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Methane dynamics in vegetated habitats in inland waters: quantification, regulation, and global significance

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Freshwater ecosystems, including lakes, wetlands, and running waters, are estimated to contribute over half the natural emissions of methane (CH_4) globally, yet large uncertainties remain in the inland water CH_4 budget. These are related to the highly heterogeneous nature and the complex regulation of the CH_4 emission pathways, which involve diffusion, ebullition, and plant-associated transport. The latter, in particular, represents a major source of uncertainty in our understanding of inland water CH_4 dynamics. Many freshwater ecosystems harbor habitats colonized by submerged and emergent plants, which transport highly variable amounts of CH_4 to the atmosphere but whose presence may also profoundly influence local CH_4 dynamics. Yet, CH_4 dynamics of vegetated habitats and their potential contribution to emission budgets of inland waters remain understudied and poorly quantified. Here we present a synthesis of literature pertaining CH_4 dynamics in vegetated habitats, and we (i) provide an overview of the different ways the presence of aquatic vegetation can influence CH_4 dynamics (i.e., production, oxidation, and transport) in freshwater ecosystems, (ii) summarize the methods applied to study CH_4 fluxes from vegetated habitats, and (iii) summarize the existing data on CH_4 fluxes associated to different types of aquatic vegetation and vegetated habitats in inland waters. Finally, we discuss the implications of CH_4 fluxes associated with aquatic vegetated habitats for current estimates of aquatic CH_4 emissions at the global scale. The fluxes associated to different plant types and from vegetated areas varied widely, ranging from−8.6 to over 2835.8 mg CH_4 m^{-2} d^{-1}, but were on average high relative to fluxes in non-vegetated habitats. We conclude that, based on average vegetation coverage and average flux intensities of plant-associated fluxes, the exclusion of these habitats in lake CH_4 balances may lead to a major underestimation of global lake CH_4 emissions. This synthesis highlights the need to incorporate vegetated habitats into CH_4 emission budgets from natural freshwater ecosystems and further identifies understudied research aspects and relevant future research directions.

KEYWORDS

carbon cycle, freshwaters, greenhouse gas, lakes, macrophytes, plant-mediated, rivers, wetlands

1 Introduction

Freshwater ecosystems, including wetlands, lakes, reservoirs, rivers, and streams, play an important role in global carbon cycling and are estimated to contribute roughly 50% to global methane (CH_4) emissions: 149 ± 15 Tg CH_4 yr^{-1} for wetlands and 151 (± 73.0) Tg CH_4 y^{-1} for lakes (Saunois et al., 2020; Rosentreter et al., 2021). Estimates of CH_4 emissions are, however, highly variable, and freshwater systems represent a major source of uncertainty in the global CH_4 budget (Saunois et al., 2020). Within freshwater systems, there are several major sources of uncertainty, that include the large temporal and spatial heterogeneity that characterizes CH_4 fluxes, as well as system and geographic biases in the extant data bases (Rosentreter et al., 2021). One additional source of uncertainty is CH_4 emissions from vegetated habitats within inland waters. Aquatic plants, and in particular emergent macrophytes, which colonize many inland waters, have been known for a relatively long time to be potentially important sources of CH_4 (Carmichael et al., 2014). Studies focusing on single systems have shown that fluxes from vegetated areas can disproportionately contribute to the total CH_4 emissions, up to 78% even when the only a limited area of the entire system is vegetated (Dacey and Klug, 1979; Holzapfel-Pschorn et al., 1986; Larmola et al., 2004; Desrosiers et al., 2022), yet these habitats are seldom accounted for in aquatic CH_4 budgets, whether at the ecosystem, regional, or global scales. A notable exception is the recent study on emergent vegetation in arctic-boreal lakes which indicates that accounting for the vegetation increases CH_4 emission estimates by 21% (Kyzivat et al., 2022). The general omission of vegetated habitats in aquatic CH_4 budgets is partly a consequence of the fact that the distribution of aquatic vegetation is itself highly heterogeneous, the information on greenhouse gas dynamics associated to this aquatic vegetation is fragmented, biased geographically and by ecosystem type, and the approaches used are often not comparable. As a result, the contribution of aquatic vegetation to whole ecosystem CH_4 budgets remains largely unquantified, and this is perhaps one of the largest sources of uncertainty in the current global inland water CH_4 budget.

Clearly, the contribution of vegetated areas to total system emissions from inland waters depends on the extent of vegetation coverage on the one hand and the impact of plants on CH_4 dynamics on the other. CH_4 emissions reported from vegetated sites vary widely—being higher or lower—than those of surrounding unvegetated sites (see an overview in e.g., Kosten et al., 2016), although they tend to be in the upper range of aquatic fluxes (Kyzivat et al., 2022). This large variability has been attributed to differences in the influence on CH_4 production, CH_4 oxidation, and CH_4 transport (Fritz et al., 2011; Dean et al., 2018; Grasset et al., 2018). The influence of vegetation on these processes varies among plant species (Holzapfel-Pschorn et al., 1986; Yoshida et al., 2014; Villa et al., 2020) and depends on a variety of variables, including plant biomass (particularly below-ground biomass; e.g., Liu et al., 2019), CH_4 concentration around the roots (Struik et al., 2022), plant growth dynamics (Kankaala et al., 2003), plant tissue composition (Grasset et al., 2019), sediment temperature (Kankaala et al., 2004), sediment composition (Kankaala et al., 2005), water depth (Ding et al., 2002) and herbivory (Dingemans et al., 2011), all of which vary seasonally, leading to seasonal differences in CH_4 emissions. This long list highlights the complexity of the mechanistic underpinnings of plant impacts on CH_4 fluxes and the challenges associated with understanding and predicting these processes, to be able to accurately extrapolate and upscale CH_4 emissions from aquatic vegetated areas across ecosystems at regional and even global scales.

Insight into the quantitative effect of aquatic vegetation on CH_4 fluxes is in part hampered by the wide range of different approaches that have been used to assess plant effects on CH_4 emissions, which vary in the type of fluxes they include. Some studies have focused exclusively on the flow of CH_4 through the plant tissue—mostly in emergent plants (Sanders et al., 2007) -, whereas other studies have assessed CH_4 fluxes more generally within vegetated habitats. Within the latter, a few have made the distinction between direct and indirect plant effects; some have included the effect of plants on ebullition (Davidson et al., 2018; Desrosiers et al., 2022), others have explicitly excluded ebullition (e.g., Petruzzella et al., 2015). This diversity of approaches complicates comparison among studies, and is also reflected in the rather inconsistent use of the term "plant-mediated" or "plant-associated" fluxes to indicate both direct plant-mediated emissions (direct transport by the plants), and emissions that occur in habitats that are dominated by plants, which include both direct fluxes from plants and other effects plants have on CH_4 emissions in the habitat. While both definitions are linguistically correct, the pathways and implications are very different. To avoid ambiguities, we use the term plant-associated CH_4 fluxes generically to denote CH_4 fluxes occurring in vegetated habitats, and these include direct plant-mediated fluxes and other CH_4 emission pathways that occur in these vegetated habitats. In this work, we aim to advance the understanding of the effect of aquatic vegetation on the CH_4 dynamics and emissions in inland waters, to advance the quantification of CH_4 emissions from vegetated habitats, and to identify knowledge gaps. We conducted a semi-quantitative literature review, aiming at (i) providing an overview of the different ways aquatic vegetation can influence CH_4 production, consumption, and transport (Section 2), (ii) providing an overview of approaches applied to measure CH_4 fluxes associated to aquatic plants and the determine the potential effect of aquatic vegetation on CH_4 dynamics (Section 2), and (iii) summarizing the extant data on CH_4 fluxes of vegetated areas and its variation (Section 3). Finally, we discuss the implications of CH_4 fluxes from vegetated habitats in inland waters for current global CH_4 estimates (Section 4).

2 The impact of vegetation on CH_4 dynamics

This section summarizes the effects of aquatic vegetation on CH_4 production, oxidation, and transport (Figure 1). For a more elaborate discussion on plant effects on CH_4 emissions in different ecosystems, we refer to Bastviken et al. (2023). More details on the physiology of plant CH_4 transport can be found in Vroom et al. (2022).

