Methane Fluxes of Vegetated Areas in Natural Freshwater Ecosystems:

Assessments and Global Significance

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Abstract

Freshwater ecosystems, including wetlands, lakes, and running waters, are estimated to contribute roughly 40% to global emissions of methane (CH_4), a highly potent greenhouse gas. The emission of CH_4 to the atmosphere entails the diffusive, ebullitive, and plant-mediated pathway. The latter, in particular, has been largely understudied and is neither well understood nor quantified. We have conducted a semi-quantitative literature review to (i) provide a synthesis of the different ways vegetated habitats can influence CH_4 dynamics (i.e., production, consumption, and transport) in freshwater ecosystems, (ii) provide an overview of methods applied to study the fluxes from vegetated habitats, and (iii) summarize the existing data on CH_4 fluxes associated to different types of vegetated habitats and their range of variation. 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. We identified 13 different aspects in which plants impact CH_4 dynamics (three related to gaseous CH_4 flux pathways) and ten approaches used to study and quantify fluxes from vegetated habitats. The variability of the fluxes from vegetated areas was very high, varying from -454.4 mg CH_4 m^{-2} d^{-1} (uptake) to 2882.4 mg CH_4 m^{-2} d^{-1} (emission). 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.

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 40% to global methane (CH_4) emissions: 149 TgCH_4 yr^{-1} for wetlands and 159 TgCH_4 y^{-1} for lakes (1, 2). Estimates of CH_4 emissions are, however, highly variable, and freshwater systems present an important source of uncertainty in the global CH_4 budget (1). Of the identified natural sources, the contribution of vegetation to the global CH_4 budget is least well understood (3). This is an important caveat as studies focusing on single systems indicate that emissions from vegetated areas can contribute up to 46% of the CH_4 efflux of the entire system (4) and sometimes even surpasses 90% (5).

Clearly, the contribution of vegetated areas to the total system emission depends on the vegetation coverage on the one hand and the impact of plants on CH_4 emissions on the other. CH_4 emissions from vegetated sites can differ considerably – being higher or lower - from those from unvegetated sites (see, e.g., an overview in 6). These contrasting findings have been attributed to differences in the impact on CH_4 production, CH_4 oxidation, and CH_4 transport (7–10). The impact of vegetation on these processes varies among species (5, 11, 12) and depends on a variety of variables, including plant biomass (particularly below-ground biomass; e.g., 13), plant growth dynamics (14), plant tissue composition (8), sediment temperature (15), type of sediment (16), water depth (17) and herbivory (18) which all vary seasonally leading to seasonal differences in CH_4 emissions. This long list highlights that mechanistic understanding of the impact of plants on CH_4 fluxes is needed to accurately extrapolate single CH_4 emissions to annual emissions and upscale to system-wide or even global CH_4 emissions from vegetated areas.

Insight into the quantitative effect of vegetation on CH_4 fluxes is in part hampered by the fact that, at least up to recently, most studies have been conducted in high-latitude areas. Moreover, a wide range of different methods has been used to assess plant effects on CH_4 emissions. These methods vary in the type of fluxes they include. Some studies, for instance, explicitly exclude ebullition, while others have found that the effect of plants on ebullition can be substantial (19). These discrepancies complicate comparison among studies. The inconsistent use of the term “plant-mediated” flux further hinders comparisons. While some authors define it as the flow of CH_4 through the plant tissue (20), others use the term to indicate the overall effect of plants on CH_4 emission, i.e., a combination of different flux pathways (21, 22). While both definitions are linguistically correct, the corresponding flux intensities can vary substantially. Therefore, in this review, we refrain from using the term “plant-mediated transport” and instead refer to CH_4 fluxes of vegetated areas, acknowledging the complexity of affected aspects of vegetation in relation to CH_4 dynamics.

In this review, we aim to advance the understanding of the effect of vegetation on aquatic CH_4 fluxes, to advance the quantification of CH_4 emissions from vegetated areas, and to identify knowledge gaps. We conducted a semi-quantitative literature review to (i) provide an overview of the different ways aquatic vegetation can influence CH_4 production, consumption, and transport, (ii) provide an overview of methods applied to study the effect of aquatic vegetation on CH_4 processes, and (iii) obtain insight in CH_4 fluxes of vegetated areas and its variation. Finally, we discuss the implications of plant-habitat-mediated CH_4 fluxes for current global CH_4 estimates.

2 Material and Methods

2.1 Literature search

To obtain an overview of studies on CH_4 fluxes of vegetated areas, we used two approaches. Firstly, we selected four key papers (cited at least 200 times in GoogleScholar; 26th of November 2020) dealing with the topic: Laanbroek (23), Brix et al. (24), Sebacher et al. (25), and Ström et al. (26). We then exported the references citing these key papers. Secondly, a literature search was done using Web of Science on the 26th of November 2020. Search inquiry for Web of Science consisted of the following keywords: *plant** (asterisk was used to consider singular and plural), *mediated,* and *methane.* The combination of keywords resulted in the following formula: TS= (plant* AND mediated AND methane), TS meant that the search was done in the title, keywords, and the abstract of papers. The search terms were used with no restriction on publication year.

The data from the search inquiry, together with studies that had cited above mentioned key papers, were integrated into a database, focusing on flux data without any experimental alterations (e.g., nutrient additions). Data were taken from the main text and of supplementary material. If the relevant data was not reported in the text, we used the WebPlotDigitizer tool (https://automeris.io/WebPlotDigitizer/) to read values from graphs. One study can have multiple entries, while one entry is an average of multiple observations. 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), and some were removed due to the irrelevance of study, meaning that they were not focusing on CH_4 fluxes. Additionally, we constrained this review by focusing on natural freshwater ecosystems or mesocosms mimicking natural systems. Hence papers on rice, 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 vegetation-flux database, we did review the methods used in rice field research and discuss their applicability in freshwater ecosystems.

Based on the data from relevant articles (n = 159), we compiled a database with specific information, such as the genus of the dominant plant, as well as mean and range of CH_4 fluxes. To explore the geographical distribution of performed studies, climate zones were assigned according to the latitude of reported coordinates: 60 – 90° arctic; 60 - 45° boreal; 45 – 20° temperate; 20 – 0° tropic. 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.

2.2 Data analysis

2.2.1 Differences between types of plants and ecosystems

After compiling the data obtained from the literature, we conducted the following steps: Firstly, for 37% of the 372 entries, we calculated the average since it was not presented in the respective publications. This was done by using the minimum and maximum value (62%), a time range presented (36%), or from replicates (2%). Secondly, all fluxes were converted to mg CH_4 m^{-2} d^{-1}. Thirdly, 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 (arctic, boreal, temperate, tropic) on CH_4 fluxes of vegetated areas (response variable). Because the model with the full range of CH_4 fluxes of vegetated areas data (-454.4 to 2882.4 mg CH_4 m^{-2} d^{-1}) was not valid (i.e., residuals were not normally distributed), we built the model for the range of -96.0 to 2882.4 mg CH_4 m^{-2} d^{-1}, excluding the minimum value of the dataset (-454.4 mg CH_4 m^{-2} d^{-1}). In a second LME, we zoomed in on the emergent plants, for which we had most data. We tested the fixed effects plant genus (34 individual genera), ecosystem type (lakes, wetlands; there were no studies of emergent plants in running waters), study period (growing, non-growing), and climate zone (arctic, boreal, temperate, tropic) on CH_4 fluxes of emergent plants (response variable). We used the “lmer” function of the R-package “lme4” (27) 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” (28). 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) + 4) 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” (29).

2.2.2 Global importance

To estimate the global importance of plant effects on CH_4 fluxes in lakes, we performed a Monte Carlo simulation including and excluding the plant effects of CH_4 fluxes.

