, 439–471. [[CrossRef](#)]
120. Nguyen, N.L.; Yu, W.J.; Gwak, J.H.; Kim, S.J.; Park, S.J.; Herbold, C.W.; Kim, J.G.; Jung, M.Y.; Rhee, S.K. Genomic insights into the acid adaptation of novel methanotrophs enriched from acidic forest soils. *Front. Microbiol.* **2018**, *9*, 1982. [[CrossRef](#)]
121. Ambus, P.; Zechmeister-Boltenstern, S.; Butterbach-Bahl, K. Sources of nitrous oxide emitted from European forest soils. *Biogeosciences* **2006**, *3*, 135–145. [[CrossRef](#)]
122. Bodelier, P.L.E.; Laanbroek, H.J. Nitrogen as regulatory factor of methane oxidation in soils and sediments. *FEMS Microbiol. Ecol.* **2004**, *47*, 265–277. [[CrossRef](#)]
123. Bodelier, P.L.E.; Steenbergh, A.K. Interactions between methane and the nitrogen cycle in light of climate change. *Curr. Opin. Env. Sustain.* **2014**, *9*, 26–36. [[CrossRef](#)]
124. Mochizuki, Y.; Koba, K.; Yoh, M. Strong inhibitory effect of nitrate on atmospheric methane oxidation in forest soils. *Soil Biol. Biochem.* **2012**, *50*, 164–166. [[CrossRef](#)]
125. Steudler, P.A.; Bowden, R.D.; Melillo, J.M.; Aber, J.D. Influence of nitrogen fertilization on methane uptake in temperate forest soils. *Nature* **1989**, *341*, 314–316. [[CrossRef](#)]
126. Saari, A.; Rinnan, R.; Martikainen, P.J. Methane oxidation in boreal forest soils: Kinetics and sensitivity to pH and ammonium. *Soil Biol. Biochem.* **2004**, *36*, 1037–1046. [[CrossRef](#)]
127. Reay, D.S.; Nedwell, D.B.; McNamara, N.; Ineson, P. Effect of tree species on methane and ammonium oxidation capacity in forest soils. *Soil Biol. Biochem.* **2005**, *37*, 719–730. [[CrossRef](#)]

128. Li, Q.; Peng, H.; Zhang, J.; Li, Y.; Song, X. Nitrogen addition decreases methane uptake caused by methanotroph and methanogen imbalances in a Moso bamboo forest. *Sci. Rep.* **2021**, *11*, 5578. [[CrossRef](#)]
129. Jo, G.G.; Kim, J.H. Changes in terpenes of three kinds of pine needles during litter decomposition. *J. Ecol. Field Biol.* **2010**, *33*, 175–186. [[CrossRef](#)]
130. Wilt, F.M.; Miller, G.C.; Everett, R.L.; Hackett, M. Monoterpene concentrations in fresh, senescent and decaying foliage of single-leaf pinyon (*Pinus monophylla* Torr. & Frem.: *Pinaceae*) from the western great Basin. *J. Chem. Ecol.* **1993**, *19*, 185–194.
131. Amaral, J.A.; Knowles, R. Inhibition of methane consumption in forest soils by monoterpenes. *J. Chem. Ecol.* **1998**, *24*, 723–734. [[CrossRef](#)]
132. Wu, B.; Mu, C. Effects on Greenhouse Gas (CH₄, CO₂, N₂O) Emissions of Conversion from Over-Mature Forest to Secondary Forest and Korean Pine Plantation in Northeast China. *Forests* **2019**, *10*, 788. [[CrossRef](#)]
133. Pacheco, A.; Lindner, A.S. Effects of Alpha-pinene and trichloroethylene on oxidation potentials of methanotrophic bacteria. *Bull. Environ. Contamin. Toxicol.* **2005**, *74*, 133–140. [[CrossRef](#)]
134. Dannenmann, M.; Gasche, R.; Ledebuhr, A.; Holst, T.; Mayer, H.; Papen, H. The effect of forest management on trace gas exchange at the pedosphere-atmosphere interface in beech (*Fagus sylvatica* L.) forests stocking on calcareous soils. *Eur. J. For. Res.* **2007**, *126*, 331–346. [[CrossRef](#)]
135. Hanson, P.J.; O'Neill, E.G.; Chambers, M.L.S.; Riggs, J.S.; Joslin, J.D.; Wolfe, M.H. Soil respiration and litter decomposition. In *North American Temperate Deciduous Forest Response to Changing Precipitation Regimes. Ecological Studies (Analysis and Synthesis)*; Hanson, P.J., Wullschlegel, S.D., Eds.; Springer: New York, NY, USA, 2003; Volume 166, pp. 163–189.