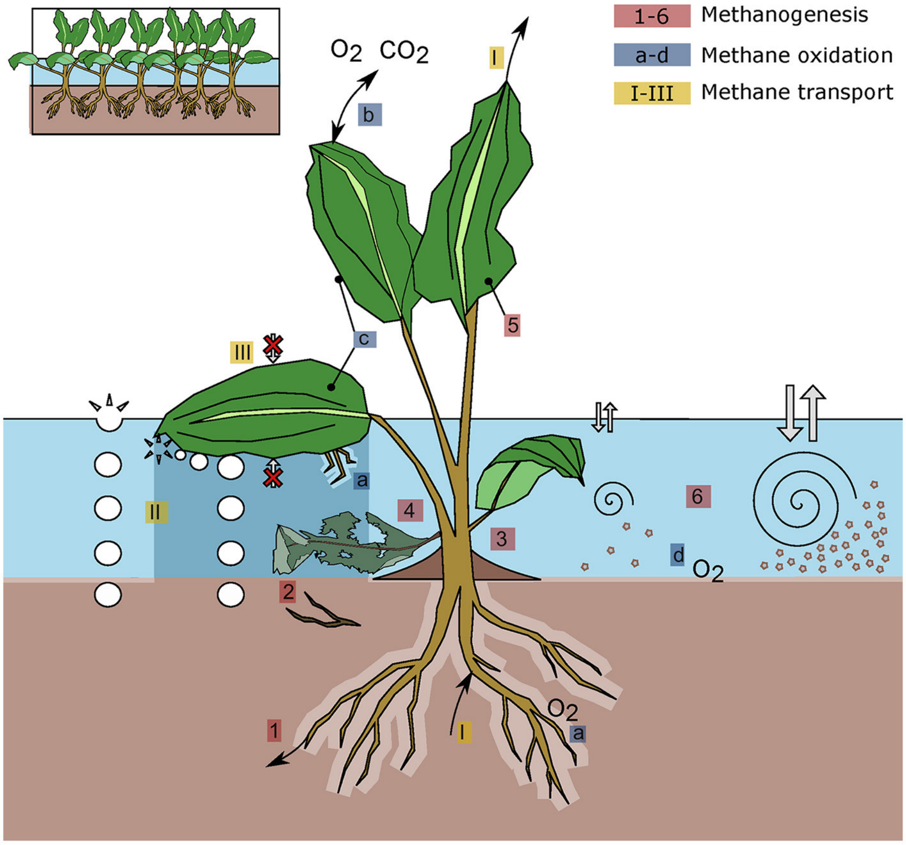

FIGURE 1
Plant-mediated processes that influence methane (CH_4) emissions from freshwater systems. The depicted plant represents a hybrid of emergent, floating, and submerged vegetation to illustrate the main processes of these three different functional groups. The water layer is divided into an oxic (light blue) and anoxic (dark blue) zone. The processes illustrated are related to CH_4 production (1-6, red), CH_4 oxidation (a-d, blue) and CH_4 transport (I-III, yellow). Plant-associated effects on CH_4 production include the provision of organic carbon through root exudates (1) and decaying organic matter (2), sediment accumulation due to reduced water flow (3), dissolved carbon release followed by oxic methanogenesis in the water column (4), CH_4 production within the plant (5) and reduced sediment resuspension (6). CH_4 oxidation is affected by radial oxygen loss (ROL) in the root zone (a) potentially related to photosynthesis (b), CH_4 oxidation by epiphytic and endophytic methanotrophs (c), and oxygen (O_2) availability in the oxic water or sediment layer (d). Plants can alter the transport of CH_4 by serving as a bypass between the anoxic sediment and the atmosphere (I), by impeding the movement of bubbles from the water to the atmosphere (II), and by reducing water-atmosphere gas exchange (III).

2.1 CH_4 production

CH_4 is for a large part a final product of organic matter decomposition by methanogenic archae in anaerobic environments and is produced mainly in sediments (Bastviken, 2009). Plant-associated effects on CH_4 production are described below and include the provision of organic carbon through root exudates and decaying organic matter and sediment accumulation due to reduced water flow. In addition, plants release dissolved carbon in the water column—potentially followed by oxic methanogenesis—and CH_4 production may take place within the plant (Figure 1).

Decaying plant matter can enhance CH_4 production in the sediment by promoting anoxia, and by providing organic substrates for methanogens (Webster and Benfield, 1986; Segers, 1998; Marinho et al., 2015). The intensity of methanogenesis depends on plant species and composition of the decaying matter. In a study of a boreal lake, for instance, *Lemna trisulca* detritus produced twice as much CH_4 per gram biomass as *Phragmites australis* detritus (Kankaala et al., 2003). Bottles incubation experiments showed that CH_4 production was positively related to a plant's water content, and negatively related to its C:N and C:P ratio (Grasset et al., 2018, 2019). Root exudates also form an important pool of labile carbon substrates, such as acetate potentially fueling methanogenesis (Joabsson et al., 1999; Ström et al., 2003). Acetate exudation per gram root can vary considerably between plant species. For instance, *Eriophorum vaginatum* may release over seven times more acetate than *Carex rostrata* and *Juncus effusus* (Ström et al., 2005). The release of labile organic carbon could fuel methanogenesis not only in the sediment, but also in the oxic water column, as has been suggested for algae in rivers and lakes (Bogard et al., 2014; Donis et al., 2017; Mei et al., 2020). Besides enhancing methanogenesis, root exudates may suppress CH_4 oxidation by competition for electron acceptors, as was found in a thermokarst bog (Turner et al., 2020).

In addition to producing organic matter that can serve as a precursor for methanogenesis, aquatic vegetation can increase sedimentation rates by reducing water flow velocity and turbulence (Sand-Jensen and Pedersen, 1999; Clarke, 2002). In particular, fine organic sediments form an optimal environment for methanogens due to high sediment surface area and a high potential for microbial biofilm formation (Sanchez et al., 1994; Grasset et al., 2019; Bodmer et al., 2020). Methanogenesis may therefore be enhanced in vegetated areas of water bodies due to high sedimentation rates (Kankaala et al., 2005; Crawford and Stanley, 2016).

An additional CH_4 production pathway could be oxic, non-enzymatic production of CH_4 within plants (Keppler et al., 2006; Bruhn et al., 2012). This process has been observed in living and litter material of several terrestrial plant species and is likely related to the oxic chemical breakdown of pectin when a plant is exposed to UV radiation or other stressors (Keppler et al., 2008; Wang et al., 2011). This process has been suggested to take place in macrophytes as well (Hilt et al., 2022).

2.2 CH_4 oxidation

Aerobic CH_4 oxidation (i.e., consumption), performed by methane-oxidizing bacteria, is most extensive at the oxic–anoxic interface where both O_2 and CH_4 are available (Bastviken, 2009). Plants affect CH_4 oxidation by radial oxygen loss (ROL) in the root zone (potentially related to photosynthesis), CH_4 oxidation by epiphytic and endophytic methanotrophs, and O_2 availability in the oxic water or sediment layer (Figure 1).

To overcome anoxia-related problems in waterlogged soils, many vascular wetland plants transport oxygen from their shoots to below-ground tissues. O_2 is transported within gas-filled aerenchyma via diffusion and/or pressurized flow (Armstrong, 1980; Colmer, 2003; Vroom et al., 2022). This process supplies O_2 to roots and rhizomes and can also result in radial O_2 loss (ROL) to the rhizosphere. ROL enables the detoxification of harmful substances (e.g., sulphide), enhances nutrient uptake, and alters the microbial community structure (Galand et al., 2005; Robroek et al., 2015). The increased O_2 availability in the rhizosphere enhances aerobic CH_4 oxidation (Aben et al., 2022). The importance of ROL in regulating CH_4 emissions is strongly dependent on plant species and developmental stage (van der Nat and Middelburg, 1998). For example, Ström et al. (2005) showed that *Carex*-dominated vegetation in peat monoliths emitted more than twice as much CH_4 as *Eriophorum*-dominated vegetation due to a lower degree of rhizospheric CH_4 oxidation in *Carex*. In a Patagonian bog colonized by cushion plants (*Astelia pumila* and *Donatia fascicularis*), intense CH_4 oxidation as a result of ROL suppressed CH_4 emissions completely (Fritz et al., 2011). ROL can also occur in floating plants and adventitious roots, reducing dissolved CH_4 concentrations in the water column (Visser et al., 2000; Kosten et al., 2016; Fonseca et al., 2017).

Besides enhancing CH_4 oxidation, ROL can suppress methanogenesis, as O_2 availability results in the oxidation of the alternative electron acceptors nitrate, manganese (IV), iron (III), and sulphate. The use of these alternative electron acceptors in organic matter decomposition is energetically favorable compared to methanogenesis. O_2 release in the rhizosphere can, therefore, indirectly repress methanogenesis, depending on the pool of alternative electron acceptors and the magnitude of ROL (Laanbroek, 2010).

The presence of vegetation can alter O_2 concentrations not only in the sediment but also in the water column. Floating vegetation forms a barrier at the water-air interface, limiting gas exchange. This reduces O_2 diffusion into the water column and dissolved CH_4 release to the atmosphere (Attermeyer et al., 2016; Kosten et al., 2016). Additionally, light limitation by overlying vegetation can reduce O_2 supply by primary production, thereby potentially reducing CH_4 oxidation (King, 1990). On the other hand, the lower light intrusion may also increase CH_4 oxidation by preventing light inhibition (Thottathil et al., 2018). The physical barrier formed by floating plants also captures bubbles, enhancing their residence time and potential dissolution and subsequent oxidation of CH_4 (Kosten et al., 2016).

In addition to impacting microbial processes through alteration of their physical environments, certain plant species also harbor methanotrophs directly on or within their tissues. Epiphytic methanotrophs have been found on the shoots of a range of emergent and submerged plant species (Heilman and Carlton, 2001; Sorrell et al., 2002; Yoshida et al., 2014; Ávila et al., 2019). Endophytic methanotrophs have been found in *Sphagnum* mosses and several vascular peatland plants (Raghoebarsing et al., 2005; Stepniewska et al., 2018). Iguchi et al. (2019) showed that duckweed colonizing freshwater lakes are not only inhabited by methanotrophs, but the duckweed plant actually has an enhancing effect on methane oxidation. Duckweed may stimulate methanotrophic growth, presumably by contributing certain metabolites (Iguchi et al., 2019).