We used the following two equations for the Monte Carlo simulations (10’000 iterations):

Model A (vegetation not taken into account): $Global\ lake\ CH_4\ emission = global\ lake\ area\ * (diffusive\ CH_4\ flux + ebbulitive\ CH_4\ flux)$

Model B (vegetation taken into account): $Global\ lake\ CH_4\ emission = \big((global\ lake\ area\ - vegetated\ area) * (diffusive\ CH_4\ flux\ + ebullitive\ CH_4\ flux)\big) + (vegetated\ area\ * CH_4\ fluxes\ of\ vegetated\ areas)$

We used the global distribution of lake areas provided by DelSontro et al. (30) (based on 31), which includes the global area of lakes and impoundments, separated in eight size class bins (bin 1: 0.001 - 0.01 km^2, bin 2: 0.01 - 0.1 km^2, bin 3: 0.1 - 1 km^2, bin 4: 1 - 10 km^2, bin 5: 10 - 100 km^2, bin 6: 100 - 1000 km^2, bin 7: 1000 - 10’000 km^2, bin 8: 10’000 - 1 * 10^6 km^2). Subsequently, we subset the global dataset of diffusive and ebullitive fluxes (from 30) according to the same size class bins (both fluxes in mg C-CH_4 m^{-2} d^{-1}). For the areal vegetation coverage, we used 83 South

American shallow lakes from the Salga data set (32) and 109 lakes around the world from the data set of Zhang et al. (33). For the Salga data set, we summed the areal coverage of all three vegetation types (i.e., floating, emergent, and submerged); if the sum was higher than 100%, we fixed the value to 100%. For the Zhang data set, we calculated the average coverage (either floating, emergent, or submerged, or different combinations of these; in %) of all available years. For the CH_4 fluxes of vegetated areas, we used the lake fluxes of the compiled database of this study (in mg C-CH_4 m^{-2} d^{-1}).

As for the CH_4 fluxes of vegetated areas from our data set, we combined all data from different study periods (i.e., growing, non-growing, and all year data), as well as from all climate zones since none of these parameters has a significant effect on the CH_4 fluxes of vegetated areas (see Table 2). Although the vegetation type significantly influences CH_4 fluxes of vegetated areas (Table 2), we combined all data of different vegetation types to simplify the analysis and increase the data power (i.e., number of observations).

Both models (A and B) were run using random sampling of the Monte Carlo simulations based on the probability density functions (PDF) fit to the original data with few exceptions: We fit the ebullitive and diffusive CH_4 fluxes of the first seven bins to a PDF (ebullitive: all log-normal distribution except normal distribution for first bin; diffusive: all log-normal distribution). Bin 8 had too few ebullitive and diffusive CH_4 flux data to fit a proper PDF; hence the data were sampled from the original data. Lake CH_4 fluxes of vegetated areas and lake vegetation coverage data were as well fit to a log-normal PDF. Since fitting PDF to data also introduces negative values, we truncated the PDF at zero when negative values are physically impossible (vegetation coverage, ebullitive flux) or when no negative data were in the original data sets (diffusive fluxes as well as CH_4 fluxes of vegetated areas).

For global estimates, we summed the estimates of all eight bins for each simulation and multiplied these data times 365 days and 10^{-15}, expressing the data in Tg C-CH_4 yr^{-1}. We tested if the resulting distributions of models A and B are different with a Two-sample Kolmogorov-Smirnov test using the “ks.test” function.

We consider this global upscaling exercise as a first attempt to obtain a rough idea about the potential relevance of vegetated lake areas for global CH_4 fluxes. The advantage of using Monte Carlo simulations is that we can run the models with and without vegetation with partially the same input data, in a consistent way, and get an idea about and highlight the uncertainty of the global estimates in the form of the interquartile range. We acknowledge that figures obtained in this way should be viewed with caution due to the limited data of CH_4 fluxes of vegetated areas and areal estimates of vegetation cover in lakes.

For running waters, even less data was available, which impeded us from assessing the potential impact of vegetation on global riverine CH_4 emissions. The incorporation of vegetation in existing wetland CH_4 models varies, which we discuss in a separate section (see section 3.4.1).

All statistical analyses were performed using the statistical programming language R (34).

3 Results and discussion

3.1 The impact of vegetation on CH_4 emission

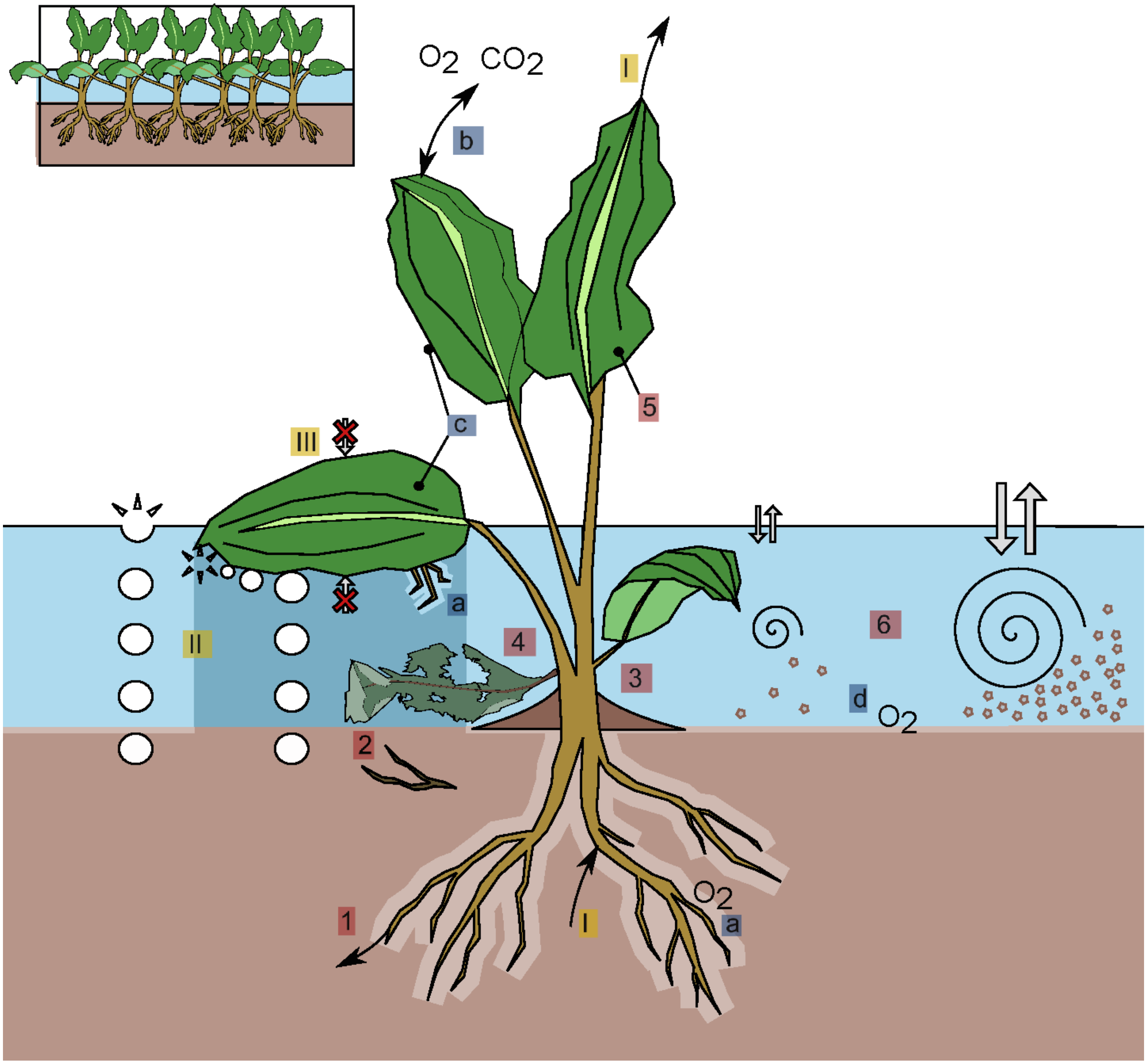

Figure 1. Plant-mediated processes that influence methane (CH_4) emissions from freshwater systems. The depicted plant represents a hybrid of emergent, floating, and submerged vegetation to illustrate the main processes of these three different functional groups. The water layer is divided into an oxic (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-mediated 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).