136. Ataka, M.; Kominami, Y.; Jomura, M.; Yoshimura, K.; Miyama, T.; Kosugi, Y.; Tani, M. CO₂ efflux from decomposing leaf litter stack is influenced by the vertical distribution of leaf litter water content and its temporal variation. *J. Agric. Meteorol.* **2015**, *71*, 263–270. [[CrossRef](#)]
137. Wilson, T.B.; Kochendorfer, J.; Meyers, T.P.; Heuer, M.; Sloop, K.; Miller, J. Leaf litter water content and soil surface CO₂ fluxes in a deciduous forest. *Agric. For. Meteorol.* **2014**, *192*, 42–50. [[CrossRef](#)]
138. Ataka, M.; Kominami, Y.; Yoshimura, K.; Miyama, T.; Jomura, M.; Tani, M. In situ CO₂ efflux from leaf litter layer showed large temporal variation induced by rapid wetting and drying cycle. *PLoS ONE* **2014**, *9*, e108404. [[CrossRef](#)] [[PubMed](#)]
139. Sardans, J.; Peñuelas, J. Drought decreases soil enzyme activity in a Mediterranean *Quercus ilex* L. forest. *Soil Biol. Biochem.* **2005**, *37*, 455–461. [[CrossRef](#)]
140. Fekete, I.; Kotroczó, Z.; Varga, C.; Hargitai, R.; Townsend, K.; Csányi, G.; Várbiró, G. Variability of organic matter inputs affects soil moisture and soil biological parameters in a European detritus manipulation experiment. *Ecosystems* **2012**, *15*, 792–803. [[CrossRef](#)]
141. Veres, Z.; Ktroczó, Z.; Magyaros, K.; Tóth, J.A.; Tóthmérész, B. Dehydrogenase activity in a litter manipulation experiment in temperate forest soil. *Acta Silv. Lignaria Hung.* **2013**, *9*, 25–33. [[CrossRef](#)]
142. Beni, A.; Soki, E.; Lajtha, K.; Fekete, I. An optimized HPLC method for soil fungal biomass determination and its application to a detritus manipulation study. *J. Microbiol. Methods* **2014**, *103*, 124–130. [[CrossRef](#)]
143. Buchmann, N. Biotic and abiotic factors controlling soil respiration rates in *Picea abies* stands. *Soil Biol. Biochem.* **2000**, *32*, 1625–1635. [[CrossRef](#)]
144. Yan, W.; Peng, Y.; Zhan, C.; Chen, X. The manipulation of aboveground litter input affects soil CO₂ efflux in a subtropical liquidambar forest in China. *iForest* **2019**, *12*, 181–186. [[CrossRef](#)]
145. Tate, K.R.; Ross, D.J.; Scott, N.A.; Rodda, N.J.; Townsend, J.A.; Arnold, G.C. Post-harvest patterns of carbon dioxide production, methane uptake and nitrous oxide production in a *Pinus radiata* D. Don plantation. *For. Ecol. Manag.* **2006**, *228*, 40–50. [[CrossRef](#)]
146. Huang, Z.; Clinton, P.W.; Davis, M.R.; Yang, Y. Impacts of plantation forest management on soil organic matter quality. *J. Soils Sediments* **2011**, *11*, 1309–1316. [[CrossRef](#)]
147. Molchanov, A.G.; Kurbatova, Y.A.; Olchev, A.V. Effect of clear-cutting on soil CO₂ emission. *Biol. Bull.* **2017**, *44*, 218–223. [[CrossRef](#)]
148. Wang, H.L.; Liu, J.; Jiang, P.K.; Zhou, G.M.; Li, Y.F.; Wu, J. Effect of management practices on methane uptake in forest soils. *Sci. Silvae Sin.* **2017**, *53*, 156–163.