2.3 CH_4 transport

Besides affecting CH_4 production and consumption processes, aquatic vegetation plays a key role in CH_4 transport. On the one hand, plants can affect two main pathways of CH_4 emission from freshwater ecosystems to the atmosphere diffusion across the air-water interface and ebullition (escape of CH_4 in gas bubbles directly from the sediments to the atmosphere) (Figure 1) On the other hand, emergent rooted aerenchymous plants represent a direct conduit for CH_4 from the sediment to the atmosphere, allowing CH_4 to bypass oxidation in oxic sediment and water layers (Chanton and Dacey, 1991; Vroom et al., 2022). This has also been observed for floating plants rooting in the sediments of shallow waters (Oliveira-Junior et al., 2018). As CH_4 transport is a side effect of ROL, it can be affected by plant functional traits and the presence of pressurized flow (Brix, 1993). Similar to ROL, plant-mediated CH_4 transport is affected by, among other factors, temperature, light intensity, plant tissue porosity, ambient rates of photosynthesis, and stomatal conductance, and may therefore vary diurnally and seasonally (Yavitt and Knapp, 1995; Whiting and Chanton, 1996; Kim et al., 1999). Damage or herbivory may result in enhanced CH_4 transport: CH_4 emissions of damaged (clipped) plants increased to 160% of control values for *Carex aquatilis* (Schimel, 1995), and similar results were observed for herbivore-induced damage in a wetland plant community (Dingemans et al., 2011). This "chimney effect" has in fact been the focus of the plant impact on CH_4 fluxes and has been measured in a relatively large number of emergent and floating plant species. Although measured rates vary widely as a function of both the species and the environmental condition, overall, the results agree that emergent vegetation has the capacity to sustain extremely high fluxes of CH_4 to the atmosphere. For example, it is estimated that direct plant-mediated transport may contribute 55 to 85% to total CH_4 fluxes in peatlands (Dean et al., 2018). Analysis of paired measurements in open water and emergent vegetation in a compiled dataset of 66 lakes furthermore indicated that on a per-area basis emissions from emergent vegetation is 6.1 times higher than from open water (Kyzivat et al., 2022). However, aquatic vegetation not only affects the emission intensity, but also may affect the emission pathway. Plant-mediated transport may reduce sediment CH_4 concentrations to such an extent that it reduces ebullition. For example, in an experimental set-up with *Phragmites australis*, plant clipping resulted in a 5 to 10-fold increase in ebullition, whereas the total emission, including plant-associated transport, was about 1.8 times higher in the presence of intact plants (van den Berg et al., 2020).

2.4 Effect of plants on overall CH_4 emissions: a whole habitat perspective

The effect of aquatic plants on the whole habitat CH_4 budget is at present difficult to predict, because as discussed in the sections above, the presence of plants influences CH_4 dynamics and emissions in multiple ways, and in addition, there have been relatively few studies that have assessed the complete CH_4 budget of vegetated habitats in freshwaters. The common denominator of studies that have assessed total CH_4 fluxes from vegetated habitats in lakes and wetlands is that these tend to be high relative to adjacent, non-vegetated sites and to open water, pelagic habitats (Kankaala et al., 2004; Larmola et al., 2004; Wang et al., 2006; Marinho et al., 2015; Jeffrey et al., 2019; Desrosiers et al., 2022). It is interesting to note that whereas total CH_4 emissions tend to be consistently high in vegetated habitats, the pathways that contribute to these emissions are highly variable. For example, Jeffrey et al. (2019) reported an average annual contribution of plant-mediated fluxes to total habitat CH_4 emissions of around 59% in a tropical wetland dominated by floating lilies, with diffusion and ebullition each accounting for roughly 20%, and studies in temperate vegetated lake habitats have also reported dominance of direct plant-mediated fluxes (Chu et al., 2014). A recent study showed that in vegetated habitats in a boreal lake colonized by *Typha* sp., ebullitive and diffusive fluxes were suppressed because their dense root mats acted as both a barrier for the vertical flux of bubbles and also greatly suppressed turbulence, yet CH_4 emissions from the habitat were nevertheless extremely high, driven by direct plant-mediated CH_4 transport (Desrosiers et al., 2022). In contrast, in an adjacent vegetated habitat in the same lake dominated by the rooted, floating *Brassenia* sp., the authors reported extremely high ebullitive fluxes, presumably driven by plant-enhanced sediment methanogenesis, with direct plant-mediated fluxes contributing much less to total CH_4 fluxes in this habitat (Desrosiers et al., 2022). Ebullitive flux was reported to be of the same magnitude as plant-mediated emissions at the outermost *Phragmites* reed band but contributed much less within the *Phragmites* bed in a boreal lake (Kankaala et al., 2004), and Marinho et al. (2015) also reported elevated rates of CH_4 ebullition in littoral habitats of tropical lake colonized by the emergent *Schoenoplectus californicus*, yet total CH_4 emissions were nevertheless dominated by diffusion. The pattern that emerges is that the dominant pathway of CH_4 emission may vary greatly between ecosystems and even between habitats within the same ecosystem, as a function of the plant functional type and density, sediment and water properties, and other environmental factors, and also seasonally with plant succession and climatic factors. Direct plant-associated transport often dominates the CH_4 budget in these habitats, but not always depending on the season and dominant plant type. Modeling and upscaling total CH_4 fluxes from vegetated freshwater habitats is therefore challenging, involving multiple pathways and complex interactions, yet this is important because regardless of what the main pathways of emission are, there is increasing evidence that vegetated habitats in lakes, wetlands and rivers, tend to contribute disproportionately to whole ecosystem emissions (Juutinen et al., 2003; Desrosiers et al., 2022). The large influence of vegetated habitats on overall CH_4 fluxes extends to seasons when plants may not be present. For example, the vegetated littoral contributed disproportionately (66–78%) to winter CH_4 emissions from two boreal lakes (Larmola et al., 2004).

2.5 Methods to assess CH_4 fluxes of vegetated areas

A wide variety of methods have been used to assess CH_4 fluxes in vegetated areas, all with different strengths and drawbacks. The main differences between the approaches are the different CH_4 flux pathways that they incorporate, and the spatial and temporal resolution of this coverage (Table 1). These approaches can be grouped into four main categories: (1) Those that quantify the plant-associated fluxes with whole plant chambers (Figure 2A), and those focusing on plant-mediated fluxes including submerged whole plant chambers (Figure 2B), leaf chambers (Figure 2C), inverted water filled bottles to capture stem flux (Figure 2D), stacked chambers to capture both submersed and emergent plant fluxes (Figure 2E), gas sampling from plant tissue (Figure 2F), experimental determination of diffusion potential of specific plant parts (Figure 2G), porewater sampling to determine potential root transport (Figure 2H) and incubation of plant material to measure potential CH_4 production (Figure 2I); (2) approaches to determine ebullitive fluxes, which include inverted funnels (Figure 2J) and porewater sampling (Figure 2H); (3) approaches to quantify diffusive fluxes, which include floating chambers (Figure 2A) and measurements of gas concentration in the surface water combined with gas exchange (Figure 2K); (4) approaches to estimate whole habitat CH_4 emissions, which include eddy covariance towers (Figure 2L). Note that some of these approaches overlap: Floating chambers, which are typically used in aquatic studies to measure diffusive fluxes and gas exchange, have also been used to determine ebullition and plant-mediated fluxes, whereas porewater sampling has been used for multiple purposes, including quantification of sediment CH_4 production, diffusion from sediment, ebullition, and plant-mediated transport.

TABLE 1 **Summary of methods used to determine CH_4 fluxes of vegetated areas with some examples of method related pros and cons.**

Method	Description	Pros	Cons	Exemplary references
Chamber (Figure 2A)	Transparent plexiglass chamber with a fan placed over the vegetation (floating or on a frame/base; measurement of headspace CH_4 increase over time)	Relatively straight forward, enables multiple measurements across different vegetation within reasonable time	Captures a mix of plant-mediated CH_4 and diffusive CH_4 fluxes (and potentially ebullition)	Joabsson and Christensen, 2001; Öquist and Svensson, 2002; Ribaudo et al., 2012; Davidson et al., 2016
Submerged chamber (or bag) (Figure 2B)	Capturing CH_4 release of submerged plants by submerged bags (e.g., made of a multi-layer clear film of saran and PVC with low CH_4 permeability)	Captures specifically plant-mediated CH_4 flux	Labor and time intensive, only individual submerged plants can be measured	Dacey and Klug, 1979; Heilman and Carlton, 2001
Leaf chamber (Figure 2C)	Transparent plastic storage boxes sealed with rimmed weather stripping and large binder clips (measurement of headspace CH_4 increase over time)	Enables targeting specific parts of a plant	Generalization of fluxes to vegetated habitat area is limited	Villa et al., 2020
Inverted water-filled vial (Figure 2D)	Clipping of main stem and placing an inverted water-filled vial over it (leaving vial for a defined amount of time)	Enables targeting specific parts of a plant	Intrusive method with potential effect of clipping deviating from natural plant-mediated CH_4 flux	Sanders et al., 2007
Stacked chamber (Figure 2E)	Installing two chambers with different diameters: larger one covering water surface with lid sealed around the plant, smaller one only enclosing plant	Clear distinction of diffusive and plant-mediated CH_4 flux possible	Dealing with different vegetation and vegetation heights is challenging	Butterbach-Bahl et al., 1997; van Bodegom et al., 2001
Gas sampling from plant tissue (Figure 2F)	Measurement of CH_4 concentration within plant stem (e.g., 1 cm below the waterline via a syringe)	Enables targeting specific plant parts	Converting concentrations to fluxes requires several assumptions; generalization of fluxes to vegetated habitat area is limited	Chanton et al., 1992, 1993
Diffusion potential of specific plant parts (Figure 2G)	A single plant part (e.g., leaves, panicles, nodes, or internodes) is inserted in the hole of a rubber stopper fitted onto a flask filled with CH_4 enriched water; the flask stands in a water-filled container to provide a water lock for the chamber covering the plant part. CH_4 emission rates are determined by temporal increase in concentration in the chamber.	Enables targeting specific parts of the plant	As plant parts are detached, diffusion potential may be altered; generalization of fluxes to vegetated habitat area is limited	Wang et al., 1997
Porewater sampling (Figure 2H)	Sampling of CH_4 concentration in porewater near and away from roots (with vials connected to rhizons)	When combined with flux measurements, it provides insight in plant effects on processes within the sediment	Estimating the effects of plants on CH_4 fluxes based on this method requires several assumptions	van der Nat and Middelburg, 2000; Davidson et al., 2016
Bottle incubation (Figure 2I)	Measuring plant-associated CH_4 production and/or oxidation by incubating in the dark, e.g., roots, rhizomes, or tillers in glass bottles measuring headspace CH_4 partial pressure over time	Enables to manipulate environmental variables; enables targeting specific parts of the plant	As plant parts are detached processes may be altered; generalization of fluxes to vegetated habitat area is limited	Frenzel and Rudolph, 1998
Inverted funnel (Figure 2J)	Using an inverted funnel to trap, and measure volume and concentration of CH_4 bubbles (e.g., placed at the surface and a deeper depth)	Insight into effects on plant-associated effects on ebullition	Only covers ebullition; when applied in areas with floating vegetation it is unclear if bubbles captured by the funnel would reach the atmosphere or be trapped in the plants	Sugimoto and Fujita, 1997; Sanders et al., 2007; Flury et al., 2010
Concentration measurement and k value (Figure 2K)	Developing a model based on laboratory and field results to estimate the gas exchange coefficient based on temperature and wind speed.	Concentration measurements are fast, enabling multiple measurements across different vegetation within reasonable time	Assessing gas exchange coefficient is complex and strongly plant-cover and wind dependent	Barber et al., 1988
Eddy covariance (EC) flux tower (Figure 2L)	Place in such a way that the EC footprint represents vegetated and/or unvegetated areas	Efficient way of assessing integrative CH_4 flux from vegetated areas	Costly; footprint varies with wind speed and direction complicating attribution of fluxes to vegetated area; not applicable for small vegetation patches	Kim et al., 1998; Chu et al., 2014; van den Berg et al., 2020