3.1.1 CH_4 production

Decaying plant matter can fuel CH_4 production in the anoxic sediment by providing organic matter, a precursor of the substrate for methanogens (35, 36). The intensity of methanogenesis depends on the water content and quality of this organic matter (e.g., C:N and C:P ratios) (7, 8). In a study of a boreal lake, for instance, *Lemna trisicula* produced twice as much CH_4 per gram biomass as *Phragmites australis* (14).

In addition to decaying organic matter, an important pool of labile carbon substrate is formed by root exudates, such as acetate (37, 38). Acetate exudation per gram root can vary considerably between species. For instance, *Eriophorum vaginatum* may release over seven times more acetate than *Carex rostrata* and *Juncus effusus* (26). Furthermore, Turner et al. (39) found a suppressing effect of root exudates on CH_4 oxidation in a thermokarst bog, presumably resulting from competition for electron acceptors. In addition to enhancing sediment methanogenesis, the release of labile organic carbon could also fuel methanogenesis in the oxic water column, as has been suggested for algae in rivers and lakes (40–42).

Besides producing organic matter as a precursor for methanogenesis, aquatic vegetation can reduce water flow velocity and thus increase sedimentation rates (43, 44). In particular, fine sediments rich in organic matter form an optimal environment for methanogens due to high sediment surface area and a high potential for microbial biofilm formation (8, 45, 46). Reduced flow velocity may therefore enhance methanogenesis in vegetated water bodies (16, 47).

Although oxygen (O_2) generally suppresses methanogenesis, Wilmoth et al. (48) showed that temporary exposure of Sphagnum peat to O_2 can increase CH_4 yields up to 2000- fold during subsequent anoxic conditions compared to Sphagnum peat without O_2 exposure due to functional shifts in the microbiome of the redox- oscillated peat.

An additional CH_4 production pathway could be oxic, non-enzymatic production of CH_4 within plants (49, 50). 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 pectine when a plant is exposed to UV radiation or other stressors (51, 52).

3.1.2 CH_4 oxidation

To overcome anoxia-related problems in waterlogged soils, much 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-through (53, 54). 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 (55, 56). The increased O_2 availability in the rhizosphere enhances aerobic CH_4 oxidation. The importance of ROL in regulating CH_4 emissions is strongly dependent on plant species and developmental stage (57). For instance, Ström et al. (26) showed in peat monoliths that Carex-dominated vegetation 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*), CH_4 oxidation as a result of ROL even eliminated CH_4 emissions completely (9).

Besides enhancing CH_4 oxidation, O_2 release in the rhizosphere can also 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 lead to repression of methanogenesis, depending on the pool of alternative electron acceptors and the magnitude of ROL (23). In addition to altering the availability of substrate and electron acceptors, plants can influence methanogenesis and methanotrophy by altering nutrient availability, affecting the microbial community, including methanogens and methanotrophs (58, 59).

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 (6, 60). Additionally, vegetation can limit light intrusion into the water and thus reduce primary production and CH_4 oxidation (61). The physical barrier formed by floating plants not only impedes diffusion but also captures bubbles, enhancing their residence time and potential oxidation (6). ROL can also occur in floating plants and adventitious roots, reducing dissolved CH_4 concentrations in the water column (6, 62, 63). O_2 availability and, therefore, potential CH_4 oxidation will thus strongly depend on the plant species and water column depth.

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 submersed plant species (12, 64–66). Endophytic methanotrophs have been found in Sphagnum mosses and several vascular peatland plants (67, 68). Beyond harboring, Iguchi et al. (69) showed that duckweeds living in freshwater lakes are not only inhabited by methanotrophs, but the duckweed plant actually has an enhancing effect on methane oxidation. Duckweeds may stimulate methanotrophic growth, presumably by contributing certain metabolites (69).

3.1.3 CH_4 transport

Besides affecting CH_4 production and consumption processes, aquatic vegetation plays a vital role in CH_4 transport. Most notably, aerenchymous plants form a direct conduit for CH_4 from the sediment to the atmosphere, causing CH_4 to bypass oxidation in oxic sediment and water layers (70). This has also been observed for floating plants rooting in the sediments of shallow waters (22). Depending on plant species characteristics, CH_4 transport through the plant can take place by diffusion (driven by differences in concentration) or by convective flow (driven by differences in pressure) (71). These processes result in the abovementioned transport of O_2 to the root zone and the opposite flow of CH_4 from roots to shoots. Plant-mediated CH_4 transport is affected by, among other factors, temperature, light intensity, plant porosity, rates of photosynthesis, and stomatal conductance, and may therefore vary diurnally and seasonally (e.g., 72–74). This “chimney effect” is estimated to contribute 55 to 85% to total CH_4 fluxes in peatlands (10). 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* (75), and similar results were observed for herbivore-induced damage in a wetland plant community (18).

Plant-mediated transport may reduce sediment CH_4 concentrations to such an extent that it reduces ebullition. In an experimental set-up with *Phragmites australis*, for instance, plant clipping resulted in a 5 to 10-fold increase in ebullition, whereas the total emission, including plant-mediated transport, was about 1.8 times higher in intact plants (76).

3.2 Methods to assess CH_4 fluxes of vegetated areas and geographical distribution of studies

A wide variety of methods is used to assess CH_4 fluxes in vegetated areas, all with different strengths and drawbacks. The principal difference between the approaches is the scale of the CH_4 fluxes they incorporate, thereby incorporating single or multiple emission pathways in the vegetated areas. In addition, there is a strong bias towards 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 (77).

In the screened literature (159 studies, 372 entries; some studies applied multiple methods), in total ten methods were applied to measure CH_4 fluxes of vegetated areas (Fig. 2; Table 1): (i) chamber (141 studies; 343 entries; Fig. 2A), (ii) porewater sampling (14 studies; 23 entries: Fig. 2B), (iii) eddy covariance flux tower (10 studies; 19 entries; Fig. 2C), (iv) inverted funnel (6 studies; 10 entries; Fig. 2D), (v) concentration measurement and k value (6 studies; 9 entries; Fig. 2E), (vi) bottle incubation (2 studies; 7 entries; Fig. 2F), (vii) gas sampling from plant tissue (2 studies; 4 entries; Fig. 2G), (viii) submerged chamber (2 studies; 3 entries; Fig. 2H), (ix) leaf chamber (1 studies; 3 entries; Fig. 2I), and (x) inverted water-filled vial (1 study; 1 entry; Fig. 2J).

