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Review

How tree traits modulate tree methane fluxes: A review

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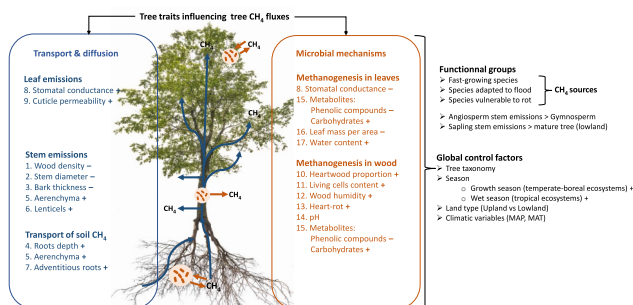
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HIGHLIGHTS

- Tree traits can modulate methane transport and microbial mechanisms in trees.
- Functional traits can help to predict the role of trees in methane flux regulation.
- Flood-adapted and fast-growing tree species could be important methane sources.
- Tree taxonomy and age, season, and land type influence tree methane fluxes.

GRAPHICAL ABSTRACT



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ABSTRACT

Trees can play different roles in the regulation of fluxes of methane (CH₄), a greenhouse gas with a warming potential 83 times greater than that of carbon dioxide. Forest soils have the greatest potential for methane uptake compared to other land uses. In addition to their influence on soil CH₄ fluxes, trees can act directly as a source or sink of CH₄, by transporting CH₄ produced in the soil and harbouring the key microorganisms involved in CH₄ production and consumption (methanogens and methanotrophs). Tree CH₄ fluxes can vary between species characterized by different traits that influence transport and modify the availability of CH₄ reaction substrates as well as the habitat for methanogens and methanotrophs. Despite their important role in modulating CH₄ fluxes from forest ecosystems, the identity and role of tree traits influencing these fluxes are poorly consolidated in the literature. The objectives of this paper are to 1) Review the functional traits of trees associated with their role in the regulation of CH₄ emissions; 2) Assess the importance of inter-specific variability in CH₄ fluxes via a global analysis of tree methane fluxes in the literature. Our review highlights that differences in CH₄ fluxes between tree species and individuals can be explained by a diversity of traits influencing CH₄ transport and microbial production of CH₄ such as wood density and secondary metabolites. We propose a functional classification for trees

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based on the key traits associated with a function in CH₄ emissions. We identified the fast-growing species with low wood density, species adapted to flood and species vulnerable to rot as functional groups which can be net sources of CH₄ in conditions favorable to CH₄ production. The global analysis further demonstrated the importance of taxonomy, with other factors such as land type and season in explaining variability in tree CH₄ fluxes.

1. Introduction

In the context of climate change, it is essential to better understand the factors that regulate methane (CH₄) fluxes, resulting from the balance between methanogenesis (CH₄ production) and methanotrophy (CH₄ consumption). The 20-years warming potential of methane is 83 times greater than that of carbon dioxide (IPCC, 2021). Forest soils have the greatest potential for methane consumption (i.e., methanotrophy) compared to other land uses (e.g., cultivated fields, grasslands), due to soil properties that influence gas diffusion and favor methanotrophy, and represent an important sink in the global methane budget (Boeckx et al., 1997; Feng et al., 2023). However, there is still a lot of uncertainty about the methane budget and regulation mechanisms in forest ecosystems (Feng et al., 2020).

Trees can play different roles in the regulation of methane fluxes (Bastviken et al., 2023). First, they influence methane fluxes through the modulation of soil properties (i.e., moisture, oxygen availability, pH, soil structure, organic matter, and nitrogen content), and abundance and activity of key microorganisms involved in CH₄ production/consumption in soils, with consequences for CH₄ emissions (Shvaleva et al., 2015; Bastviken et al., 2023). For instance, forest ecosystems maintain soil humidity at a level favorable to the presence of methanogens (Shvaleva et al., 2015), producing CH₄ and contributing to the maintenance of the potential of methanotrophy by making its substrate (i.e., CH₄) available. The structure of methanogen and methanotroph microbial communities is also influenced by root density which is greater in forests (Lejon et al., 2005; Sjögersten et al., 2020). The rhizosphere is an important habitat for methanotrophs due to soil oxygenation by the roots, which promotes CH₄ oxidation at the root-soil interface (Halmeemäki et al., 2017). Tree litter and root exudates stimulate microbial degradation and respiration in the rhizosphere and can support methanogenesis via the generation of substrates and electron acceptors necessary for microbial mechanisms (Shvaleva et al., 2015; Welch et al., 2019). Studies also show relationships between soil CH₄ fluxes and tree physiological processes, including photosynthesis, which influences CH₄ production/consumption via carbon input and subsequent stimulation of microbial respiration/degradation, as well as tree transpiration, which modulates soil moisture and oxygen availability (Megonigal and Schlesinger, 1997; Vann and Megonigal, 2003).

In addition to modulating the methane cycle in soils, tree stems can also act as a CH₄ source by emitting CH₄ produced in the soil (Pangala et al., 2013; Maier et al., 2018). At the ecosystem scale, methane fluxes from trees can either increase the methane source, offset the soil sink, or in some cases contribute to the soil sink by capturing methane. The influence and quantitative contribution of plants and trees can differ among different ecosystems (Bastviken et al., 2023). The role of trees in the transport and subsequent release of methane into the atmosphere has been highlighted in wetlands, known hotspots of CH₄ production (Pangala et al., 2013, 2015; Jeffrey et al., 2020; Schindler et al., 2020; Sjögersten et al., 2020; Moldaschl et al., 2021). Tree emission rates and their contribution to the ecosystem emissions are particularly important when soil moisture is high (Sjögersten et al., 2020). The highest tree emission rates have been reported from tropical forests, with the Amazon floodplain in first rank (Pangala et al., 2013, 2017). Moreover, Jeffrey et al. (2021a, 2021b) showed that this emission pathway can facilitate the release of CH₄ from the soil into the atmosphere and increase net ecosystem emissions due to the bypass of the oxidation zone at the oxic water-sediment interface in a flooded forest. Net methane

emissions from tree trunks have also been observed in upland ecosystems although their contributions to the ecosystem fluxes were less important (Machacova et al., 2016; Wang et al., 2016; Pitz and Megonigal, 2017; Warner et al., 2017; Maier et al., 2018; Barba et al., 2019; Plain et al., 2019). In addition, the tree leaves may also exhibit net methane emissions or uptake, resulting from a balance between fluxes associated to transpiration, photochemical CH₄ production, and microbial CH₄ production/consumption inside leaf tissues (Keppler et al., 2006; Rice et al., 2010; Sundqvist et al., 2012; Machacova et al., 2016; Putkinen et al., 2021; Gorgolewski et al., 2022b; Vainio et al., 2022). A glossary of terms related to methane fluxes mediated by trees is provided in Box 1.

It has recently been highlighted in the literature that above-ground tissues of trees (i.e. the phyllosphere) can harbor communities of methanogens and methanotrophs that are distinct from those found in the soil. Those methanogens and methanotrophs can play a role in the tree CH₄ emissions. Studies show predominance of hydrogenotrophic methanogens in the heartwood of poplars and their role in intrinsic CH₄ production, regulated by wood water content as well as O₂ and H₂ availability (Wang et al., 2017; Yip et al., 2019; Li et al., 2020; Feng et al., 2022). Jeffrey et al. (2021a, 2021b) identified a bacterial community dominated by methanotrophs (*Methylomonas*) in the bark of *Melaleuca quinquenervia*, responsible for reducing methane emissions from tree stems. Putkinen et al. (2021) identified methanogens in the needles of *Picea abies*, suggesting that anoxic microenvironments necessary for methanogenic activity may also exist in leaves. Methane can also be produced aerobically by plants (Keppler et al., 2006; Kirschbaum et al., 2006). A proposed mechanism for this production involves the reaction between a variety of leaf compounds (e.g., pectin, lignin, cellulose, methionine, wax) and reactive oxygen species (ROS) that can result from UV exposure or from tree physiological processes (i.e., natural metabolism of respiration and photosynthesis or stress response) (McLeod et al., 2008; Viganò et al., 2008; Messenger et al., 2009; Wang et al., 2009; Bruhn et al., 2014).