149. Ström, L.; Falk, J.M.; Skov, K.; Jackowicz-Korczynski, M.; Mastepanov, M.; Christensen, T.R.; Lund, M.; Schmidt, N.M. Controls of spatial and temporal variability in CH₄ flux in a high arctic fen over three years. *Biogeochemistry* **2015**, *125*, 21–35. [[CrossRef](#)]
150. Tate, K.R. Soil methane oxidation and land-use change—From process to mitigation. *Soil Biol. Biochem.* **2015**, *80*, 260–272. [[CrossRef](#)]
151. Fontaine, S.; Bardoux, G.; Abbadie, L.; Mariotti, A. Carbon input to soil may decrease soil carbon content. *Ecol. Lett.* **2004**, *7*, 314–320. [[CrossRef](#)]
152. Schaefer, D.A.; Feng, W.; Zou, X. Plant carbon inputs and environmental factors strongly affect soil respiration in a subtropical forest of southwestern China. *Soil Biol. Biochem.* **2009**, *41*, 1000–1007. [[CrossRef](#)]
153. Graglia, E.; Jonasson, S.; Michelsen, A.; Schmidt, I.K.; Havström, M.; Gustavsson, L. Effects of environmental perturbations on abundance of subarctic plants after three, seven and ten years of treatments. *Ecography* **2001**, *24*, 5–12. [[CrossRef](#)]
154. Cornelissen, J.H.; Van Bodegom, P.M.; Aerts, R.; Callaghan, T.V.; Van Logtestijn, R.S.P.; Alatalo, J.; Chapin, F.S.; Gerdol, R.; Gudmundsson, J.; Gwynn-Jones, D.; et al. Team. *Global negative vegetation feedback to climate warming responses of leaf litter decomposition in cold biomes*, *Ecol. Lett.* **2007**, *10*, 619–627.

155. Rinnan, R.; Michelsen, A.; Bååth, E.; Jonasson, S. Mineralization and carbon turnover in subarctic heath soil as affected by warming and additional litter. *Soil Biol. Biochem.* **2007**, *39*, 3014–3023. [[CrossRef](#)]
156. Rinnan, R.; Michelsen, A.; Jonasson, S. Effects of litter addition and warming on soil carbon, nutrient pools, and microbial communities in a subarctic heath ecosystem. *Appl. Soil Ecol.* **2008**, *39*, 271–281. [[CrossRef](#)]
157. Venterea, R.T.; Groffman, P.M.; Verchot, L.V.; Magill, A.H.; Aber, J.D. Gross nitrogen process rates in temperate forest soils exhibiting symptoms of nitrogen saturation. *For. Ecol. Manag.* **2004**, *194*, 129–142. [[CrossRef](#)]
158. Tuchman, N.C.; Wetzel, R.G.; Rier, S.T.; Wahtera, K.A.; Teeri, J.A. Elevated atmospheric CO₂ lowers leaf litter nutritional quality for stream ecosystem food webs. *Glob. Chang. Biol.* **2002**, *8*, 163–170.
159. Pancotto, V.A.; van Bodegom, P.M.; van Hal, J.; van Logtestijn, R.S.P.; Blokker, P.; Toet, S.; Aerts, R. N deposition and elevated CO₂ on methane emissions: Differential responses of indirect effects compared to direct effects through litter chemistry feedbacks. *J. Geophys. Res.* **2010**, *115*, G02001.