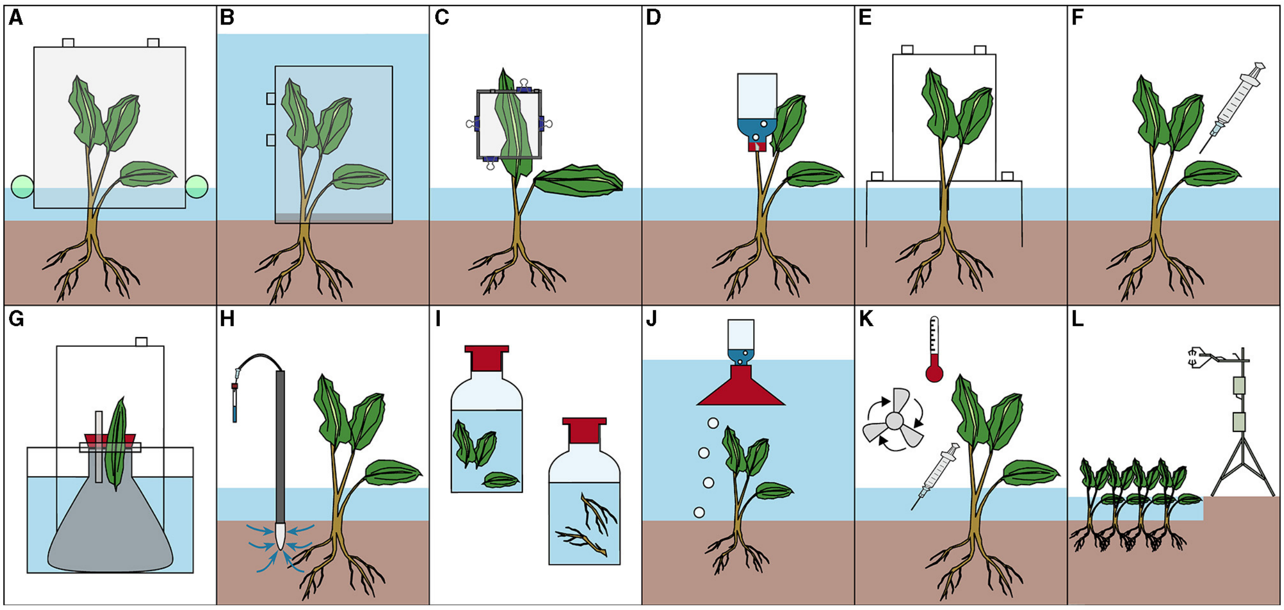

FIGURE 2
Methods to investigate CH_4 fluxes of vegetated areas (field and laboratory): Chamber **(A)**, Submerged chamber **(B)**, Leaf chamber **(C)**, Inverted water-filled vial **(D)**, Stacked chamber **(E)**, Gas sampling from plant tissue **(F)**, Diffusion potential of specific plant parts **(G)**, Porewater sampling **(H)**, Bottle incubation **(I)**, Inverted funnel **(J)**, Concentration measurement and k value **(K)**, Eddy covariance flux tower **(L)**.

3 Analysis of extant data from vegetated areas in freshwaters

In this section we discuss existing plant-associated CH_4 fluxes of a semi-quantitative literature search. Specifically, we discuss a compilation of the frequency of measurement approaches used and their specificities and limitations. In addition, we provide an overview of flux intensities associated with vegetated habitats among aquatic ecosystems, seasons, and plant types, and geographic regions.

3.1 Literature review and data compilation

To obtain an overview of studies on CH_4 fluxes of vegetated areas in inland waters, we used two approaches. First, we selected four key papers (cited at least 200 times in Google Scholar; 4th of April 2023) dealing with the topic in distinct ways: Laanbroek (2010), reviewing microbial processes, Brix et al. (1996), focusing on *Phragmites*, Sebacher et al. (1985), investigating a large range of aquatic plants, and Ström et al. (2005), focusing on carbon turnover in multiple wetland plant species. We then exported the references citing these key papers. Secondly, a literature search was carried out using Web of Science on the 4th of April 2023. Search inquiry for Web of Science consisted of the following keywords: *plant** or *macrophyte** and *aquatic* or *freshwater*, and *methane* (asterisks where used to consider singular and plural), *mediated,* and *methane.* The combination of keywords resulted in the following formula: "TS = ((plant* OR macrophyte*) AND (aquatic OR freshwater) AND methane)" TS = (plant* AND mediated AND methane), TS meant that the search was done in the title, keywords, and the abstract of research papers. The search terms were used with no restriction on publication year. Lastly, we added papers from an earlier search with slightly different keywords (see Bodmer et al., 2021) and other relevant papers that we encountered while evaluating above-mentioned papers.

The data from the search inquiry, together with studies that had cited above mentioned key papers and the additional papers, were integrated into a database, and we retained CH_4 flux data that were not associated to experimental manipulations (e.g., nutrient additions). We point out that the data collected in our search have been derived from papers that focused mostly on determining direct, plant-associated CH_4 fluxes, usually of individual plant taxa, sometimes of mixed stands. There is a limited number of studies that have focused more broadly on various pathways of CH_4 emission in vegetated habitats in inland waters, and there is often overlap between these two categories since the latter sometimes also determine direct plant-associated fluxes. Although we have not quantitatively reviewed other CH_4 related processes in vegetated habitats (e.g., ebullition) because of the sparseness of available data, we do discuss the potential significance of these processes in the section below. Data were taken from the main text or from the Supplementary material of the retained papers. If the relevant data was not reported in the text, we used the WebPlotDigitizer tool (https://automeris.io/WebPlotDigitizer/) to read values from graphs. Some studies reported CH_4 emissions e.g., under different circumstances or plant genera and hence have multiple entries, whereas other studies only reported averages of multiple observations and hence have only one entry in the database. Non-English and non-peer-reviewed papers were excluded, the rest of the papers were screened according to the title (if the title was not clear, the abstract was screened). If publications did not include original CH_4 flux data (e.g., reviews) or did not include vegetation, we did not include them in the dataset. Additionally, we constrained this review by focusing on natural freshwater ecosystems or mesocosms mimicking natural systems. Hence papers on rice fields, constructed wetlands receiving wastewater, and water treatment facilities were not considered. Although we excluded papers dealing with CH_4 fluxes from rice fields from our vegetated habitat flux database, we did review the methods used in rice field research and discuss their applicability in other freshwater systems.

Based on the data from relevant articles (188), we compiled a database with specific information (437 entries), including the genus of the dominated plant, range of CH_4 fluxes, description of study site, and—when applicable—the type of experimental approach. To explore the geographical distribution of the studies, climate zones were assigned according to the latitude of reported coordinates: 60–90° northern; 60–40° temperate; 40–20° subtropical; 20–0° tropical (Delwiche et al., 2021). For experimental studies (e.g., based on mesocosms), we considered the location of the experiment, which does not necessarily represent the geographical location of the mimicked ecosystem.

3.2 Data analysis

After compiling the data obtained from the literature, we conducted the following steps: First, for 37% of the 437 entries, we calculated the average for each entry when this was not given (but when a range was published, for example). This was done by using the minimum and maximum value (geometric mean to consider mostly skewed data; applied in 31% of the cases), a time range presented (60%) or from replicates (9%). Second, all fluxes were converted to mg CH_4 m^{-2} d^{-1}. Third, we classified studies into three main groups: running waters (stream + river), lakes (ponds + lakes), and wetlands (bog + marsh + fen + mire + swamp).

In a first linear mixed-effect model (LME), we tested the fixed effects ecosystem type (running waters, lakes, wetlands), study period (growing, non-growing), plant type (emergent, submerged, floating), and climate zone (northern, temperate, subtropical; tropical) on CH_4 fluxes of vegetated areas (response variable). In a second LME, we zoomed in on the emergent plants, for which we had most data. We tested the fixed effects plant genus (48 individual genera), ecosystem type (lakes, wetlands; there were no studies of emergent plants in running waters), study period (growing, non-growing season), and climate zone (arctic, boreal, temperate, tropic) on CH_4 fluxes of vegetated areas (response variable). We used the "lmer" function of the R-package "lme4" (Bates et al., 2015) with Maximum Likelihood estimation. For the LMEs, we included study ID as a random effect on the intercept to account for the fact that one study can have multiple entries. Statistical significances of fixed effects were assessed with likelihood ratio tests using the function "drop1" (Zuur et al., 2009). The LMEs were followed by a model validation, checking the residuals for normal distribution and homogeneity of variances. For both LMEs, we transformed the response variable [log10(plant_flux) + min(plant_flux) + 1] to improve the model performance and validity. Both LMEs were followed by a pairwise comparison posthoc test (Tukey adjustment for multiple comparisons), comparing the individual levels of the significant fixed effects using the R-package "emmeans" (Lenth, 2019).