The intensity of tree fluxes is likely to differ between species that differ in traits affecting methane transport, methanogenesis/methanotrophy, and non-microbial CH₄ production (Pangala et al., 2013; Wang et al., 2017; Sjögersten et al., 2020; Epron et al., 2022; Soosaar et al., 2022; Ge et al., 2024). Studies also report important variation in emissions among tree individuals (Flanagan et al., 2021; Sakabe et al., 2021; Machacova et al., 2023), suggesting that within-species trait variation can also be important for predicting ecosystem CH₄ fluxes. However, the identity and role of tree traits on the directionality and intensity of CH₄ fluxes remains poorly consolidated in the literature (Barba et al., 2021). Previous reviews have covered the current knowledge on mechanisms regulating tree methane fluxes (Feng et al., 2020; Bastviken et al., 2023; Ge et al., 2024), and Ge et al. (2024) discussed traits that can influence methane transport in plants. However, no review to date focused on tree-specific traits influencing transport and microbial mechanisms in the tree phyllosphere, as well as assessed the importance of inter-specific variability based on the existing data on tree CH₄ fluxes. The objectives of this article are therefore to: 1) Review the functional tree traits associated with the role of trees in the regulation of methane fluxes, in relation to transport and diffusion, and to the presence and activity of key methane cycling microorganisms in the phyllosphere; 2) Assess the importance of inter-specific variability of methane fluxes compared to other factors of influence (e.g., land, ecosystem, season) via a global analysis of tree methane fluxes in the literature.

2. Traits associated with inter-specific variability in tree methane fluxes

2.1. Inter-specific variability in tree methane fluxes

Studies that have measured methane fluxes for more than one species from the same site, under the same environmental conditions, have shown that tree fluxes can differ in their intensity, vertical patterns, and temporal patterns between species. Under the same conditions, some species show substantial stem CH₄ emissions while other species have negative, or negligible fluxes (Covey et al., 2012; Pangala et al., 2013; Wang et al., 2016; Warner et al., 2017; Jeffrey et al., 2020; Sjögersten et al., 2020; Epron et al., 2022). For instance, in the study by Warner et al. (2017) in a temperate forest, stem CH₄ emissions from *Nyssa sylvatica*, *Liriodendron tulipifera* and *Fagus grandifolia* were higher than those from *Acer rubrum*, *Betula lenta*, *Quercus* spp., which were negligible or null. Similar interspecific contrasts have also been shown in upland temperate forests (Covey et al., 2012; Epron et al., 2022), tropical peatlands (Pangala et al., 2013), flooded subtropical forest (Jeffrey et al., 2020) and mangroves (Zhang et al., 2022). Leaf methane fluxes can also be species dependent as shown in the study of Gorgolewski et al. (2022b) who observed variable net uptake rates between species in temperate upland forest.

2.2. Traits regulating methane transport and diffusion in trees

Wood density (Fig. 1.1) and **tree diameter** (Fig. 1.2) are two traits that have been shown to influence methane emissions between species. These effects take place through the influence of wood and bark density on molecular diffusion inside the trunk (Wang et al., 2016; Epron et al., 2022). Many studies observed differences in emissions between species that were explained by the trunk diameter and wood density, the stem CH₄ emissions being negatively correlated with both traits (Pangala et al., 2013, 2015; van Haren et al., 2021; Soosaar et al., 2022). As density of wood is negatively related to the growth rate, fast-growing species are more likely to have higher diffusion coefficients (Fajardo, 2022). For instance, Welch et al. (2019) associated the higher CH₄ emissions of *Simarouba amara* to its low wood density and the formation of vessels of greater diffusivity resulting from its fast growth. Among hardwood species, molecular diffusion of gas is lower for ring-porous species (e.g., *Fraxinus excelsior*) compared to diffuse-porous species (e.g., *Fagus sylvatica*) (Sorz et al., 2006; Teskey et al., 2008). Wood density depends on environmental conditions that affect growth, such as the intensity and frequency of flooding, which could therefore influence

methane emissions (Whittman et al., 2006; Chave et al., 2009; Boakye et al., 2023). The relationship between soil humidity and wood density is mixed (Moles, 2018). In the case in which species adapted to water-logging are associated with low wood density (Pavanetto et al., 2024), this trait could favor higher tree emissions in wetlands, where the production of CH₄ in soil is also important. Conversely, higher wood density in wetlands has also been observed, which could limit the stem CH₄ emissions (Whittman et al., 2006; Moles, 2018; Yang et al., 2024). Angiosperms, which are characterized by high water transport capacity due to their water conductive cells, are better adapted to lowland environments than gymnosperms (Chave et al., 2009) and their dominance may favor high CH₄ emissions in such environments. Although conifers have lower wood density, the length of conducting element can lead to lower diffusion coefficients in comparison to hardwood species (Sorz et al., 2006). Overall, the interaction between the trait, which is associated with CH₄ transport capacity, and the environmental selection of trees may determine the importance of tree CH₄ emissions.

The **structure of the bark** (Fig. 1.3), including its thickness and its irregularities, may also influence stem emissions by the trunk, since bark acts as a barrier to gas diffusion (Teskey et al., 2008; Wang et al., 2016). Thicker bark may limit diffusion while irregularities in the bark may represent CH₄ exit pathways. For instance, the structure of *Melaleuca quinquenervia* bark, a paper-like bark with layers and interstitial spaces, was identified as a feature that could be associated with its high emissions (Jeffrey et al., 2020, 2021a, 2021b). To verify the relationship between methane emissions and bark smoothness, measurements on a variety of tree species are required.

The **root distribution** (Fig. 1.4) in the soil may also explain inter-specific differences in methane emission by determining the availability of CH₄ that the tree can uptake and then re-emit from the soil. The distribution of *Picea abies* roots in soil close to the surface, where CH₄ is oxidized by methanotrophs, could explain the lower stem CH₄ emissions compared to *Betula pubescens* which has deeper roots (Vainio et al., 2022). In the study of Plain et al. (2019), the detection of emissions at the trunk of *Quercus petraea*, despite an absence of emission from the soil, was associated with the morphology of the root system of the species enabling it to reach the methane production zone.

The species adaptations to flood, including the presence of **aerenchyma** (Fig. 1.5), **high lenticel density** (Fig. 1.6), and the presence of hypertrophied lenticels, promote gas exchanges and are associated to substantial CH₄ emissions from tree stems when soil moisture conditions are favorable to methane production (Terazawa et al., 2007; Pangala et al., 2014, 2017; Sjögersten et al., 2020). For instance, *Alnus glutinosa*, which forms aerenchyma and lenticels, had higher methane emissions

Box 1

Glossary on methane-related terms in the context of tree-mediated methane fluxes.

Consumption: Microbial oxidation of methane through methanotrophy.

Diffusion transport: Refers to the movement of methane molecules into intercellular spaces and aerenchyma.

Emission: Positive flux resulting in methane release towards the atmosphere.

Flux: Movement of gas in a direction (positive or negative) in terms of amount per unit area per time units.

Net flux: Difference between positive fluxes (emissions) and negative fluxes (uptake).

Production: Microbial synthesis of methane through methanogenesis.

Source: Which presents a positive net flux, adding methane to the atmosphere.

Sink: Which presents a negative net flux, taking up methane from the atmosphere.

Transpiration transport: Refers to the transport of methane dissolved in water through the xylem through the flux of water in the tree caused by evaporation of water from leaves.

Uptake: Negative flux resulting in methane capture (the result of methanotrophy).