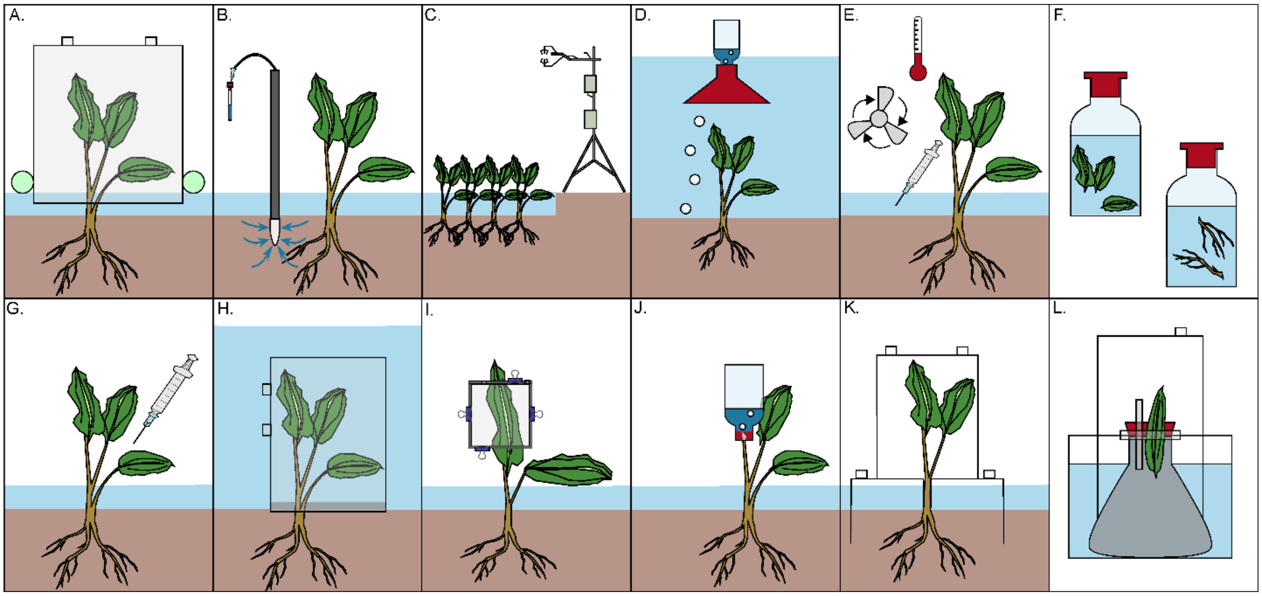

Figure 2. Methods to investigate CH_4 fluxes of vegetated areas (field and laboratory): chamber (A), porewater sampling (B), eddy covariance flux tower (C), inverted funnel (D), concentration measurement and k value (E), bottle incubation (F), gas sampling from plant tissue (G), submerged chamber (H), leaf chamber (I), inverted water-filled vial (J), stacked chamber (K), diffusion potential of specific plant parts (L).

331 **Table 1.** Summary of methods used to determine CH_4 fluxes of vegetated areas.

Method	Description	Exemplary references
<u>Natural freshwater systems</u>		
Chamber (Fig. 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)	(78–80)
Porewater sampling (Fig. 2B)	Sampling of CH_4 concentration in porewater near and away from roots (with vials connected to rhizons)	(80, 81)
Eddy covariance (EC) flux tower (Fig. 2C)	Placed in such a way that the EC footprint represents vegetated and/or unvegetated areas	(76, 82, 83)
Inverted funnel (Fig. 2D)	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)	(20, 84, 85)
Concentration measurement and k value (Fig. 2E)	Developing a model based on laboratory and/or field results to estimate the gas exchange coefficient based on temperature and wind speed	(86)
Bottle incubation (Fig. 2F)	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	(87)
Gas sampling from plant tissue (Fig. 2G)	Measurement of CH_4 concentration within plant stem (e.g., 1 cm below the waterline via a syringe)	(88, 89)
Submerged chamber (Fig. 2H)	Capturing CH_4 release of submerged plants by submerged bags (e.g., made of a multi-layer	(4, 64)

	clear film of saran and PVC with low CH_4 permeability)	
Leaf chamber (Fig. 2I)	Transparent plastic storage boxes sealed with rimmed weather stripping and large binder clips (measurement of headspace CH_4 increase over time)	(11)
Inverted water-filled vial (Fig. 2J)	Clipping of main stem and placing an inverted water-filled vial over it (leaving vial for a defined amount of time)	(20)
<u>Rice literature</u>		
Stacked chamber (Fig. 2K)	Installing two chambers with different diameters: larger one covering water surface with lid sealed around the plant, smaller one only enclosing plant	(90, 91)
Diffusion potential of specific plant parts (Fig. 2L)	A single plant part (e.g., leaf, panicle, node, or internode) 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.	(92)

The majority of the reviewed studies applied floating chambers. 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 plant. Disturbance of vegetation may liberate gas bubbles inducing a peak emission; in addition, the chamber alters moisture, light, and carbon dioxide (CO_2) concentrations which impacts stomata and may consequently influence CH_4 fluxes. Secondly, often the chamber does not cover the entire plant; when part of the root system exchanges gas with the overlying water outside the chamber area, these fluxes may be missed (e.g., 93). Thirdly, fluxes measured in floating chambers integrate plant-mediated and diffusive fluxes, complicating the disentangling of different flux pathways.

The stacked chamber approach, used in rice studies (90, 91), could be used to better differentiate between actual plant-mediated CH_4 fluxes, diffusion, and/or ebullition, avoiding the potentially misleading integration discussed above. The diffusion potential method (92) can be used to scan for possible within-plant hotspots of CH_4 flux.

Most of all reviewed studies (159 studies, 372 entries; one study performed both approaches) were performed in the field (134 studies; 297 entries) compared to mesocosm experiments (26 studies; 75 entries). Studies on all scales are valuable to both obtain mechanistic understanding and enable 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 159 compiled studies (of which one study was performed on two continents), 70 were performed in North America (154 entries), followed by 62 in Europe (161 entries), and 21 (48 entries), 5 (7 entries), 1 (1 entry), and 1 (1 entry) in Asia, South America, Oceania, and Australia, respectively (Fig. 3). Besides missing data in, e.g., Africa, there are only a handful of studies in South America (e.g., 94, 95), where some of the largest inland aquatic systems are located (e.g., Amazon and Pantanal). Consequently, our current understanding of the magnitude of CH_4 fluxes of vegetated areas is strongly biased.