3.3 Geographical distribution of studies and methods used in the literature

We found that out of the screened literature (a total of 188 studies, 437 entries), the majority of studies used chamber measurements (162 studies; 382 entries), mostly with the objective of determining plant-associated fluxes. In a practical sense, this method seems straightforward, but it comes along with certain issues. Firstly, it is difficult to place the floating chamber on top of emerging and floating vegetation without disturbing the plants. Disturbance of vegetation may liberate gas bubbles therefore artificially inflating emissions; in addition, the chamber alters moisture, light, temperature, and carbon dioxide (CO_2) concentrations which impacts stomata and may consequently influence CH_4 fluxes. Secondly, often the chamber does not capture the plant's entire root system; when part of the root system exchanges gas with the overlying water outside the chamber area or other plant shoots with which they are connected (e.g., in case of Typha), these fluxes may be missed (e.g., Bansal et al., 2020). Thirdly, and more importantly, fluxes measured in floating chambers integrate direct plant-associated, diffusive water-atmosphere and potentially ebullitive pathways that are not always easy to differentiate, although some studies have attempted to disentangle these pathways, for example by modeling diffusive fluxes based on surface water concentrations (e.g., Desrosiers et al., 2022). The stacked chamber approach, used in rice studies (Butterbach-Bahl et al., 1997; van Bodegom et al., 2001) could be used to better differentiate between actual plant-associated CH_4 fluxes, diffusion, and/or ebullition, avoiding the potentially misleading integration discussed above. The diffusion potential method (Wang et al., 1997) can be used to scan for possible within-plant hotspots of CH_4 flux, but these approaches have been applied much less frequently.

The remainder of the studies used one or more of the other approaches listed in Table 2, sometimes singly, often in combination: porewater sampling (17 studies; 27 entries), eddy covariance flux tower (14 studies; 23 entries), inverted funnel (12 studies; 22 entries), concentration measurement and k value (9 studies; 18 entries), gas sampling from plant tissue (6 studies; 10 entries), bottle incubation (3 studies; 11 entries), submerged chamber (3 studies; 4 entries), leaf chamber (1 studies; 3 entries), and inverted water-filled bottles (1 study; 1 entry). Most of these approaches, but not all, target direct plant-associated fluxes, so they are not all strictly comparable, and there are very few studies that have reported the total CH_4 emission from vegetated habitats (i.e., diffusive + ebullitive + plant-mediated).

Of the reviewed studies (188 studies, 437 entries; 7 studies contained a field and mesocosm component), most were performed in the field (157 studies; 333 entries) compared to mesocosm experiments (38 studies; 104 entries). Studies on all scales are valuable to both obtain mechanistic understanding and enable

TABLE 2 Results of the linear mixed model testing effects of ecosystem type (running water, lake, wetland), study period (growing, non-growing), plant type (emergent, floating, submerged), climate zone (arctic, boreal, temperate, tropic) on CH_4 fluxes of vegetated areas (A), and testing the effects of plant genus (48 individual genera), ecosystem type (lake, wetland), study period (growing, non-growing), and climate zone (arctic, boreal, temperate, tropic), on CH_4 fluxes of vegetated areas of emergent plants (B).

Response variable	Fixed effect	χ^2 (1)	*p*
(A) Testing combined CH_4 fluxes of vegetated areas			
CH_4 fluxes of vegetated areas*	Ecosystem type	3.12	0.210
	Study period	2.70	0.100
	Plant type	4.18	0.123
	Climate zone	9.62	**0.022**
(B) Testing CH_4 fluxes of vegetated areas of emergent plants			
CH_4 fluxes of vegetated areas*	Plant genus	139.68	**<0.001**
	Ecosystem type	0.27	0.602
	Study period	2.28	0.131
	Climate zone	7.77	0.051

Study ID was included as a random effect on the intercept. Significances of fixed effects were assessed with likelihood ratio tests with degrees of freedom = 1. Significant p values <0.05 are in bold.

*Transformation: log10 (CH_4 fluxes of vegetated areas + abs (min (CH_4 fluxes of vegetated areas)) +1); (A) Marginal R^2 = 0.049, conditional R^2 = 0.628, sample size = 363; (B) Marginal R^2 = 0.233, conditional R^2 = 0.777, sample size = 320.

upscaling efforts. Furthermore, mesocosm experiments can be used to simulate running waters/flow conditions, which would help to constrain and to understand CH_4 fluxes of vegetated areas in running waters.

From the 188 compiled studies (of which seven studies were performed on two continents), 79 were performed in North America (162 entries), followed by 67 in Europe (171 entries), and 36 (84 entries), 7 (10 entries), 5 (9 entries), and 1 (1 entry) in Asia, South America, Oceania, and Africa, respectively (Figure 3). For some regions we found but one study—e.g., Africa, and in other regions there are only a handful of studies conducted, e.g., in South America (e.g., Silva et al., 2016; Oliveira-Junior et al., 2020), yet this is where some of the most extensive inland aquatic systems are located (e.g., Amazon and Pantanal). In addition, there is a strong bias toward growing season-only data and focus on a small subset of genera and plant types. These biases all contribute to the large uncertainty of freshwater systems in global CH_4 budgets (Saunois et al., 2020). Consequently, our current understanding of the magnitude of CH_4 fluxes of vegetated areas is strongly biased.

3.4 CH_4 flux intensity and variability from vegetated areas

Although our systematic literature review points to major spatial and temporal data gaps, and differences in methods that complicate data comparisons, we nevertheless attempt here to provide an overview of the extant CH_4 flux estimates for freshwater vegetated habitats. We should reiterate that most of the data that we were able to collect were derived from chamber-based measurements involving emergent plants, which likely include both water-atmosphere diffusive fluxes that are more or less impacted by the plants and direct plant-mediated fluxes. These literature fluxes do mostly not fully capture ebullitive fluxes, and therefore likely significantly underestimate total CH_4 emissions from these vegetated habitats, as we have discussed in previous sections.

From an ecosystem perspective, of total 188 studies (437 entries; seven studies were performed in two different ecosystems), 156 were carried out in wetlands (357 entries), whereas only 37 (78 entries) in lakes and 2 (2 entries) in running waters. This implies that the available data are strongly imbalanced in terms of the habitats covered, and there is a clear need for more studies in standing and running waters.

CH_4 fluxes of vegetated areas ranged from−8.6 (uptake) to 2835.8 (emission) mg CH_4 m^{-2} d^{-1} {65.0 (9.3, 194.4); median [interquartile range (IQR)]} in wetlands, from 0.2 to 971.8 mg CH_4 m^{-2} d^{-1} [86.1 (28.0, 235.0)] in lakes, and from 5.4 to 39.0 mg CH_4 m^{-2} d^{-1} in running waters [22.2 (13.8, 30.6)] (Figure 4). There was no significant effect of ecosystem type on CH_4 fluxes of vegetated areas, whereas climate zone was a significant driver (p = 0.022; Table 2A).

Of all the 188 studies (437 entries), only 11 studies (16 entries) are from the non-growing season, compared to 146 studies (347 entries) performed in the growing season, while 36 studies (69 entries) include measurements throughout the year. The very similar median fluxes (Figure 5) in the growing and non-growing season calls for more attention to CH_4 fluxes of vegetated areas outside the growing season. For example, the genus *Phragmites* does not grow in winter but may facilitate CH_4 emissions by creating a direct pathway or "chimney" from the sediments to the atmosphere while the water column is sealed off from the atmosphere by ice. Fluxes outside the growing period may be considerable and need further attention.

Study period did not significantly influence CH_4 fluxes of vegetated areas (p = 0.100; Table 2A) with fluxes ranging from−8.6 to 2835.8 mg CH_4 m^{-2} d^{-1} (62.0 [9.0, 203.3]) in the growing season, and from 0.1 to 553.2 mg CH_4 m^{-2} d^{-1} (51.4 [7.7, 140.0]) in the non-growing season (Figure 5). Also, when we zoom in on emergent macrophytes alone, we find no significant effect of study