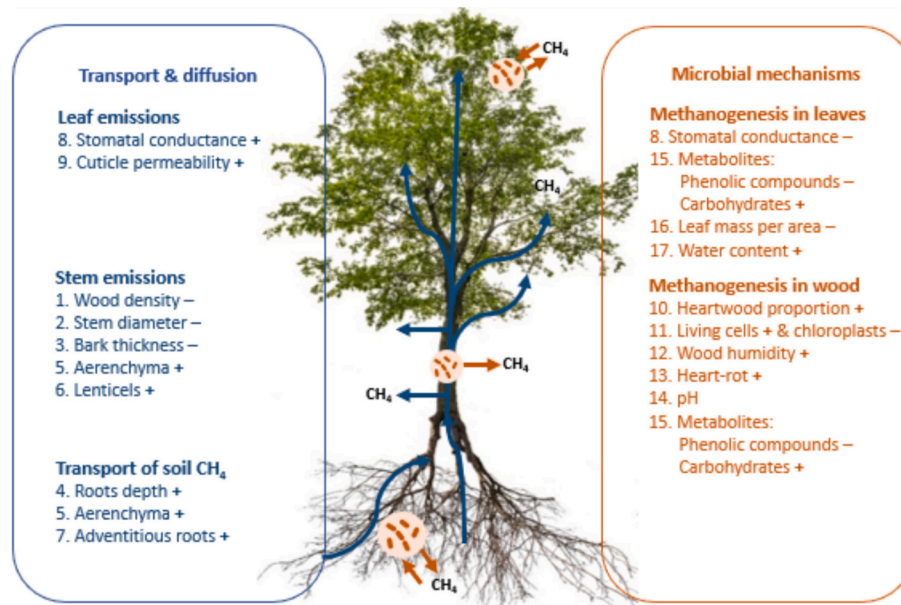


Fig. 1. Schematic diagram summarizing the traits influencing methane emissions of trees, via the modulation of the microbiome, microbial mechanisms, and gas transport. The direction of the trait effect (increase or decrease) on the processes are indicated by + and –.

during flooding than *Fagus sylvatica* lacking aerenchyma (Machacova et al., 2013). The presence of **adventitious roots** (Fig. 1.7) is another adaptation to flood that may be associated with higher emissions due to the contribution of these structures to gas exchange, as observed for *Symphonia globulifera* in the study of Sjögersten et al. (2020). The presence of pneumatophores was associated with higher emissions in a *Avicennia marina* mangrove despite lower trunk emissions from this species characterized by higher wood density and lower lenticel density (Zhang et al., 2022).

In species that do not have aerenchyma and hypertrophied lenticels (e.g., beech), methane can preferentially be released into the atmosphere via transpiration (Díaz-Pinés et al., 2016). Due to the low water solubility of methane, the amount that can be released by this transport pathway is limited and below the potential of emission through diffusion (Machacova et al., 2013). The species without aerenchyma show seasonal or diurnal variation in CH_4 emissions (Pitz et al., 2018). For example, defoliation in the fall led to a reduction in emission in *Betula pubescens*, a species that would transport CH_4 mainly through transpiration (Pangala et al., 2015). In comparison, leaf loss did not reduce methane emission in *Alnus glutinosa* for which the main pathway is likely diffusion (Pangala et al., 2015). Similarly, stem methane emissions through molecular diffusion of *Fraxinus mandshurica*, which has aerenchyma tissues in the cortex of fine roots, did not show any diurnal or seasonal (i.e., foliated vs defoliated season) pattern (Terazawa et al., 2015). Methane transport via transpiration can also result in leaf emissions for some species (Gorgolewski et al., 2022b). This could partly explain why some species exhibit canopy fluxes (e.g., *Taxodium distichum*), while others do not (e.g., *P. davidiana*, *C. cathayensis*, *Alnus glutinosa*) (Garnet et al., 2005; Pangala et al., 2014; Wang et al., 2016). Transpiration rates depend on hydraulic conductivity of stem that is influenced by xylem structure and photosynthetic capacity (Brodrribb and Feild, 2000; McCulloh et al., 2010). Since transpiration emissions are also influenced by factors that control tree transpiration rates such as temperature, soil water content, and solar radiation, emissions of methane by trees may also vary spatially or temporally as a function of these environmental variables (Ge et al., 2024). In the study of Flanagan et al. (2021), poplar emissions were related to evapotranspiration rates such that ecosystem fluxes varied with solar radiation.

Leaf anatomical structures such as thick cuticles and absence of stomata on the epidermis in species adapted to salinity and tides reduce

transpiration and indirectly inhibit CH_4 fluxes from the trunks and leaves (He et al., 2019). Garnet et al. (2005) also showed that foliar CH_4 emissions were controlled by the anatomical characteristics, namely the **stomatal conductance** (Fig. 1.8), of plant species. Reduced stomatal conductance is also an adaptation to flood in some species that may affect tree emissions via control of CH_4 transport through transpiration (Kosłowski, 1997). **Cuticle permeability** (Fig. 1.9) could also be a trait influencing methane diffusion through leaves although with less importance than stomatal conductance considering that the diffusion through stomata would be the main exit and entrance pathway of methane emitted or uptake at the leaf level (Garnet et al., 2005; Sundqvist et al., 2012).

2.3. Traits regulating the presence and activity of methane cycling microorganisms in the phyllosphere

The presence of methanogens and methanotrophs in the phyllosphere suggests that the tree microbiome could be involved in methane cycling, although only few studies have investigated methanotrophic and methanogenic communities of the phyllosphere, and much more research needs to be done to elucidate the role of tree microbiome in methane fluxes. The mechanistic of methane production and consumption in trees and the ecophysiology of methanogens and methanotrophs associated with trees are still poorly understood. For instance, only little evidence on microbial consumption of CH_4 in trees exists and methanotrophic communities could rely mostly on tree-produced methanol (Jeffrey et al., 2021a, 2021b; Putkinen et al., 2021).

In that regard, some tree traits can influence tree methane fluxes by modulating the presence and activity of methanogens and methanotrophs in the phyllosphere. The influence of traits on methanogens and methanotrophs can also be through the modulation of the global phyllosphere microbiome and interaction with other microorganisms that generate methanogenesis precursors (i.e., CO_2 , acetate, hydrogen), or favorable conditions. For instance, the respiration of microbial communities could promote the activity of methanogens by creating hypoxic conditions. The relationships between tree traits are complex and different predictions can be made about their effect on the phyllosphere methanogenic and methanotrophic communities.

First, species growth strategy and heartwood formation influence the presence and activity of methanogens in the wood. Wang et al. (2017)

showed that the **ratio of heartwood** (Fig. 1.10) on trunk diameter correlated positively with CH₄ emissions. The proportion of sapwood in the trunk varies with the species wood anatomy, especially between annular pore xylem (e.g., *Quercus* spp.) and diffuse pore xylem (e.g., *Tilia* spp.) (Hoch et al., 2003), and may partly explain the differential CH₄ emissions observed between species. Wood density may also modulate the abundance and activity of methanogens and methanotrophs by impacting oxygen levels in tree tissues (Feng et al., 2022).

Moreover, the rates of cortical photosynthesis and respiration of species, which vary according to the **proportion of living cells and chloroplast content** (Fig. 1.11) of tissues (Teskey et al., 2008), may influence methanotrophy and methanogenesis in wood via modulation of oxygen and CO₂ concentrations. Hardwoods have a larger volume of living cells that carry out respiration (Teskey et al., 2008), which could create favorable conditions for methanogenesis.

Wood humidity (Fig. 1.12) is implicated in differential CH₄ production and emissions between tree species (Wang et al., 2016, 2017). Wang et al. (2017) showed that species with different wood water content had different heartwood CH₄ concentrations: Some species (*Populus* spp., *Ulmus* spp.) had substantial concentrations ($\geq 10,000 \mu\text{L L}^{-1}$) associated with moist heartwood regardless of soil conditions; other species (*Pinus koraiensis*, *Betula platyphylla*, *Larix gmelinii*, *Acer truncatum*, *Carpinus hupeana*, *Rhus chinensis*, and *Cornus* spp.) had low or negligible methane concentrations associated with low wood humidity regardless of soil conditions; while other species (*Acer*, *Tilia*, *Juglans*, and *Quercus* spp.) had CH₄ concentrations that varied with wood water content depending on soil conditions. The edaphic preference of the species could therefore influence its emissions because of the soil water content influence on heartwood humidity as well as on soil CH₄ production. In addition, there is a negative relationship between the wood density of the species and the water saturation of sapwood (Ramanantoandro et al., 2016), suggesting that wood density can also indirectly modulate the production of methane. Wet wood promotes anoxic conditions and therefore the microbial production of methane and negatively influences the diffusion of the CH₄ produced. Methanogens are abundant in wet alkaline and carbonated wood, where the absence of oxygen, lower density, high levels of bacterial fermentation products (e.g., acetate, butyrate, propionate, ethanol, isobutyrate, isopropanol, methane) as well as destruction of ray-vessel membranes are prevalent conditions (Zeikus et al., 1975; Schink et al., 1981; Moya et al., 2009). The relationship between methane production and wood water content could also differ between species as shown by Epron et al. (2022).