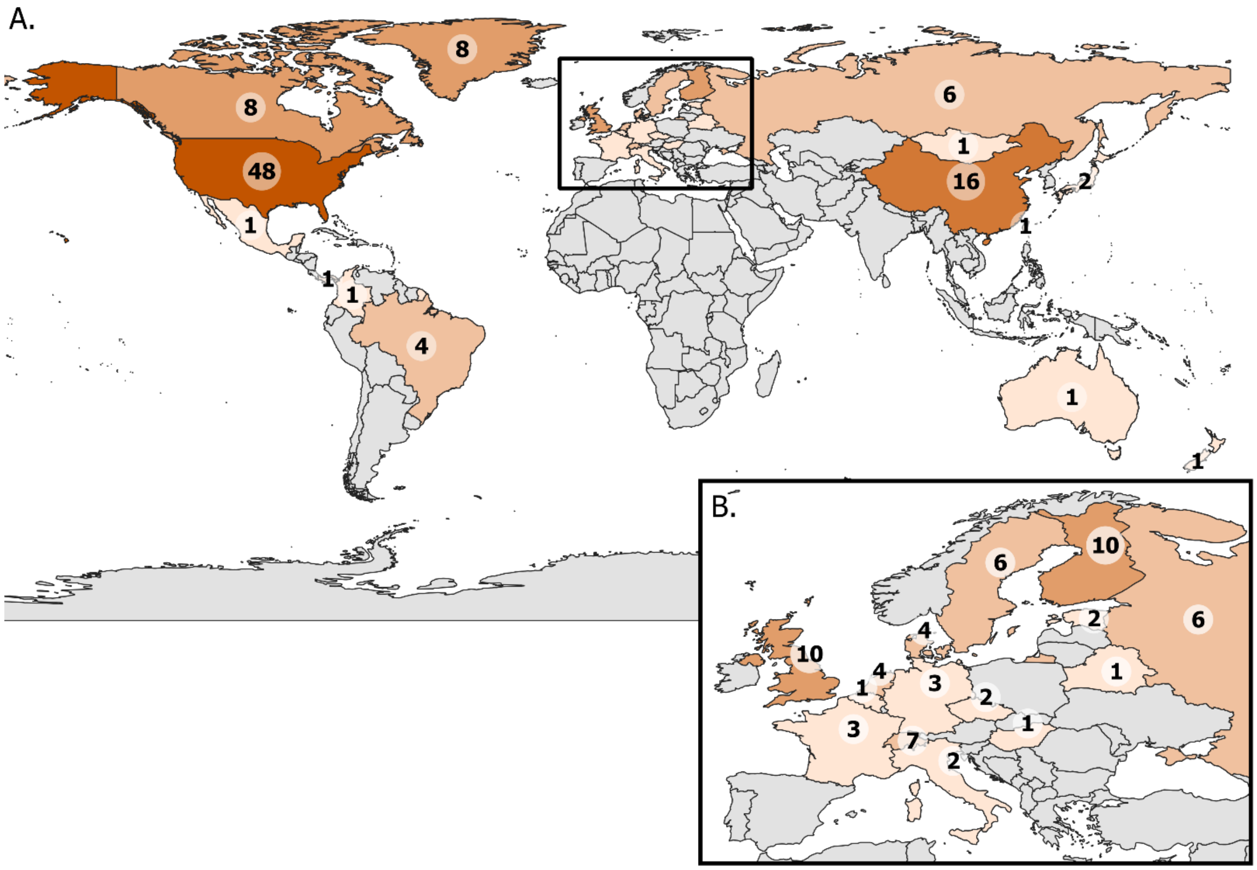

Figure 3. Geographical distribution of studies related to CH_4 fluxes of vegetated areas (A) with a zoom-in of Europe (B). The number of studies is indicated on the respective countries accompanied by different color intensities indicating the higher frequency (higher color intensity) and lower frequency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

3.3 CH_4 flux intensity and variability from vegetated areas

Although our systematic literature review points out that there are spatial and temporal data gaps and that different methods cannot readily be compared, we provide a first overview.

From an ecosystem perspective, of total 159 studies (372 entries), 136 were done in wetlands (318 entries), whereas only 22 (53 entries) and 1 (1 entry) in lakes and running waters, respectively. This implies that the available data are strongly imbalanced, urging for more studies in standing and running waters.

CH_4 fluxes of vegetated areas ranged from -454.4 (uptake) to 2882.4 mg CH_4 m^{-2} d^{-1} (emission) (62.1 [8.8, 183.8]; median [interquartile range (IQR)]) in wetlands, from 0.2 to 1960.0 mg CH_4 m^{-2} d^{-1} (76.0 [34.6, 230.0]) in lakes, and on average 5.4 mg CH_4 m^{-2} d^{-1} in running waters (only one entry available) (Fig. 4). There was neither a significant effect of ecosystem type nor climate zone on CH_4 fluxes of vegetated areas (Table 2A).

Table 2. Results of the linear mixed models testing effects of ecosystem type (running waters, lakes, wetlands), 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 (34 individual genera), ecosystem type (lakes, wetlands), study period (growing, non-growing), and climate zone (arctic, boreal, temperate, tropic), on CH_4 fluxes of vegetated areas of emergent plants (B). 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.

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	1.068	0.586
	Study period	2.698	0.100
	Plant type	9.268	**0.010**
	Climate zone	4.919	0.178
B) Testing CH_4 fluxes of vegetated areas of emergent plants			
CH_4 fluxes of vegetated areas*	Plant genus	64.601	**< 0.001**
	Ecosystem type	0.112	0.738
	Study period	2.146	0.143
	Climate zone	3.140	0.371

* Transformation: log10 (CH_4 fluxes of vegetated areas + abs (min (CH_4 fluxes of vegetated areas)) +4)

A) Marginal R^2 = 0.065, conditional R^2 = 0.537, sample size = 301.

B) Marginal R^2 = 0.260, conditional R^2 = 0.614, sample size = 192.

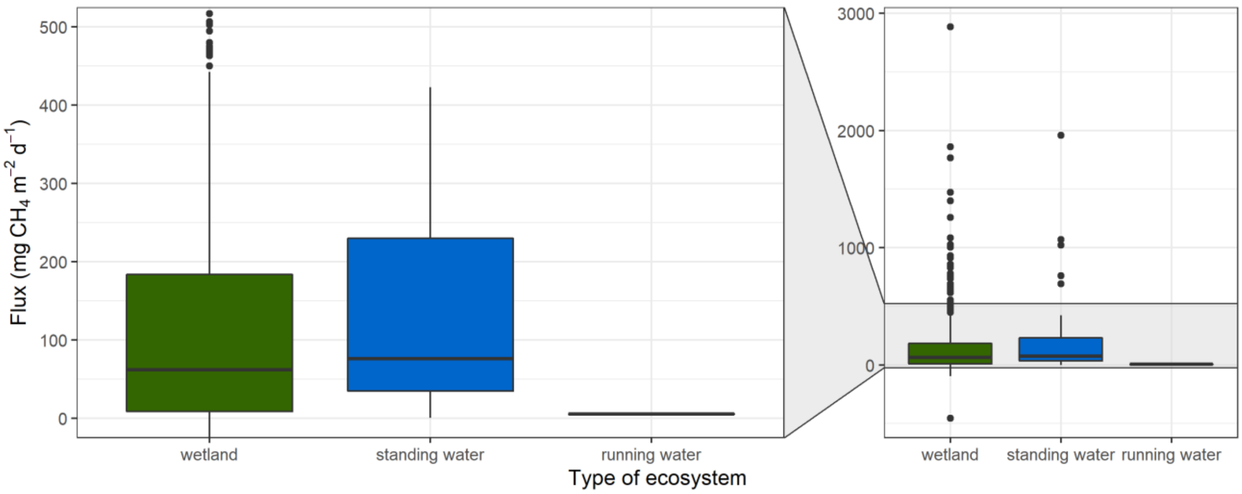

Figure 4. CH_4 fluxes of vegetated areas of different ecosystem types (wetlands, lakes, and running waters). Boxplots represent median (black line), first and third quartiles (hinges), range (whiskers), and outliers (black dots).

From all the 159 studies (372 entries), only 11 studies (20 entries) are from the non-growing season, compared to 117 studies (282 entries) performed in the growing season, while 29 studies (61 entries) include measurements throughout the year. The very similar median fluxes (Fig. 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 potentially 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 -454.4 to 2882.4 mg CH_4 m^{-2} d^{-1} (55.7 [8.5, 200.3]) in the growing season, and from 0.1 to 553.2 mg CH_4 m^{-2} d^{-1} (74.3 [7.7, 131.8]) in the non-growing season (Fig. 5). One explanation of the absent significant effect might be that organic matter supply rate (96), e.g., due to dying vegetation, could actually be more relevant in driving CH_4 production than the division of growing and non-growing seasons.