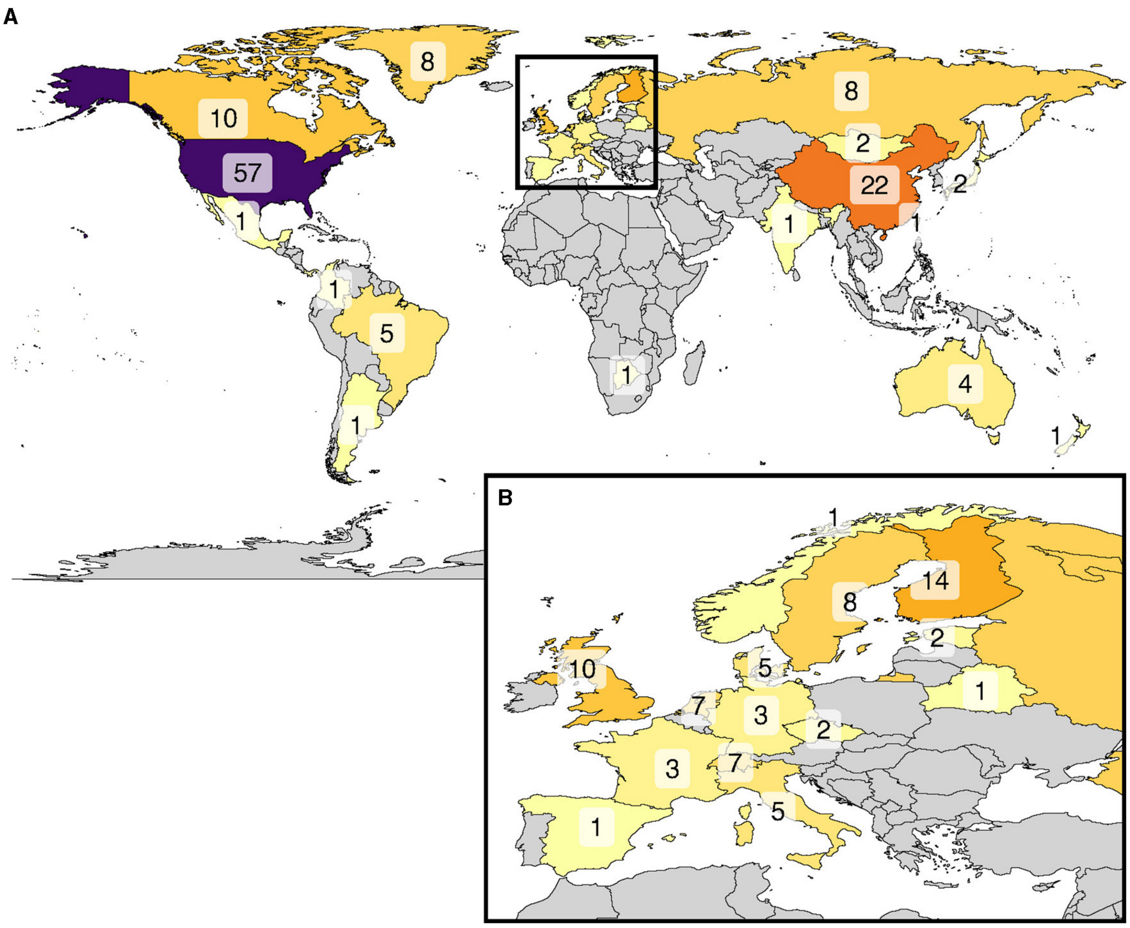

FIGURE 3
Geographical distribution of studies related to CH_4 fluxes of vegetated areas **(A)** with a zoom-in of Europe **(B)**. The number of studies is indicated on the respective countries accompanied by different color intensities indicating the higher frequency (higher color intensity) and lower frequency (lower color intensity) of performed studies. Grey areas indicate no available studies according to our literature search parameters.

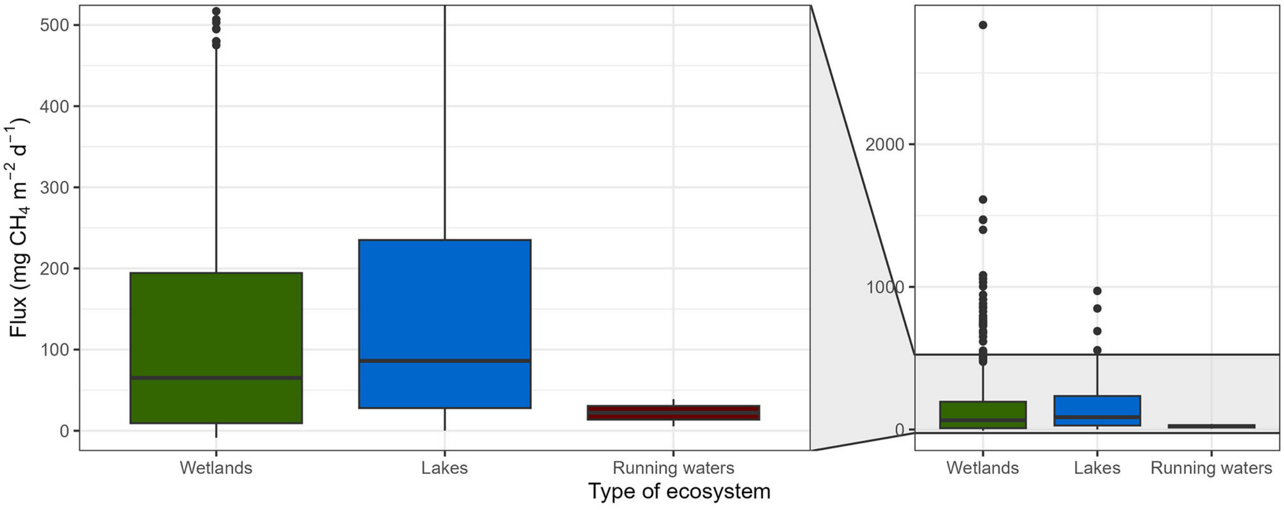

FIGURE 4
CH_4 fluxes of vegetated areas of different ecosystem types (wetlands, lakes, and running waters). Boxplots represent median (black line), first and third quartiles (hinges), range (whiskers), and outliers (black dot).

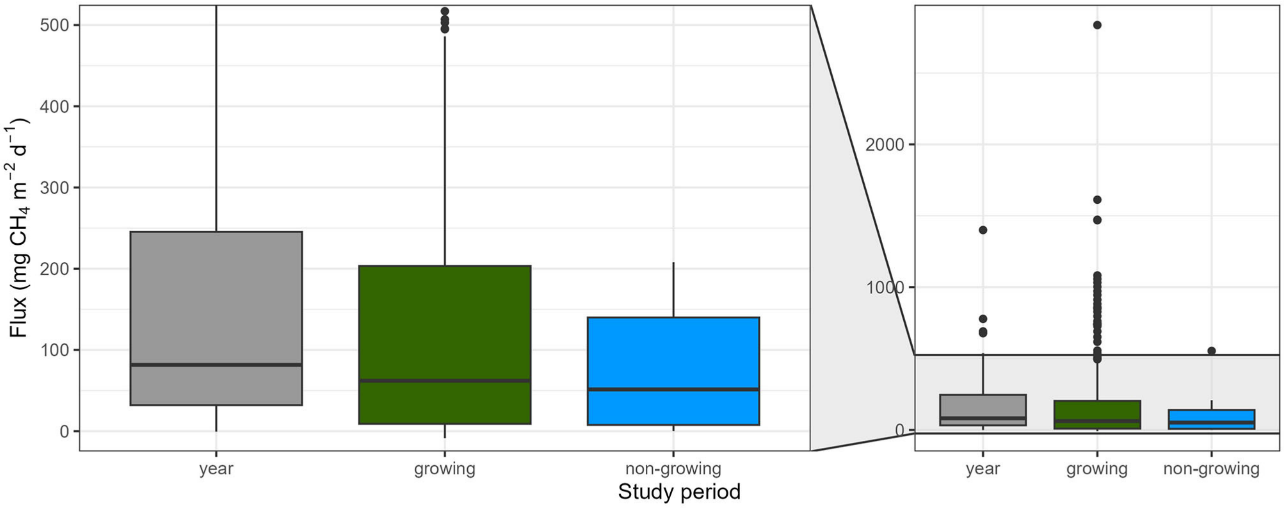

FIGURE 5
CH$_4$ fluxes of vegetated areas from different plant types combined, measured in 3 different seasons (growing and non-growing season, and year-round studies). Boxplots represent median (black line), first and third quartiles (hinges), range (whiskers), and outliers (black dot).

period ($p = 0.131$; Table 2B). One explanation for the absence of a significant effect might be that organic matter supply rate (Grasset et al., 2021), e.g., due to dying vegetation, could actually be more relevant in driving CH$_4$ production and emissions than the actual presence of growing plants. Alternatively, there may be geographic biases location of annual studies that minimize potential seasonal differences. Regardless, these annual patterns certainly deserve more attention.

There was a strong imbalance in the focus on different plant growth forms/types, with the majority of studies focusing on emergent plants, with only a few studies focusing on floating plants and barely any on submerged vegetation (Figure 6).

The fluxes for habitats with emergent plants ranged from−8.6 to 2835.8 mg CH$_4$ m^{-2} d^{-1} (66.7 [12.2, 194.6]), for floating plants from 3.9 to 1612.3 mg CH$_4$ m^{-2} d^{-1} [74.0 (17.7, 365.4)], and for submerged plants from 4.2 to 457.3 mg CH$_4$ m^{-2} d^{-1} [48.6 (15.7, 184.7)]. Fluxes from mixed stands ranged from 4.2 to 9.9 mg CH$_4$ m^{-2} d^{-1} [7.1 (5.6, 8.5)] (Figure 6). These differences however did not lead to a significant effect of plant type on CH$_4$ fluxes of vegetated areas ($p = 0.123$; Table 2A). This result underlines that none of the plant types is of lesser importance in terms of CH$_4$ emissions. Different processes may underlie the high emissions from areas with floating plants, particularly the low oxygen conditions below the floating plants resulting from the inhibition of water column photosynthesis and the decreased oxygen exchange imposed by floating plants (see also Section 2). The low oxygen availability in the water column and sediment creates favorable circumstances for methanogenesis and may impede CH$_4$ oxidation and thus large CH$_4$ build up. When floating plants are rooted in the sediment, connecting sediments and bottom waters with high CH$_4$ concentrations directly to the atmosphere through plant-associated transport, emissions may be particularly high (Oliveira-Junior et al., 2018, 2020). However, only a small fraction of studies indicated whether the studied floating plants were free-floating or rooted in the sediment. Especially since some species can be both rooted or not rooted (see e.g., Oliveira-Junior et al., 2020), this information should be definitely better considered and reported in future studies.

Within the emergent plants (384 entries), most data are from mixed plant stands (32.3%), followed by *Carex* (16.1%), *Eriophorum* (8.9%), *Phragmites* (8.6%), and *Typha* stands (5.2%). Not surprisingly, as seen in the distribution of the studies (Figure 3), emphasis has been on plants widely occurring in the subarctic, boreal and temperate regions. The remaining 43 genera/combination of genera represent <4.0% of the entries (Supplementary Table S1). Within floating plants (33 entries), 32.3% of the data are from the genus *Nuphar*, followed by *Eichhornia* (21.2%), mixed plant stands (12.1%), and *Nelumbo*, *Nymphaea*, and *Trapa* with 9.1% each (Supplementary Table S1). Finally, most data for submerged plants (18 entries) are from *Myriophyllum* (33.3%), and *Ceratophyllum*, *Ranunculus*, and *Vallisneria* with 11.1% each (Supplementary Table S1).