The vulnerability to **heart-rot and decay** (Fig. 1.13) of the species is also a trait explaining the differential production of methane between species (Covey et al., 2012; Warner et al., 2017). Indeed, substantial concentrations of CH₄ have been measured in the trunk of temperate upland species susceptible to rot (i.e., *Acer rubrum*, *Quercus rubra*, *Betula lenta*) (Covey et al., 2012). The presence of fungi influences CH₄ fluxes due to their ability to produce methanogenesis precursors. For instance, members of *Basidiomycota*, which can degrade wood into precursors of methanogenesis, have been identified in the wood of *Populus euramericana x deltoides* where methanogens were also identified (Feng et al., 2022). The vulnerability of the species to rot depends on its growth-strategy, and on the nature and physicochemical properties of the substances synthesized during heartwood formation (Wagner and Davidson, 1954). Notably high-density wood would be more resistant to decomposition (Chave et al., 2009). The progression of decomposition also differs between species according to their defense strategy (Wagner and Davidson, 1954). For instance, Gorgolewski et al. (2022a) observed that *Fagus grandifolia*, which can compartmentalize rot, had lower methane emissions than *Acer saccharum*.

Tissue **pH** (Fig. 1.14) exerts control over the presence of key methane-oxidizing microorganisms. The optimal pH for methanotrophy is 5–6.5 and it is generally reduced at pH < 4 (Chowdhury and Dick, 2013). However, there are some acidophilic and tolerant methanotrophs

(e.g., *Methylosinus*, *Methylomonas*, *Methylovulum*, *Methylocella*, *Methylocapsa*, *Methylocystis*, *Methylacidimicrobium* and *Methylacidiphilum*) (Dedysh et al., 2005, 2007; Pol et al., 2007; Kip et al., 2011; van Tee-seeling et al., 2014). For example, a bacterial community dominated by acidophilic methanotrophs, which was found responsible for reducing the tree emissions, was identified in the bark of *Melaleuca quinquenervia*, characterized by acidic and low-density tissues (Jeffrey et al., 2021a, 2021b).

In addition, the nature and levels of **secondary metabolites** (Fig. 1.15) in the wood of trees, which vary according to the species, can stimulate (carbohydrates) or inhibit (phenolic compounds) the microbial production of CH₄. Li et al. (2020) showed that the CH₄ production of wood was strongly dependent on the tree species and that the emission potential of trees was associated with the concentration and nature of wood metabolites of the species. For instance, *Salix matsudana* had a negligible production associated with a stronger inhibition of methanogenesis by the phenolic compounds of its wood, compared to *Populus davidiana* which exhibited substantial CH₄ production. The high phenolic compounds concentrations in wood of most upland species would be responsible for lower emissions due to the inhibition of methanogens. The metabolites would therefore act in concert with the taxonomic diversity of the methanogenic community to explain the differential methane production of the tree (Li et al., 2020). Besides, non-structural carbohydrates produced by photosynthesis fuel methane production by methanogenesis in living trees and their concentration varies between species. They are more concentrated in the sapwood of angiosperms than gymnosperms, which could suggest a greater potential for CH₄ production in hardwood species (Hoch et al., 2003; Würth et al., 2005; Covey and Magonigal, 2019).

Secondary metabolites (e.g., methanol, amino acids, methane, terpenes, and chloromethane) that can be released from leaves are likely to modulate the leaf microbiome (Herrmann et al., 2021). Leaf microbiome can in turn regulate the release of volatile compounds, including atmospheric trace gases (e.g. methane), into the atmosphere (Bringel and Couée, 2015). Methanol formation by physiological processes in the tree could support the growth of facultative methanotrophs (e.g., *Methylocella*) in leaves, and acetate formation in plant cells could influence acetic methanogenesis and the presence of microorganisms carrying this function (e.g., *Methanoxithrix* identified in spruce needles) (Putkinen et al., 2021). Production rates of volatile organic compounds, and the amount of structural and antimicrobial compounds produced by leaves are also traits that structure the microbiome (Whipps et al., 2008). Yadav et al. (2005) demonstrated that the content of leaf phenolic compounds explained the variation in leaf microbial colonization between different tree species, while Lajoie et al. (2020) observed a strong effect of aluminum and copper concentrations in the leaves, acting as antibiotics, on microbial functional variation between tree-hosts species.

Factors associated with the species' resource acquisition strategy, which are associated with the efficiency of photosynthetic resource use (e.g., leaf mass per area LMA, nutrient concentrations, water content, and leaf thickness), constitute functional traits influencing the microbial structure of the canopy, and thus that could have an impact on methanogens and methanotrophs (Yadav et al., 2005; Kembel et al., 2014; Laforest-Lapointe et al., 2016). The ability of a tree to be resource-conservative and to generate thicker leaves with a high leaf mass per area is likely to limit the leaching of nutrients from the interior of leaves to the surface, which may influence the functional structure of the leaf microbiome. In trees with acquisitive resource strategy, the lower LMA (Fig. 1.16) is associated with higher non-structural carbohydrates content (Zhang et al., 2024), which may favor microbial activity and could support methanogenesis inside the leaves. Conversely, sapling leaves of high LMA evergreen species are associated with higher phenolic content which could limit microbial activity including CH₄ production and consumption (Yadav et al., 2005; Poorter et al., 2009). **Leaf water content** (Fig. 1.17) and **stomatal conductance** (Fig. 1.8), which vary

between tree species, could be particularly important traits regulating the presence and activity of methanogens and methanotrophs in leaves by controlling oxygen availability. The higher leaf water content in low LMA species could favor anoxic conditions (Poorter et al., 2009). LMA is associated with several chemical and anatomical traits (Wright et al., 2004; Poorter et al., 2009) that could have different effects on methanogens and methanotrophs, making the assessment of its effect on tree CH₄ fluxes complex.

Leaf traits could also influence the non-microbial aerobic production through the photochemical reaction between leaf structural compounds and UV, and emissions of CH₄ (Vigano et al., 2008). For instance, the availability of CH₄ precursors in the leaf (e.g., pectin, cellulose, lignin, and waxes – Keppler et al., 2006; Messenger et al., 2009; Bruhn et al., 2014) could influence leaf CH₄ emissions (Wang et al., 2009). Traits influencing the leaf exposition to UV radiation, such as cuticle reflectance, UV-screening pigments or UV-photosensitizers could in turn influence leaf CH₄ emissions (McLeod et al., 2008; Messenger et al., 2009; Wang et al., 2009). Since stresses (e.g., hypoxia, physical injury, bacterial infection, and drought) could induce aerobic CH₄ production through the generation of ROS and subsequent reaction with leaf compounds (McLeod et al., 2008; Wang et al., 2009; Qaderi and Reid, 2009), other plant traits that regulate their response to stress (e.g., adaptations to flood) could likely impact CH₄ production. This could also imply inter-specific variation of the aerobic CH₄ production depending on the environmental conditions. Considering ROS are also produced through plant photosynthesis activity (Foyer et al., 2018), traits associated with higher photosynthetic rates such as low LMA (Wright et al., 2004) could likely result in higher production of ROS and subsequently higher CH₄ production. It could explain the differences in leaf CH₄ emissions among plant species, with low-LMA species having higher emissions, under aerobic conditions (Watanabe et al., 2012). More studies are needed to confirm the mechanism of CH₄ production through ROS generation inside leaf cells and, therefore, traits suggested as regulators of CH₄ production through this mechanism remain hypothetical.