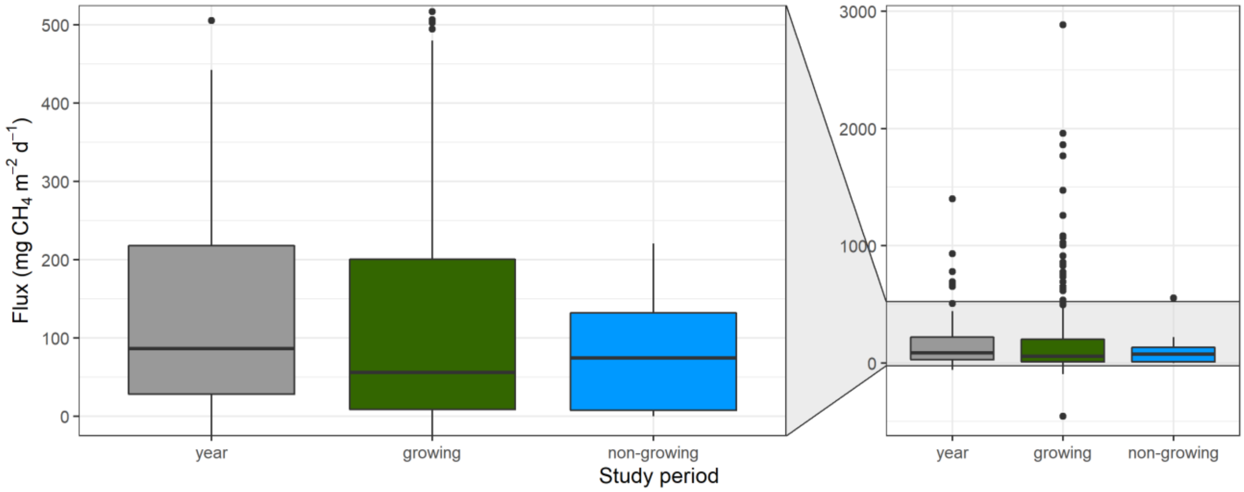

Figure 5. CH_4 fluxes of vegetated areas from different plant types combined, measured in 3 different seasons (growing and non-growing season, and year-round studies). Boxplots represent median (black line), first and third quartiles (hinges), range (whiskers), and outliers (black dots).

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

The fluxes for emergent plants ranged from -454.4 to 2882.4 mg CH_4 m^{-2} d^{-1} (62.4 [12.0, 184.4]), for floating plants from 3.9 to 1860.8 mg CH_4 m^{-2} d^{-1} (77.0 [43.5, 391.8]), and for submerged plants from 5.4 to 380.9 mg CH_4 m^{-2} d^{-1} (50.6 [15.4, 192.7]). Fluxes from mixed stands with a mix of different plant types ranged from 4.2 to 9.9 mg CH_4 m^{-2} d^{-1} (7.1 [5.6, 8.5]) (Fig. 6). These differences led to a significant effect of plant type on CH_4 fluxes of vegetated areas ($p = 0.010$; Table 2A), with significantly higher fluxes from floating plants compared to emergent plants (post hoc pairwise comparison; $p = 0.011$). Different processes may underlie the high emissions from areas with floating plants. Particularly the low oxygen conditions below the floating plants related to the inhibition of photosynthesis and the hampered oxygen intrusion into the water distinguish the floating plants from other plants (see also section 3.1). The low oxygen availability in the water column and sediment creates favorable circumstances for methanogenesis. When the floating plants are rooted in the sediment – thereby connecting the high CH_4 concentrations in the sediment directly to the atmosphere through plant-mediated transport, emissions may be particularly high (22, 94). However, only a small fraction of studies indicated whether the studied floating plants were free-floating or rooted in the sediment. This information should be better considered and reported in future studies.

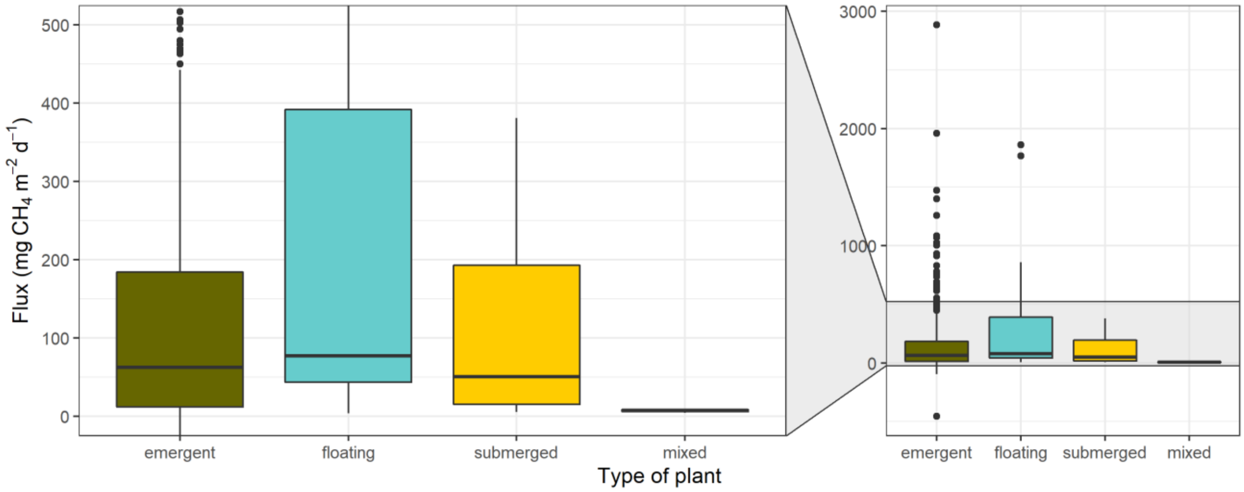

Figure 6. CH_4 fluxes of vegetated areas from different plant types. Emergent: 147 studies, 337 entries; floating: 15 studies, 24 entries; submerged: 2 studies, 9 entries; mixed: 1 study, 2 entries. Boxplots represent median (black line), first and third quartiles (hinges), range (whiskers), and outliers (black dots).

Within the emergent plants (337 entries), most data are from mixed plants (28.2%), followed by Carex (16.6%), Eriophorum (9.8%), Phragmites (9.2%), and Typha (4.5%). Not surprisingly, seen in the distribution of the studies (Fig 3), emphasis has been on plants widely occurring in the arctic, subarctic, and temperate regions. The remaining 46 genera/combination of genera represents less than 4.0% of the entries (Table S1). Within floating plants (24 entries), 33.3% of the data are from the genus Nuphar, followed by Eichhornia (25.0%) and Nelumbo and Nymphaea with 12.5% each (Table S1). Finally, most data for submerged plants (9 entries) are from Myriophyllum (33.3%) and Ranunculus (22.2%) (Table S1).

CH_4 fluxes from different genera within the different plant types are highly variable (Fig. 7 & S1). Being the strongest predictor in the LME run on fluxes of emergent plants, the genus had a significant effect ($p < 0.001$; Table 2B). Particularly Glyceria stands out with significantly higher CH_4 fluxes than Carex and Spartina (pairwise comparison posthoc; $p = 0.032$ and $p = 0.043$). 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” for climate and soil type - are likely more promising (see e.g., 56, 97).