CH$_4$ fluxes from different genera within the different plant types are highly variable (Figure 7 and Supplementary Figure S1). Genus was the strongest predictor of fluxes of emergent plants in the LME run of emergent plants ($p < 0.001$; Table 2B). Hence, there are differences among genera, e.g., *Panicum* had significantly higher emissions than *Betula*, *Mimulus*, *Cassiope*, *Salix*, and *Sphagnum*, respectively (pairwise comparison posthoc $p < 0.05$). As mentioned above, there is a strong imbalance related to the number of entries of individual genera. A higher number of entries for a specific genus (e.g., for *Phragmites*) likely leads to higher variability since it has been studied in very different systems, which creates a certain bias and an imbalanced model. We are therefore currently unable to predict CH$_4$ fluxes based on occurring genera on a large scale. Given the large variability in CH$_4$ fluxes within genera it is also questionable if reasonable genera inferred predictions of CH$_4$ fluxes can be developed. Predictions made based on vegetation types—aggregating several genera at a specific site, thereby "controlling"

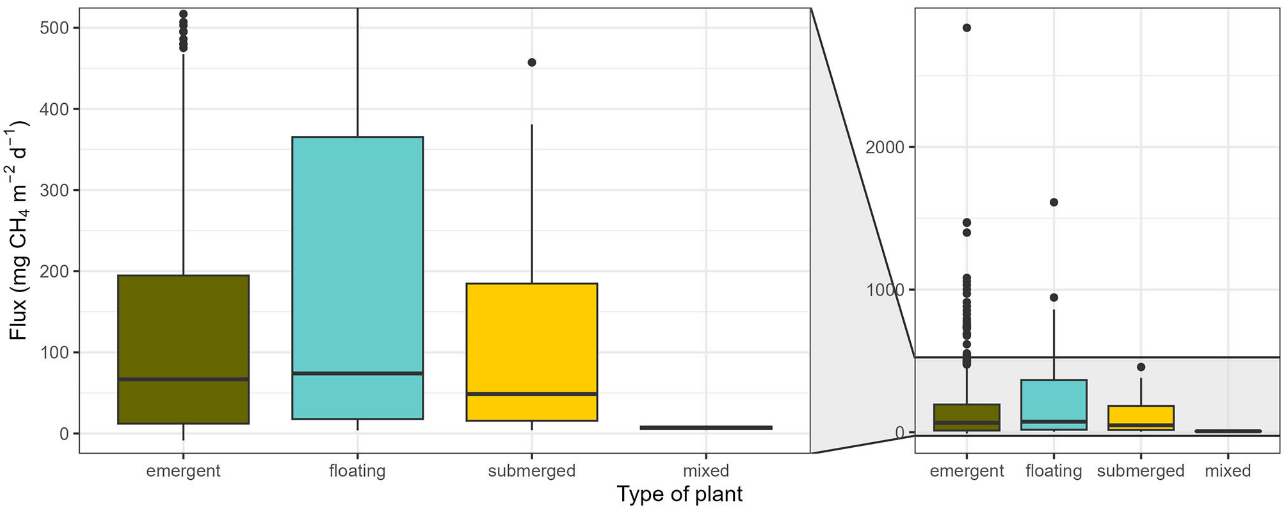

FIGURE 6
CH_4 fluxes of vegetated areas from different plant types. Emergent: 171 studies, 384 entries; floating: 22 studies, 33 entries; submerged: 8 studies, 18 entries; mixed: 1 study, 2 entries. Boxplots represent median (black line), first and third quartiles (hinges), range (whiskers), and outliers (black dot).

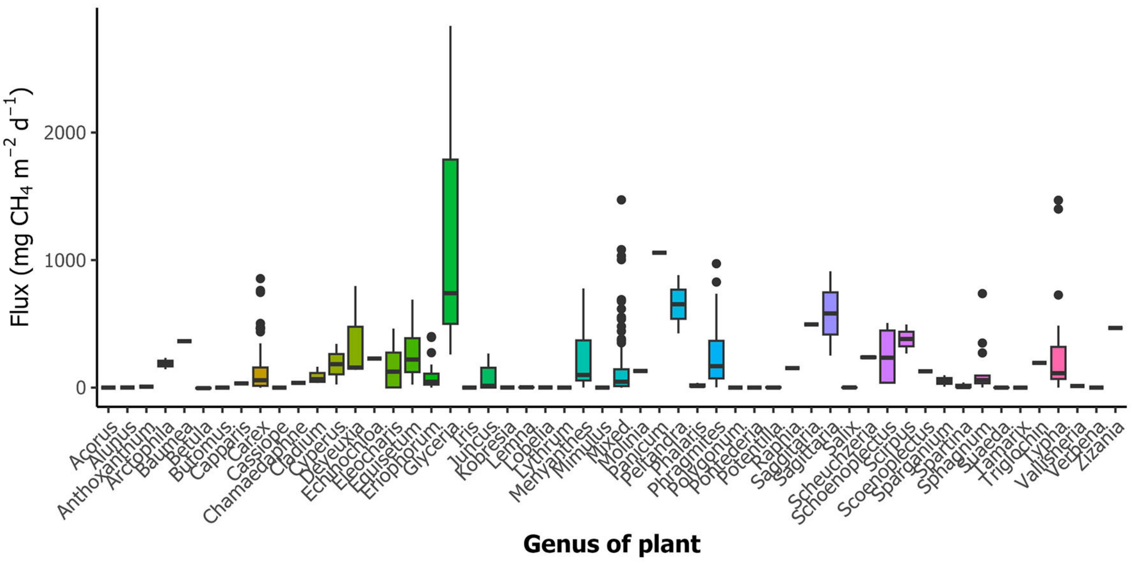

FIGURE 7
CH_4 fluxes of vegetated areas from individual genera of investigated emergent plants. Boxplots represent median (black line), first and third quartiles (hinges), range (whiskers), and outliers (black dot).

for climate and soil type—are likely more promising (see e.g., Juutinen et al., 2003; Robroek et al., 2015).

4 Plant effects on CH_4 fluxes: implications for current global CH_4 estimates from freshwaters

The extent to which CH_4 emissions from vegetated habitats have been incorporated into current local, regional, and global freshwater CH_4 budgets varies greatly and is not always specified. In the following sections we discuss some of the challenges and implications of incorporating fluxes from vegetated habitats into current global estimates of CH_4 emissions from inland waters.

4.1 Incorporating vegetated habitats into lake CH_4 budgets

Recent global lake CH_4 emission estimates range from 24.0 ± 8.4 Tg CH_4 yr^{-1} (Zhuang et al., 2023), over 41.6 ± 18.3 Tg CH_4 yr^{-1} (Johnson et al., 2022), up to 150.9 ± 73.0 Tg CH_4 yr^{-1} (Rosentreter et al., 2021). These global estimates differ in various aspects, such as lake size cut-off, global lake cartographies, upscaling approach, and consideration of seasonality and ice cover. However, these estimates have one thing in common: none of them considers plant-associated CH_4 emissions from vegetated areas. In a recent overview study on the global regulation of CH_4 emissions from lakes, the emission via vegetation is even explicitly excluded, and only open water fluxes are considered (Sanches et al., 2019). The median of plant-associated CH_4 emissions in lakes (Figure 4) is 86 mg CH_4 m^{-2} d^{-1}, i.e., 1.8 to 1.3 times higher than the median open-water lake emission estimated by Rosentreter et al. (2021; i.e., 46 mg CH_4 m^{-2} d^{-1} extracted from Figure 1) or the estimated diffusive summer emissions by Johnson et al. (2022; 68 mg CH_4 m^{-2} d^{-1}; July data extracted from Supplementary Figure S2), respectively. Vegetated areas tend to make up a considerable portion of total area of many lakes—for example the vegetated habitat (either floating, emergent, or submerged, or different combinations of these) had a median coverage of 33% in 109 lakes around the world (Zhang Y. et al., 2017). Given the consistently high emissions that characterize those areas, incorporating CH_4 fluxes from vegetated habitats will likely result in significant increases in current estimates of global CH_4 emissions.

The magnitude of plant-associated CH_4 fluxes likely varies regionally, depending on the proportion of vegetated habitat coverage. For example, Kyzivat et al. (2022) recently showed that neglecting vegetated areas leads to an underestimation of 21% of the CH_4 emission for lakes across four Arctic-boreal study areas. As pointed out in the sections above, it is important to emphasize that the median flux of 86 mg CH_4 m^{-2} d^{-1} for vegetated areas that we report here does not reflect the total CH_4 emissions of these habitats (e.g., the ebullitive flux is often missing, see Section 2.5), although it is still unclear what proportion of these emissions are accounted for by the existing data. Hence, we argue that our estimate of the importance of vegetated areas is very conservative.

4.2 Incorporating vegetated habitats into river CH_4 budgets

The current global annual CH_4 emission for rivers is estimated to be in the order of 27.9 (16.7–39.7) Tg CH_4 yr^{-1} (Rocher-Ros et al., 2023). These fluxes exclude emissions from emergent vegetation, and it is unclear to what extent they include submerged vegetation. Our literature search, unfortunately, yielded only two studies (Sanders et al., 2007; Kuhn et al., 2017) where both CH_4 emissions from vegetated river sections and unvegetated sections were explicitly included. It is therefore difficult to speculate on the relevance of vegetation for riverine CH_4 fluxes, but many rivers worldwide develop extensive vegetated habitats, particularly in lowland tropical and subtropical regions, and there is no question that global river CH_4 emissions will have to be eventually adjusted for fluxes from these habitats as new information is acquired on the extent and composition of these riverine habitats. One of the difficulties ahead is that the distinction between vegetated river habitats and wetlands is not always clear, so avoiding double accounting while effectively capturing these riverine features remains a major challenge.