2.4. Potential functional groups of trees influencing ecosystem methane fluxes

Identifying functional groups of trees that share defining traits for CH₄ fluxes could help predict the role occupied by trees in ecosystem methane fluxes. The predominance of species characterized by traits favorable to the production of CH₄ in soils and its transport through the tree or favorable to methanogens in the phyllosphere could result in the increase of ecosystem emissions. It can be particularly useful in a context of climate change which can increase the production of CH₄ in soils (Guo et al., 2023), and cause a shift of the tree-species composition and functional traits (Wu et al., 2023) that can have impact on CH₄ emissions. It could also be used to valorize taxonomic groups associated with low emission in environments with a high methane production, and thus inform forest management practice to reduce CH₄ emissions (Thomas et al., 2022). We suggest different functional groups associated with key traits that have been identified as influencing tree CH₄ fluxes between species in previous studies.

First, flood-adapted species share traits (i.e., pneumatophores, aerenchyma, hypertrophied lenticels) favorable for stem CH₄ transport and release. These traits may be responsible for increasing the proportion of soil CH₄ that will be emitted due to CH₄ uptake by roots in the CH₄ production zone and the bypass of the soil CH₄ oxidation zones. As a result, these species can form a functional group leading to increases in the net CH₄ emissions of the ecosystem. They can play a significant role in wetlands where CH₄ production in soils is favored, resulting in substantial CH₄ transport in trees. Considering the trade-off between traits of drought-tolerant species and flood-tolerant species, they may play different roles in CH₄ emissions (Niinemets and Valladares, 2006; Puglielli et al., 2021; Pavanetto et al., 2024).

In addition, species with low wood density, in particular fast-

growing species, could form a functional group characterized by a relatively high potential for diffusion and emission of CH₄. In these species, the higher water saturation potential of low-density wood could result in particularly high microbial production and emissions when edaphic conditions are favorable. Likewise, species characterized by moist wood or species vulnerable to rot can form functional groups in CH₄ fluxes through their potential for intrinsic microbial production of CH₄. On the other hand, species with rather dry and dense wood, and rot-resistant could form functional groups characterized by low or negligible CH₄ emissions.

We also suggest that species with low LMA could form a group associated with higher leaf emissions in consequence of potentially higher CH₄ production (microbial and non-microbial) resulting from the higher carbohydrates and water content, and photosynthetic activity.

Understanding the effect of climate change on these functional groups and traits can help predict the effect on tree-mediated methane fluxes. Climate change can cause a shift on traits associated with changing climatic variables (e.g. mean annual temperature and precipitations) and resistance to environmental stressors (Wieczynski et al., 2019; Kühn et al., 2021). Notably, higher wood density, which provides xylem resistance, is positively associated with environmental stress (e.g. drought) tolerance and warming temperatures (Šímová et al., 2018; Kühn et al., 2021; Wu et al., 2023). A transition from species with resource-acquisition strategy and high hydraulic efficiency towards slow-growing species with hydraulic-safety and higher wood density resulting from drought (Wu et al., 2023) could reduce the potential of methane transport in tree stems. Conversely, higher water-use efficiency and deeper roots to cope with decreasing precipitations (Kühn et al., 2021) are traits associated with higher methane transport potential. In addition, it is likely that flood-adapted species, with traits that can facilitate tree methane emissions, would be favored with increasing flood frequency and magnitude in other locations. For leaves, both lower and higher leaf mass area can be associated with tree ability to cope with increasing temperature depending on the biome (Kühn et al., 2021) which makes difficult the determination of the trait variation effect on tree methane emissions under climate change.

3. Traits associated with tree life history and development influencing methane fluxes

Methane fluxes can also vary between individuals of the same species with traits that are not associated with the taxonomy of the species but with the life history of the individual. For example, Machacova et al. (2023) showed that *Fagus sylvatica* individuals of the same age exhibited different emissions, whose contribution to the ecosystem fluxes may vary from 1.5 %, to 46.5 %. In the study of Epron et al. (2022), the potential of methane production in the heartwood varied more among individuals than species. The variability in the amount of wood rot, and the presence of wet heartwood, which can promote microbial production of CH₄, could explain the differential emissions between individuals (Flanagan et al., 2021; Machacova et al., 2023). The presence and extent of injuries are also responsible for differential emissions between individuals (Gorgolewski et al., 2022a).

Methane fluxes can also vary with tree age according to traits associated with development (i.e., ontogenic traits). For instance, higher stem emissions have been observed for saplings (Pangala et al., 2015; Sjögersten et al., 2020). Lower wood density and diameter, and higher lenticel density in young trees have been suggested as traits that may explain their higher stem emissions. Otherwise, Pitz et al. (2018), suggested that the development of a larger and deeper root system that can reach methane producing zones in the soil, and other factors such as rot development and non-structural carbohydrate levels in large mature trees, could result in higher stem emissions. The concentration of non-structural carbohydrates produced by photosynthesis can support microbial activity and thus regulate microbial production of methane in wood, and consequently stem emissions. Moreover, oxygen availability

in wood, which influences microbial methane production, may vary according to tree age. For instance, internal re-fixation of CO₂ from autotrophic respiration is generally greater for young trees due to better light transmittance of thin bark and could increase the tissue oxygenation (Teskey et al., 2008). Vulnerability to rot is a trait that also varies between individuals according to age class (Wagener and Davidson, 1954; Carmichael et al., 2014). The stage of decay influences the wood density, which influence wood emissions between individuals: advanced decay limits microbial production by methanogenesis due to the lower density and greater permeability which facilitates O₂ diffusion (Covey et al., 2012; Warner et al., 2017).

Factors that vary with individual age can also influence methanogenic and methanotrophic communities of tree leaves and their methane fluxes. Gorgolewski et al. (2022b), who observed differential leaf methane fluxes between young and mature individuals in a temperate forest, suggested that the higher rates of methane uptake by young leaves may result from the greater potential for foliage colonization by methanotrophs due to the greater proximity to soil. Tree height can also influence the microbiome due to its influence on the chemical environment and exposure to external pressures like the intensity of solar radiation reaching the leaves (Herrmann et al., 2021). It can also influence the aerobic production of CH₄ by controlling UV exposure. Putkinen et al. (2021) associated the large variation of methane fluxes of young *Picea abies* individuals to their dynamic growth phase. The greater leaf impermeability of young trees due to the intact cuticle (Whipps et al., 2008) could result in a different microbiome via modulation of the chemical environment between young and mature trees. Finally, leaf phenolics and condensed tannins can change with tree age (Wam et al., 2017), which may influence methanogenic communities and methane production as observed for wood in the study of Li et al. (2020).

4. Global analysis of tree methane fluxes according to land-type, tree age, and taxonomy

We did a global analysis on tree methane fluxes to assess the importance of inter-specific variability of methane fluxes in comparison to other factors of influence (e.g., land, age, season). We also aimed to validate the effect of key traits and associated functional groups suggested in the previous section. Based on the literature review of functional traits we delineate the following hypotheses for our global analysis: In addition to being superior in lowland environments, tree methane fluxes should be higher for younger individuals, species with low wood density, low LMA, and angiosperms.