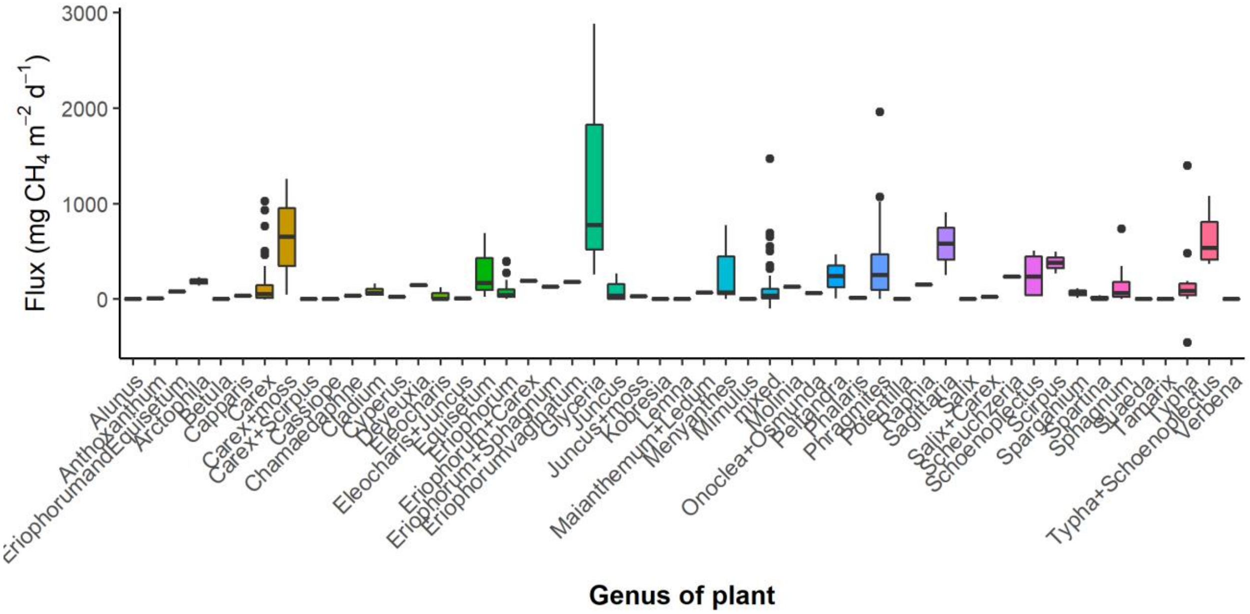

Figure 7. CH_4 fluxes of vegetated areas from individual genera of investigated emergent plants. Boxplots represent median (black line), first and third quartiles (hinges), range (whiskers), and outliers (black dots).

3.4 Plant effects on CH_4 fluxes: Implications for current global CH_4 estimates

3.4.1 Wetlands

While vegetation presence and vegetation composition are commonly used to model CH_4 emissions at local to regional scales (e.g., 98–100), the effect of vegetation on CH_4 emissions is often not included in larger-scale models. Global models of wetland-CH_4 feedbacks indicate that wetland CH_4 emissions could drive 21st-century climate change, with global wetland emissions matching or exceeding anthropogenic emissions by 2100 (101). However, modeled CH_4 emissions vary strongly (102, 103), partly due to a poor understanding of the role of vegetation in CH_4 production, oxidation, and transport (104, 105). Many wetland models (e.g., 106–109) incorporate the primary production of vegetation as it fuels carbon stocks that are subsequently available for decomposition. Only a few take the transport through plants into account (e.g., Kleinen et al. (110) using the CH_4 transport model by Riley et al. (105) and Ito & Inatomi (111)). 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 101, who included CH_4 oxidation during plant-mediated transport in their global wetland model). Upscaling of the many ways plants can impact CH_4 –as summarized in Fig. 1- is no sinecure but the lack of mechanistic processes (see examples in section 3.1). Describing CH_4 emissions from wetlands is an important caveat as it is estimated that herbaceous plants represent ca. 28 to 90% of the total ecosystem-level CH_4 flux from wetlands (3) which is a globally significant amount considering the total annual wetland CH_4 emission of 149 $TgCH_4$ yr^{-1} (1).

3.4.2 Inland waters

The global annual CH_4 emission for rivers is estimated to be 27 $TgCH_4$ yr^{-1} (112). This estimate is based on a simple bootstrapping approach using published diffusive riverine CH_4 fluxes. These fluxes exclude emissions from emergent vegetation, and it is unclear to which extent they include submerged vegetation. Our literature search, unfortunately, yielded only one study (20) where both CH_4 emissions from vegetated river sections and unvegetated sections were compared. We could therefore not estimate the relevance of vegetation for riverine CH_4 fluxes.

In a current global CH_4 emission estimate of lakes of 104 $TgCH_4$ yr^{-1} (30), vegetated areas are not explicitly considered. 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 (113). Our estimate of the global importance of CH_4 fluxes of vegetation in lakes, based on a comparison between a simulated global CH_4 flux with and without considering the effect of vegetation on CH_4 fluxes, indicates that the median global CH_4 emission of lakes neglecting vegetation is 123.9 Tg $C\text{-}CH_4$ yr^{-1} (IQR: 80.9, 202.3). The simulated CH_4 emission from lakes taking the vegetation effect into account is 180.8 Tg $C\text{-}CH_4$ yr^{-1} (IQR: 122.8, 275.5), which has a significantly different distribution compared to without vegetation (Two-sample Kolmogorov-Smirnov test; $p < 0.001$). These estimations imply that we potentially underestimate global CH_4 emissions from lakes by 46% (IQR: 36; 52). These 46% underestimations are in line with a study of Jeffrey et al. (114) which showed that plant-mediated CH_4 fluxes (seasons aggregated and weighting for changes in lily coverage) accounted for ~59% of the annual CH_4 emissions. In contrast, ebullition and diffusion each accounted for ~20%. As pointed out before in this review, it is important to consider that the flux data used for this upscaling exercise do not reflect the entirety of the habitat, and it is unclear which aspects and how much of the vegetated habitat is covered (see section 3.2). Hence, it is paramount to consider CH_4 fluxes from a vegetated habitat perspective and standardize related measurement approaches and terminologies, to improve these estimates.

4 Conclusions and outlook

CH_4 fluxes from vegetated areas are largely understudied and neither well understood nor quantified. The here presented study is, according to our knowledge, the first attempt to synthesize the many ways in which vegetation impacts CH_4 fluxes across 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 flux intensities across a geographical, seasonal, and vegetation type related spectrum and provide a first-order estimate of the significance of CH_4 fluxes from vegetated areas for global lake CH_4 emissions.

From a methodological perspective, we urge for a more standardized way of measuring CH_4 fluxes from vegetated areas. We consider not only measuring the growing season but also the non-growing season as pertinent to reduce biased estimates on an annual basis. To measure specifically plant-mediated CH_4 fluxes, we consider the stacked chamber method (Table 1) as the most appropriate one since it allows to separate the plant-mediated flux from the diffusive flux. Alternatively, we suggest trying to capture CH_4 fluxes from the vegetated areas as a whole by measuring diffusion, ebullition, and plant-mediated fluxes combined. 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.

By showing a comprehensive overview of how vegetated areas can affect CH_4 dynamics in numerous aspects, we urge further studies to consider a vegetated habitat view instead of focusing solely on plant-mediated CH_4 fluxes. The comprehensive overview given in this study may pave the way for future studies tackling vegetation-related aspects of CH_4 production, oxidation, and/or transport in the light of global and land-use change. We believe that linking the elaborated processes to quantifiable species traits is an important next step.

Despite being beyond the scope of this study, we recommend considering CO_2 and nitrous oxide fluxes beside CH_4 fluxes to fully capture the role of vegetated areas in the carbon and greenhouse gas cycle. If CH_4 fluxes are described on their own, it is important to consider that those vegetated areas also store carbon; otherwise, we might exaggerate their potential radiative effect. Although not specifically accounting for plant-mediated CH_4 fluxes, it has been shown that CH_4 emissions partially offset “blue carbon” burial in mangroves (115). Similar assessments in freshwater systems are scarce (but see 116, 117).