4.3 Wetlands

Current estimates of global wetland CH_4 emissions are in the order of 149 Tg CH_4 yr^{-1} (Rosentreter et al., 2021), and global models of wetland-methane feedbacks indicate that wetland CH_4 emissions could play a significant role in driving 21st-century climate forcing, with global wetland emissions potentially matching or exceeding anthropogenic emissions by 2100 (Zhang B. et al., 2017). It is therefore of key importance to improve our understanding of the magnitude, regulation and sources of uncertainty of wetland CH_4 emissions, which necessarily implies a better accounting for the role of vegetation. Contrary to the situation with lakes and rivers, where vegetated habitats have been systematically excluded from estimates of whole ecosystem CH_4 emission, and therefore from global inland CH_4 budgets, wetland CH_4 budgets have variously incorporated emissions from plants and from vegetated habitats. Regional (Ito, 2021) and global (Ito and Inatomi, 2012) wetland CH_4 estimates have been derived using process-based models. For example, the VISIT (the Vegetation Integrative Simulator for Trace gases) and other wetland process models (Cao et al., 1996; Walter and Heimann, 2000; Hodson et al., 2011; Arora et al., 2018; Parker et al., 2018) have incorporated wetland CH_4 modules that integrate CH_4 diffusive, ebullitive, and plant-mediated CH_4 fluxes. The latter have been modeled on the basis of vegetation coverage and composition (e.g., Bubier et al., 1995; Dias et al., 2010; Robroek et al., 2017), and primary production of vegetation as it fuels carbon stocks that are subsequently available for decomposition. Only a handful of models have explicitly incorporated the transport through plants in wetlands (e.g., Riley et al., 2011; Ito and Inatomi, 2012; Kleinen et al., 2020). Potentially influential factors such as the impact of vegetation community composition on transport through plants, as well as plant effects on CH_4 oxidation, are generally not included in larger-scale models (but see Knoblauch et al., 2015 and Zhang B. et al., 2017, the latter included CH_4 oxidation during plant-associated transport in their global wetland model). Modeled wetland CH_4 emissions vary greatly and not always coherently (Melton et al., 2013; Ciais et al., 2014), and it is clear that there is still much to be learnt concerning the role of vegetation in CH_4 production, oxidation, and transport (Berrittella and van Huissteden, 2011; Riley et al., 2011). These uncertainties may partly underlie the large discrepancies that still exist between inverse modeling and bottom-up estimates of the global and regional CH_4 budgets, which have been at least in part attributed to problems with estimates of wetland emissions (Bohn et al., 2015; Saunois et al., 2017, 2020). These uncertainties are related to the extent of global wetland distribution, as well as to our lack of understanding of the key underlying CH_4 processes, notably the contribution of plants themselves (Bloom et al., 2017; Peltola et al., 2019). In wetlands in particular, herbaceous plants (Carmichael et al., 2014) and trees (Covey and Megonigal, 2019) are emerging as major contributors to wetland CH_4 emissions, yet their role has yet to be fully quantified and incorporated in wetland models. The literature that we collected and the statistical models we developed of plant-associated fluxes do not allow us to further speculate on a potential impact of plant associated fluxes on wetland CH_4 emissions, because on the one hand, we do not have herbaceous and tree flux data, and on the other, it is at present, very difficult to assess to what extent the aquatic plant fluxes are explicitly incorporated in current global wetland emission estimates, and if they are, how accurate they are.

5 Conclusions and outlook

CH_4 fluxes from vegetated areas in inland waters, especially in lakes and rivers, are largely understudied and neither well understood nor quantified. Our review represents, to our knowledge, the first attempt to synthesize the many ways in which submerged, floating, and emergent vegetation may influence CH_4 fluxes in different freshwater ecosystems, combined with a compilation of methodological approaches used to assess vegetation effects on CH_4-related processes. Moreover, we provide an overview of published CH_4 fluxes from vegetated habitats from various types of ecosystems across a geographical, seasonal, and vegetation types, and assess the potential significance of CH_4 fluxes from vegetated areas for global lake CH_4 emissions.

From a methodological perspective we urge for a more standardized approach of measuring CH_4 fluxes from vegetated areas. We emphasize the importance of considering not only the growing season in order to obtain more robust annual estimates, since the influence of plants extends well beyond their growing period. To specifically capture direct plant-associated CH_4 fluxes we suggest the stacked chamber method (Table 1) as the most appropriate one, since it allows to separate the direct plant-mediated emission from the diffusive flux. Further, we suggest assessing if plants are rooted or non-rooted when measuring fluxes from floating plants, since this information is relevant for future upscaling or generalization efforts. More importantly perhaps, our review highlights the need for studies that capture total CH_4 emissions from the vegetated habitats, by simultaneously measuring diffusion, ebullition, and direct plant-associated—also referred to as plant-mediated—fluxes. The few studies that have done so suggest that the magnitude of these pathways and their contribution to overall CH_4 emission can vary greatly between vegetated habitats, and therefore focusing on any given pathway yields an incomplete and biased perspective of CH_4 dynamics in these systems.

The presence of emergent and submerged vegetation influences CH_4 dynamics in multiple ways. Although it is challenging, disentangling the effects of plants on CH_4 production, oxidation, and transport is important to understand and model CH_4 emissions from vegetated areas, and particularly to predict how plants will affect future CH_4 emissions. Aerenchyma development and root organic carbon release, for instance, will respond differently to increasing atmospheric carbon dioxide levels, warmer temperatures, and altered precipitation and soil moisture patterns (Armstrong, 1980; Gregory et al., 1995; Cheng, 1999; Visser et al., 2000; Leakey, 2009) thereby influencing the plant effects on CH_4 emission in potentially synergistic but possibly also antagonistic ways. Future studies should therefore focus on vegetation-related aspects of CH_4 production, oxidation, and/or transport in the light of global and land-use change and link these processes to quantifiable plant traits as a way to facilitate modeling of CH_4 dynamics in vegetated habitats.

Although beyond the scope of this study, we recommend incorporating CO_2 and N_2O fluxes besides CH_4 pathways to fully capture the role of vegetated areas in the carbon and greenhouse gas balance of inland waters (see e.g., Aben et al., 2022). It is important to consider that these vegetated habitats, while generally being hotspots of CH_4 emission, may also take up and store significant amounts of carbon, and also have variable roles in terms of N_2O dynamics; their radiative balance can therefore only be determined if a complete GHG is carried out. For example, it has been shown that CH_4 emissions partially offset "blue carbon" burial in mangroves (Rosentreter et al., 2018), yet similar assessments in freshwater systems are scarce (but see Bastviken et al., 2011; van Bergen et al., 2019).

At present, upscaling CH_4 fluxes from vegetated areas to the ecosystem, landscape, and global scale is challenging [but see Kyzivat et al. (2022) for an example of how vegetated areas can be included on a regional scale]. We have shown here that although plant-associated fluxes are extremely variable, depending on plant type and habitat, they tend to be consistently high relative to pelagic non-vegetated areas (Desrosiers et al., 2022; Kyzivat et al., 2022), such that vegetated habitats in inland waters tend to contribute disproportionately to whole ecosystem CH_4 emissions on an areal basis. In this regard, our preliminary assessment suggests that inclusion of vegetated habitats would likely increase current estimates of global lake CH_4 emissions. We cannot at present derive a similar assessment for rivers, but in all likelihood, it will not be negligible either because many lowland rivers in the world develop extensive vegetated areas, so efforts should be made to collect the data necessary to carry out this exercise in the near future.

To narrow down estimates of the global contribution of this source depends on (i) more standardized methods with clear accounting for and disentangling of different CH_4 flux pathways or making sure that the vegetated habitat is captured as a whole, (ii) flux measurements taken across the complete geographic extent and vegetation type (i.e., emergent, floating, and submerged), and (iii) a better and more complete assessment of vegetation cover, for example using remote sensing techniques (e.g., Silva et al., 2008; Melack and Hess, 2023). General trends in plant coverage in inland waters as a function of environmental and climate change are difficult to predict (Zhang Y. et al., 2017), and differ among types of vegetation (i.e., emergent, floating, submerged) and regions. Specifically, global change seems to favor floating over submerged vegetation (Netten et al., 2011; Peeters et al., 2013) and may lead to an increase in invasive vegetation (Shih and Finkelstein, 2008; Emilson et al., 2018) which may profoundly impact CH_4 budgets of aquatic systems (Tong et al., 2012; Beyene et al., 2022). Hence, the understudied and likely globally underestimated CH_4 emissions from vegetated areas might become more relevant due to global warming, land-use change, and shifts in species distributions. CH_4 emissions from vegetated habitats are largely unaccounted for in current global estimates of lake and river CH_4 emission, and it is clear that these emissions merit more attention.

Data availability statement

The dataset compiled for this study can be found on figshare [dx.doi.org/10.6084/m9.figshare.24847161].

Author contributions

PB: Conceptualization, Data curation, Formal analysis, Methodology, Project administration, Validation, Visualization, Writing—original draft, Writing—review & editing. RV: Data curation, Validation, Visualization, Writing—review & editing, Writing—original draft. TS: Conceptualization, Data curation, Validation, Writing—review & editing. PdG: Conceptualization, Resources, Supervision, Writing—review & editing. SK: Conceptualization, Methodology, Resources, Supervision, Writing—review & editing.

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Conflict of interest

The authors declare that the research was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

Publisher's note

Supplementary material

The Supplementary Material for this article can be found online at: https://www.frontiersin.org/articles/10.3389/frwa.2023.1332968/full#supplementary-material

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