4.1. Method

To conduct the global analysis of methane fluxes with the aim to assess the importance of interspecific variation in methane fluxes, a search in the existing literature was performed as follows. First, a search in Scopus, Science direct and Google scholar databases using the searching terms presented in Table S1 identified a total of 607 papers. Based on the title, papers respecting the inclusion and exclusion criteria presented in Table S2 were selected for content assessment. Afterwards, studies on CH₄ fluxes from soil, global ecosystem (e.g., from Eddy covariance measurements), non-natural ecosystems (e.g., landfill sites, urban sites, or mesocosms), plants other than trees, or coarse woody debris, were excluded. After reading the abstract of remaining papers, studies on in situ tree stem or tree leaf CH₄ fluxes from chamber measurements were kept, excluding papers on fluxes from incubations or other in vitro experiments. We consider that studies relying on syringe gas sampling method, tissue incubation in laboratory, and greenhouse experiments, where conditions could be non-representative of the natural environment, could include particularly important methodological biases (Kamakura et al., 2012; Salas-Rabaza et al., 2023), so we chose not to include them in the analysis. Duplicates from the research results of the three databases were removed, resulting in 57 articles

downloaded. Those papers were read thoroughly to extract methane flux data. Among them, papers that did not include in situ flux measurement data from chambers in natural ecosystems, or that only reported fluxes on ground area, were also excluded. Finally, papers presenting only the mean for a group of species were excluded from species fluxes comparison. In the end, 50 publications were kept for the global analysis of tree methane fluxes, resulting in 156 data points for taxonomic comparison. Those papers cover different ecosystems including temperate, tropical, subtropical, intertropical, boreal forests and wetlands, and mangroves. Methane fluxes were converted in $\mu\text{mol m}^{-2} \text{h}^{-1}$. When fluxes intervals were reported, the median was calculated. The methane fluxes by study, species and ecosystem type in uplands and lowlands are presented in Table S3.

Methane flux data were categorized according to land type (upland or lowland), ecosystem, site with its mean annual precipitation and temperature, tree species, tree age (mature or sapling), phyllosphere compartment (stem, leaf) and methane flux measurement details (height of measurements and season). Data analyses, including descriptive statistics and data visualisation, were conducted in the R statistical programming environment (R Core Team, 2021). The distribution of fluxes according to land type, ecosystems, tree age (mature or sapling), and taxonomy (clade: gymnosperm or angiosperm, genus, and species) was visualised using the functions of the *ggplot2* R package. We then performed ANOVA (function *aov*, package *stats*) to test the effect of land type, taxonomy and tree age on stem and leaf fluxes. To overcome the limited number of comparable studies for species fluxes comparison, genus level comparisons were performed. Only genera for which multiple values ($n \geq 4$) were available were included in this comparison. Post-hoc tests (function *TukeyHSD*, R package *stats*) were also performed to assess which tree genera differed in terms of CH₄ fluxes. The effect of wood density and LMA of tree species based on data obtained from TRY Plant Trait Database and Global Wood Density Database (Chave et al., 2009; Kattge et al., 2020). Our analysis on the effect of traits on tree fluxes was limited to wood density and LMA because of the lack of data availability for other traits. We tested for the correlation of stem and leaf CH₄ fluxes with wood density and LMA (function *cor.test*, method "Pearson", R package *stats*). The relationship of stem fluxes with wood density and LMA was plotted using the *geom_smooth* function (R package *ggplot2*). Finally, a linear regression model that explains the stem CH₄ fluxes of mature trees based on different factors of influence was built using the functions *lm* (R package *stats*) and *stepAIC* (R package *MASS*). The distribution of the residuals was verified to ensure the model error was normally distributed and stochastic. The importance of the factors identified was assessed by calculating the proportion of variance explained by the regressors using *calc.relimp* function (R package *rela. impo*).

4.2. Results and discussion

We observed that stems have positive fluxes and act mainly as methane sources. The mean stem flux tended to be higher in lowlands ($396.09 \mu\text{mol m}^{-2} \text{h}^{-1}$) than in uplands ($1.64 \mu\text{mol m}^{-2} \text{h}^{-1}$) although it was not statistically significant (ANOVA *P-value* = 0.09) (Fig. 2a). It became significantly different when nested on the ecosystem or site (*P-value* < 0.05). For instance, in warm-temperate ecosystems, stem fluxes were significantly higher in lowlands (mean of $26.67 \mu\text{mol m}^{-2} \text{h}^{-1}$) than in uplands (mean of $3.86 \mu\text{mol m}^{-2} \text{h}^{-1}$). For leaf fluxes, we observed negative mean for upland fluxes ($-0.95 \mu\text{mol m}^{-2} \text{h}^{-1}$) compared to positive mean ($6.04 \mu\text{mol m}^{-2} \text{h}^{-1}$) for lowland fluxes, indicating that leaves can act as a source or sink depending on the land type (ANOVA *P-value* < 0.01). This could be associated with higher methane production in lowland soils resulting in more important transport of methane in trees via transpiration, as demonstrated in previous studies (Jeffrey et al., 2020; Moldaschl et al., 2021).

We observed differences in stem fluxes between young and mature trees. For stem fluxes in lowlands, the mean flux of saplings was

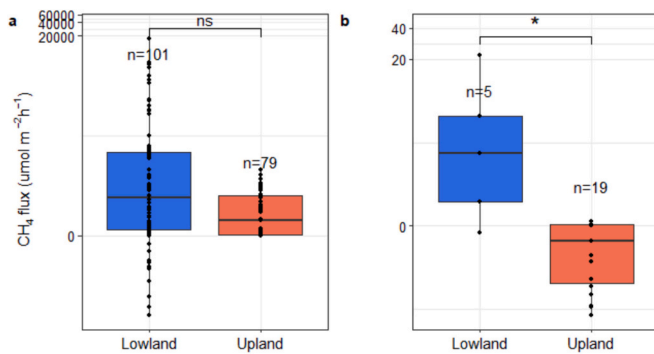


Fig. 2. Distribution of stem (a) and leaf (b) CH_4 fluxes ($\mu\text{mol m}^{-2} \text{h}^{-1}$) (under an inverse hyperbolic sine transformation) obtained from the literature between land types. Asterisk indicates a significant difference according to the ANOVA test. The horizontal bar of the boxplots represents the median, and the lower and upper hinges represent the first and third quartile of flux data.

significantly higher than mature trees (3630.3 vs $259.19 \mu\text{mol m}^{-2} \text{h}^{-1}$, ANOVA P -value < 0.01) (Fig. 3a). This could be explained by higher lenticel density on sapling stems and lower wood density (Pangala et al., 2014). Upland fluxes tended to be lower for saplings (mean of 0.06 vs $2.69 \mu\text{mol m}^{-2} \text{h}^{-1}$), although it was not statistically significant and sapling fluxes only came from *Quercus petraea* (Fig. 3b). Otherwise, larger, and deeper root systems that can reach methane producing zones, higher levels of wood carbohydrates and vulnerability to rot that fuel methane production by methanogenesis could be traits of mature trees resulting in higher stem methane emissions (Covey et al., 2012; Warner et al., 2017).

Higher leaf emissions were observed for saplings compared to mature trees in lowlands (mean of 16.70 vs $1.46 \mu\text{mol m}^{-2} \text{h}^{-1}$)

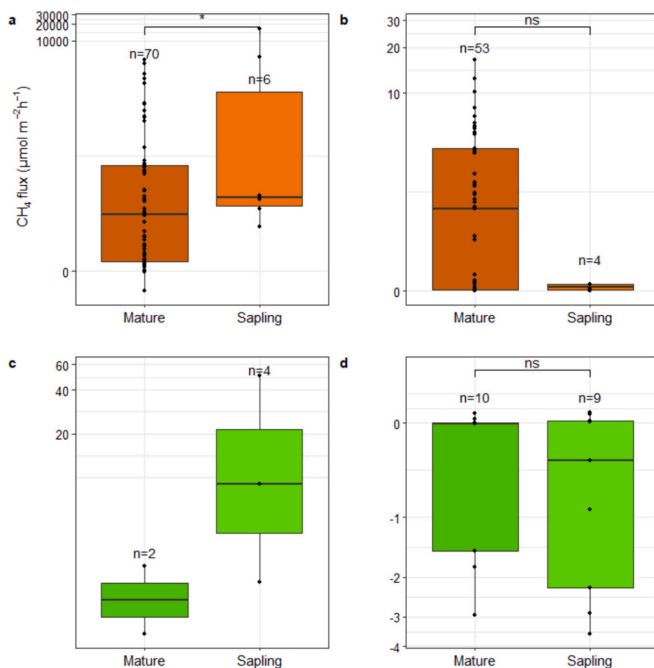


Fig. 3. Distribution of tree stem (a, b) and leaf (c, d) CH_4 fluxes ($\mu\text{mol m}^{-2} \text{h}^{-1}$) (under an inverse hyperbolic sine transformation) obtained from the literature between mature trees and saplings in lowlands (a, c) and uplands (b, d). Asterisk indicates significant difference while ns indicates nonsignificant difference according to the ANOVA test. ANOVA test was not performed for leaf fluxes in lowlands since $n < 4$ for mature trees. The horizontal bar of the boxplots represents the median, and the lower and upper hinges represent the first and third quartile of flux data.