160. Brumme, R.; Borken, W. Site variation in methane oxidation as affected by atmospheric deposition and type of temperate forest ecosystem. *Glob. Biogeochem. Cycles* **1999**, *13*, 493–501. [[CrossRef](#)]
161. Seidl, R.; Klöner, G.; Rammer, W.; Essl, F.; Moreno, A.; Neumann, M.; Dullinger, S. Invasive alien pests threaten the carbon stored in Europe's forests. *Nat. Commun.* **2018**, *9*, 1626. [[CrossRef](#)]
162. Flower, C.E.; Gonzalez-Meler, M.A. Responses of temperate forest productivity to insect and pathogen disturbances. *Annu. Rev. Plant Biol.* **2015**, *66*, 547–569. [[CrossRef](#)] [[PubMed](#)]
163. Grüning, M.M.; Germeshausen, F.; Thies, C. Increased forest soil CO₂ and N₂O emissions during insect infestation. *Forests* **2018**, *9*, 612. [[CrossRef](#)]
164. Kainulainen, P.; Holopainen, J.K. Concentrations of secondary compounds in Scots pine needles at different stages of decomposition. *Soil Biol. Biochem.* **2002**, *34*, 37–42. [[CrossRef](#)]
165. Veraart, A.J.; Garbeva, P.; van Beersum, F.; Ho, A.; Hordijk, C.A.; Meima-Franke, M.; Zweepers, A.J.; Bodelier, P.L.E. Living apart together-bacterial volatiles influence methanotrophic growth and activity. *ISME J.* **2018**, *12*, 1163–1166. [[CrossRef](#)]
166. Yamada, Y.; Kuzuyama, T.; Komatsu, M.; Shin-ya, K.; Omura, S.; Cane, D.E.; Ikeda, H. Terpene synthases are widely distributed in bacteria. *Proc. Natl. Acad. Sci. USA* **2015**, *112*, 857–862. [[CrossRef](#)] [[PubMed](#)]
167. Butterbach-Bahl, K.; Kock, M.; Willibald, G.; Hewett, B.; Buhagiar, S.; Papen, H.; Kiese, R. Temporal variations of fluxes of NO, NO₂, N₂O, CO₂, and CH₄ in a tropical rain forest ecosystem. *Glob. Biogeochem. Cycles* **2004**, *18*, GB3012. [[CrossRef](#)]
168. Menyailo, O.V.; Hungate, B.A.; Abraham, W.-R.; Conrad, R. Changing land use reduces soil CH₄ uptake by altering biomass and activity but not composition of high-affinity methanotrophs. *Glob. Change Biol.* **2008**, *14*, 2405–2419. [[CrossRef](#)]
169. Bowden, R.D.; Nadelhoffer, K.J.; Boone, R.D.; Melillo, J.M.; Garrison, J.B. Contributions of aboveground litter, belowground litter, and root respiration to total soil respiration in a temperate mixed hardwood forest. *Can. J. For. Res.* **1993**, *23*, 1402–1407. [[CrossRef](#)]
170. Sun, L.; Teramoto, M.; Liang, N.; Yazaki, T.; Hirano, T. Comparison of litter-bag and chamber methods for measuring CO₂ emissions from leaf litter decomposition in a temperate forest. *J. Agric. Meteorol.* **2017**, *73*, 68–76. [[CrossRef](#)]
171. Xiao, W.; Ge, X.; Zeng, L.; Huang, Z.; Lei, J.; Zhou, B.; Li, M. Rates of litter decomposition and soil respiration in relation to soil temperature and water in different-aged *Pinus massoniana* forests in the Three Gorges Reservoir area, China. *PLoS ONE* **2014**, *9*, e101890.
172. Yan, W.D.; Chen, X.Y.; Tian, D.L.; Peng, Y.Y.; Wang, G.J.; Zheng, W. Impacts of changed litter inputs on soil CO₂ efflux in three forest types in central south China. *Chin. Sci. Bull.* **2013**, *58*, 750–757. [[CrossRef](#)]
173. Ming, A.; Yang, Y.; Liu, S.; Wang, H.; Li, Y.; Li, H.; Nong, Y.; Cai, D.; Jia, H.; Tao, Y.; et al. Effects of near natural forest management on soil greenhouse gas flux in *Pinus massoniana* (Lamb.) and *Cunninghamia lanceolata* (Lamb.) Hook plantations. *Forests* **2018**, *9*, 229. [[CrossRef](#)]
174. Wang, H.; Liu, S.; Mo, J.; Zhang, T. Soil-atmosphere exchange of greenhouse gases in subtropical plantations of indigenous tree species. *Plant Soil* **2010**, *335*, 213–227. [[CrossRef](#)]