Although general global trends in plant coverage in the light of global change are difficult to predict (33), they seem to differ among vegetation types (i.e., emergent, floating, submerged). Specifically, global change trends seem to favor floating over submerged vegetation (118, 119). However, the data basis for this trend is still weak. It was furthermore shown that invasive vegetation has the potential to increase CH_4 emissions from a subtropical tidal estuarine wetland (120). Hence, the understudied and highly likely underestimated CH_4 fluxes from vegetated areas might get even more relevant due to global warming and land-use change.

At present, upscaling CH_4 flux from vegetated areas to the landscape and global scale is challenging. 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 using, e.g., remote sensing techniques (e.g., 121). Despite the uncertainties, it is clear that CH_4 emissions from vegetated areas are an important source of global CH_4 emissions from freshwater systems. Especially studies of lakes and running waters may be missing an important pathway of the total CH_4 flux. This omission introduces a major degree of uncertainty in the global estimation of CH_4 emissions from freshwater systems.

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Supplementary material

Table S1. Individual genera of investigated emergent plants (total n = 337), floating plants (total n = 24), and submerged plants (total n = 9); percentage of the number of entries (n) for individual genera in relation to the total number of entries was calculated.

Emergent plants					
Plant genus	**n**	**%**	**Plant genus**	**n**	**%**
mixed	95	28.2	*Scirpus*	2	0.6
Carex	56	16.6	*Sparganium*	2	0.6
Eriophorum	33	9.8	*Suaeda*	2	0.6
Phragmites	31	9.2	*Alunus*	1	0.3
Typha	15	4.5	*Anthoxanthum*	1	0.3
Sphagnum	13	3.9	*Arctagrostis+Carex+Dupontia+EriophorumandEquisetum*	1	0.3
Cladium	8	2.4	*Betula*	1	0.3
Juncus	8	2.4	*Capparis*	1	0.3
Typha+Schoenoplectus	7	2.1	*Carex+Scirpus*	1	0.3
Menyanthes	5	1.5	*Cassiope*	1	0.3
Schoenoplectus	4	1.2	*Chamaedaphne*	1	0.3
Eleocharis	3	0.9	*Cyperus*	1	0.3
Equisetum	3	0.9	*Eleocharis+Juncus*	1	0.3
Glyceria	3	0.9	*Eriophorum+Carex*	1	0.3
Phalaris	3	0.9	*Eriophorum+Sphagnum*	1	0.3
Potentilla	3	0.9	*Eriophorumvaginatum*	1	0.3
Spartina	3	0.9	*Juncus+moss*	1	0.3
Arctophila	2	0.6	*Kobresia*	1	0.3
Carex+moss	2	0.6	*Maianthemum+Ledum*	1	0.3
Deyeuxia	2	0.6	*Mimulus*	1	0.3
Lemna	2	0.6	*Molinia*	1	0.3
Peltandra	2	0.6	*Onoclea+Osmunda*	1	0.3
Sagittaria	2	0.6	*Raphia*	1	0.3
Scheuchzeria	2	0.6	*Salix*	1	0.3

Emergent plants (continuation)

Plant genus	**n**	**%**
Salix+Carex	1	0.3
Tamarix	1	0.3
Verbena	1	0.3

Floating plants

Plant genus	**n**	**%**
Nuphar	8	33.3
Eichhornia	6	25.0
Nelumbo	3	12.5
Nymphaea	3	12.5
mixed	1	4.2
Nuphar+Potamogeton+Mentha+Hippuris+Berula	1	4.2
Potamogeton	1	4.2
Trapa	1	4.2

Submerged plants

Plant genus	**n**	**%**
Myriophyllum	3	33.3
Ranunculus	2	22.2
Cabomba	1	11.1
Ceratophyllum	1	11.1
Hottonia	1	11.1
Lagarosiphon	1	11.1

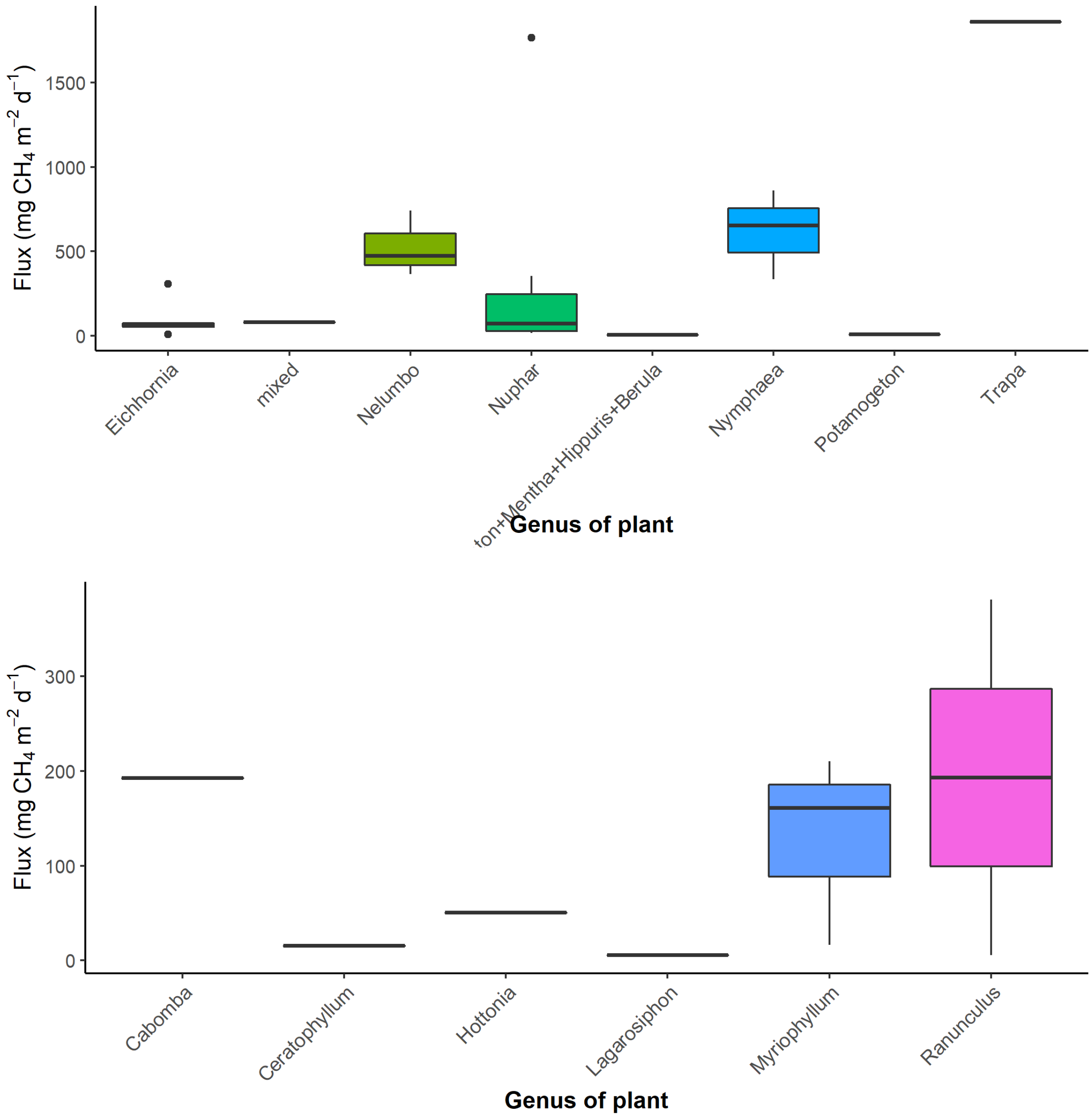

Figure S1. CH$_4$ fluxes of vegetated areas from individual genera of investigated floating plants (upper panel) and submerged plants (lower panel). Boxplots represent median (black line), first and third quartiles (hinges), range (whiskers), and outliers (black dots).