although there was not enough data to test the statistical significance (Fig. 3c). The smaller surface of sapling stems could result in higher leaf emissions in lowlands. We observed a higher mean uptake for saplings in uplands (-1.08 vs $-0.83 \mu\text{mol m}^{-2} \text{h}^{-1}$) although the ANOVA test indicated that sapling fluxes were not significantly different from mature trees (P -value > 0.05 , Fig. 3d). A higher uptake for saplings in uplands could be associated with a greater foliage colonization by methanotrophs as suggested by Gorgolewski et al. (2022b). We suggest that the influence of tree age on stem and leaf CH_4 fluxes could differ between uplands and lowlands, but more data are needed to assess the effect of age class on tree methane fluxes. Leaf and sapling fluxes measured in situ are particularly scarce. The relative contribution of the microbial mechanisms, resulting from a different microbiome between saplings and mature trees, could be more important in uplands while variability associated to differential transport could be more important in lowlands where important concentrations of soil-produced methane can be transported.

For the taxonomic comparisons, there was no significant difference of lowland fluxes between tree genera (ANOVA P -value = 0.07) (Fig. 4a). The global analysis of methane fluxes in uplands showed a significant effect of tree taxonomy on stem emissions (ANOVA P -value < 0.05) (Fig. 4b). *Populus* spp. had significantly higher stem emissions (mean of $6.87 \mu\text{mol m}^{-2} \text{h}^{-1}$) than *Betula* spp., *Fagus* spp. and *Quercus* spp. (mean of 0.04 , 2.24 and $0.34 \mu\text{mol m}^{-2} \text{h}^{-1}$). A functional trait that can explain the lower emission rates observed for *Betula* spp., *Fagus* spp., and *Quercus* spp. is their resistance to rot, associated with their capacity to compartmentalize infected tissues (Shigo and Shortle, 1979; Rademacher et al., 1984), which can limit intrinsic methane production from wood decay as suggested in Warner et al. (2017). The higher stem emissions for *Populus* spp. could be associated with its low-density wood which facilitates methane diffusion. Stem methane fluxes of trees in uplands were negatively correlated with wood density which also confirms the importance of the trait in regulating tree methane emissions (Pearson correlation $R = -0.31$, $p < 0.05$) (Fig. 5b). This correlation was not observed for lowland fluxes. A positive correlation was observed ($R = 0.32$, P -value < 0.05), while it became not significant when excluding outliers (i.e. fluxes from Jeffrey et al., 2020, 2021b) ($R = 0.05$, P -value > 0.05) (Fig. 5a).

Although there were less flux data for gymnosperms, we observed a lower and close to zero ($0.03 \mu\text{mol m}^{-2} \text{h}^{-1}$) mean stem flux compared to a positive mean ($2.84 \mu\text{mol m}^{-2} \text{h}^{-1}$) for angiosperms in uplands (ANOVA P -value < 0.05) (Fig. 6b). The higher fluxes of angiosperms could be linked to functional traits favorable to methane transport such as the presence of vessel elements that results in higher transport capacity (Chave et al., 2009). Carbohydrates that are more concentrated in the sapwood of angiosperms than in gymnosperms may also fuel methanogenesis in the wood (Hoch et al., 2003; Covey and Megonigal, 2019).

For leaf fluxes, we observed taxonomic differences for upland fluxes at the genus and clade level (ANOVA P -value < 0.05) (Figs. 4c, 6d). Angiosperms (i.e. *Acer* spp.) had a higher mean CH_4 uptake ($-1.80 \mu\text{mol m}^{-2} \text{h}^{-1}$) compared to gymnosperms (i.e. *Picea* and *Pinus* spp.) ($-0.44 \mu\text{mol m}^{-2} \text{h}^{-1}$). Angiosperms could support higher methanotrophic activity due to higher nutrient leaching, lower phenolic content, and less anoxic conditions in leaves, although microbial analysis are needed to verify this hypothesis. There was no significant correlation between leaf fluxes and LMA ($R = -0.68$ and -0.65 , P -value > 0.05) (Fig. 5c, d). More data on different species are needed to assess the relationship with LMA and verify the flux trend between angiosperms and gymnosperms.

We built linear regression models to explain the stem CH_4 fluxes in lowlands and uplands that include different explanatory factors. Factors explaining the upland and lowland fluxes and their relative contributions are different (Tables S4–S6). The best model explaining upland fluxes ($R^2 = 0.70$, P -value < 0.01) includes, in order of importance, tree genus, season, mean annual temperature (MAT) and precipitation (MAP). Notably, growth-season of temperate and boreal ecosystems had

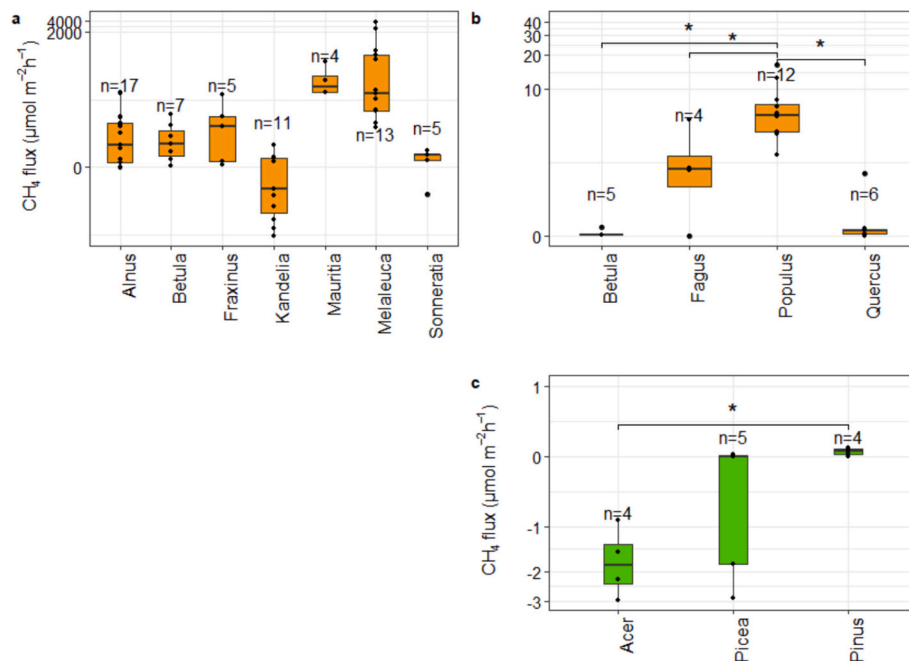


Fig. 4. Distribution of tree stem (a, b) and leaf (c) CH₄ fluxes ($\mu\text{mol m}^{-2} \text{h}^{-1}$) (under an inverse hyperbolic sine transformation) obtained from the literature for different genera ($n \geq 4$) in uplands (b, c) and lowlands (a). Asterisk indicates significant differences according to the post-hoc Tukey test. There was not enough data to perform the taxonomic comparisons of leaf fluxes in lowlands ($n < 4$) which are therefore not presented here. The horizontal bar of the boxplots represents the median, and the lower and upper hinges represent the first and third quartile of flux data.

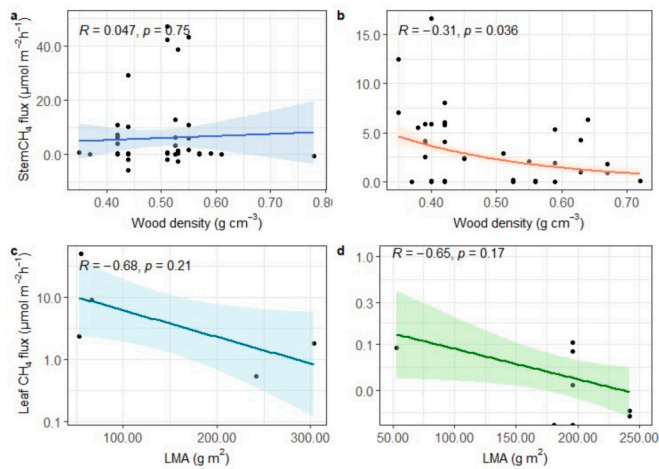


Fig. 5. Regression (Pearson correlation) between stem CH₄ fluxes ($\mu\text{mol m}^{-2} \text{h}^{-1}$) and wood density (data obtained from TRY Plant Trait and Global Wood Density databases) in lowlands (a) and uplands (Poisson distribution, link = log) (b), and between leaf CH₄ fluxes ($\mu\text{mol m}^{-2} \text{h}^{-1}$) (under log scale) and leaf mass area (g m^{-2}) (data obtained from TRY Plant Trait) in lowlands (c) and uplands (d).

a positive effect on upland stem fluxes, which means higher stem methane fluxes are observed during this time of year. The best model explaining lowland fluxes ($R^2 = 0.63$, $P\text{-value} < 0.01$) includes, in order of importance, tree genus, season, measurement height, and longitude. Notably, the wet season had a significant positive effect on lowland tree fluxes.

Variability in environmental conditions, type of data (e.g., median vs mean), and measurement height limits the reliability of flux comparisons between studies and the assessment of taxonomy effect on flux differences. Moreover, differences in measurement methods (e.g., chamber design, gas analyzer) can create a bias that makes comparisons

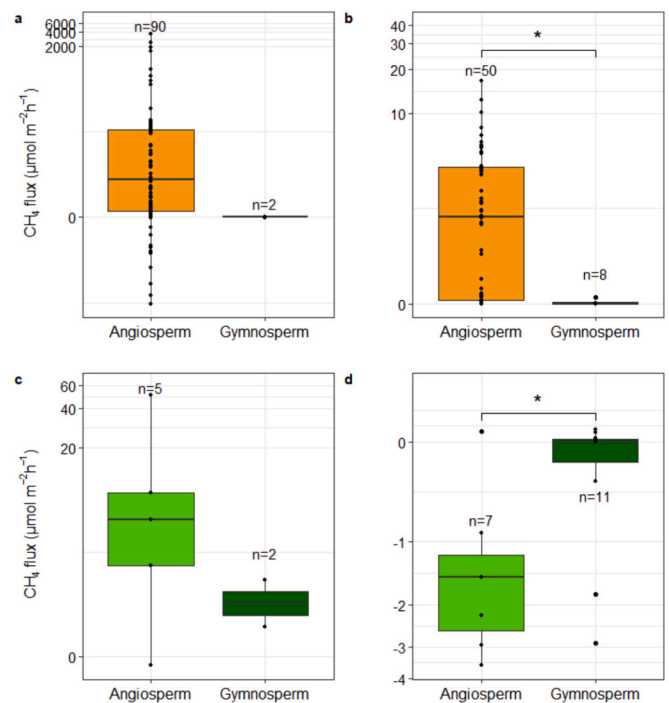


Fig. 6. Distribution of tree stem (a, b) and leaf (c, d) CH₄ flux data ($\mu\text{mol m}^{-2} \text{h}^{-1}$) (under an inverse hyperbolic sine transformation) for tree clade in lowlands (a, c) and uplands (b, d). Asterisk indicates a significant difference according to the ANOVA test. There was not enough data for the comparisons of fluxes in lowlands ($n < 4$ for gymnosperms). The horizontal bar of the boxplots represents the median, and the lower and upper hinges represent the first and third quartile of flux data.

between studies difficult and thus have a negative impact on the reliability of a global analysis for identifying species effect. For instance, measurement duration can impact concentration buildup and lead to an underestimation of fluxes (Salas-Rabaza et al., 2023). The chamber design can impact CH₄ leak and consequently flux estimations (Salas-Rabaza et al., 2023). The use of UV-opaque vs translucent chambers for measurement of leaf fluxes could represent an important bias since UV controls the aerobic production of methane (Kohl et al., 2023). Other potential biases include the interference of volatile organic compounds (VOC) that can result in measurement of artefacts rather than methane. It varies with the analyzer used and could be particularly important for leaf flux measurements (Kohl et al., 2019). Controlling and accounting for leak and VOC interference in flux calculation can influence estimations.

Despite the limitations of the global analysis, we were able to identify consistent factors explaining the variability of methane fluxes. Taxonomy and season were the factors with the greatest explanatory potential of tree methane fluxes. The importance of taxonomy can indicate the effect of tree functional traits in methane cycling associated with the taxonomy. This is a first step in assessing the importance of inter-specific variability in tree CH₄ fluxes globally. More studies that target multiple species in the same ecosystem with trait measurements are needed to better assess how methane fluxes differ between tree species according to their features. Considering the low amount of data, especially for leaf and sapling fluxes, we suggest that more studies should focus on measuring these fluxes, and that the results of this global analysis should be taken with caution. Because some functional traits differ between individuals rather or as well as species, it would be interesting to assess the contribution of individuals and their traits in methane fluxes variability (e.g., Mochidome and Epron, 2024).

5. Conclusion

The review highlighted that differences in methane fluxes between tree species and individuals can be explained by a diversity of taxonomic and ontogenetic traits influencing methane transport and microbial production of methane. For instance, wood density was identified as a trait influencing methane emission, which was verified in the global analysis. The global analysis demonstrated the importance of taxonomy as an important control factor of stem CH₄ fluxes, along with season. Knowledge on functional traits enables the identification of functional taxonomic groups that share key traits in methane cycling which can help predict the role played by trees in the ecosystemic methane budget based on the forest composition. It is important to better understand, quantify and predict tree methane fluxes considering they can play an important role in modulating the ecosystemic methane budget. Modeling tree CH₄ fluxes, based on environmental conditions, tree taxonomic composition and traits could be an interesting avenue to include trees in ecosystemic methane budgets. Anttila et al. (2024) built a model which integrates CH₄ transport in stems for boreal tree species, based on sap flow, axial advection, and radial diffusion, with meteorological forcing variables and soil CH₄ concentrations. More studies are needed to incorporate tree traits (aerenchyma, wood structural properties, wood humidity) which influence transport mechanisms to these equations. These models should also include equations for microbial mechanisms based on wood and leaf chemistry (e.g., humidity, pH, metabolites), and non-microbial production of CH₄ based on leaf traits (e.g., LMA). More data is needed to test and define the precise functions between tree traits and these mechanisms. We suggest that the relationship between leaf fluxes and LMA should be investigated since it could regulate different mechanisms, and thus be an important variable in models. The interaction between different tree traits should also be assessed and accounted for in models. Traits that have additive or opposite effects on CH₄ fluxes can result in different relationships with tree CH₄ emissions between species. In future studies, an effort should be made to simultaneously measure tree CH₄ fluxes of different species and

individuals, environmental conditions (e.g., soil humidity, UV exposure), tree traits, and investigate the presence of methanogens and methanotrophs within the phyllosphere. This should be done in different ecosystems and seasons to account for interactions between traits and environmental conditions. Both methane emissions and plant traits could change under climate change, further supporting the need to better understand the relationships between traits and environmental conditions.

CRedit authorship contribution statement

Marie-Ange Moisan: Writing – original draft, Formal analysis, Conceptualization. **Geneviève Lajoie:** Writing – review & editing, Validation. **Philippe Constant:** Writing – review & editing, Validation. **Christine Martineau:** Writing – review & editing, Validation, Supervision, Funding acquisition, Conceptualization. **Vincent Maire:** Writing – review & editing, Validation, Supervision, Funding acquisition, Conceptualization.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Data availability

Data associated to this article are available in Supplementary material.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.scitotenv.2024.173730>.

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