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### 3 **The importance of plants for methane emission at the ecosystem scale**

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#### 18 **Highlights**

- 19 • Plants have major indirect influence on global emissions of methane.
- 20 • Improved quantitative knowledge on plant-methane interactions is needed.
- 21 • Systematic long-term observations of both methane and plant communities are key.

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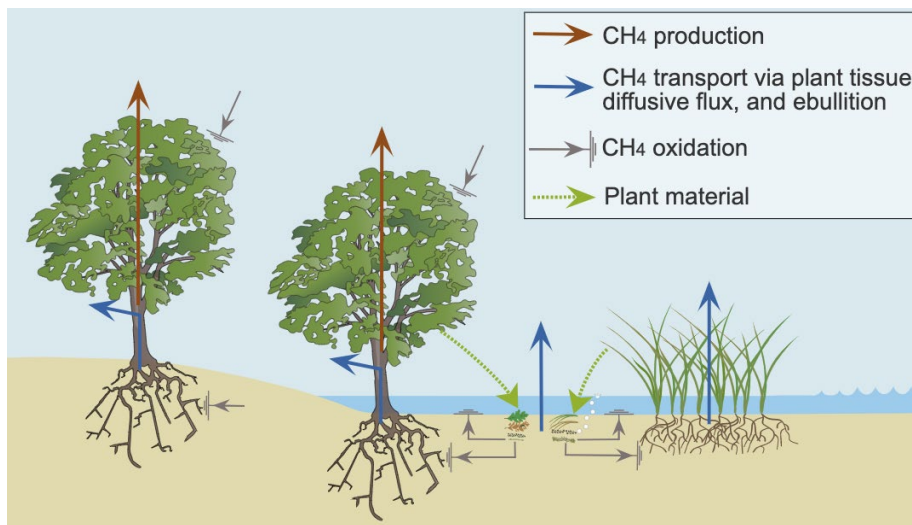
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30 **Graphical abstract**



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35 **Abstract**

36 Methane (CH<sub>4</sub>), one of the key long-lived atmospheric greenhouse gases, is primarily produced from  
37 organic matter. Accordingly, net primary production of organic matter sets the boundaries for CH<sub>4</sub>  
38 emissions. Plants, being dominant primary producers, are thereby indirectly sustaining most global  
39 CH<sub>4</sub> emissions, albeit with delays in time and with spatial offsets between plant primary production  
40 and subsequent CH<sub>4</sub> emission. In addition, plant communities can enhance or hamper ecosystem  
41 production, oxidation, and transport of CH<sub>4</sub> in multiple ways, e.g., by shaping carbon, nutrient, and  
42 redox gradients, and by representing a physical link between zones with extensive CH<sub>4</sub> production in  
43 anoxic sediments or soils and the atmosphere. This review focuses on how plants and other primary  
44 producers influence CH<sub>4</sub> emissions with the consequences at ecosystem scales. We outline  
45 mechanisms of interactions and discuss flux regulation, quantification, and knowledge gaps across  
46 multiple ecosystem examples. Some recently proposed plant-related ecosystem CH<sub>4</sub> fluxes are  
47 difficult to reconcile with the global atmospheric CH<sub>4</sub> budget and the enigmas related to these fluxes  
48 are highlighted. Overall, ecosystem CH<sub>4</sub> emissions are strongly linked to primary producer  
49 communities, directly or indirectly, and properly quantifying magnitudes and regulation of these links  
50 are key to predicting future CH<sub>4</sub> emissions in a rapidly changing world.

51

## 52           **1. Introduction**

53 Methane (CH<sub>4</sub>), one of the most important greenhouse gases (GHGs), is currently under scrutiny  
54 because of its high global warming potential in combination with uncertainties in the CH<sub>4</sub> budget  
55 (Kirschke et al., 2013; Saunio et al., 2020). Major sources of atmospheric CH<sub>4</sub> are both  
56 anthropogenic and natural and include extraction and handling of fossil fuels, combustion processes,  
57 landfills, ruminants, rice cultivation, and emissions from wildfires. Other key CH<sub>4</sub> sources are  
58 wetlands, marine- and freshwater environments (lakes, reservoirs, ponds, and streams) (Saunio et  
59 al., 2020). The two main CH<sub>4</sub> sinks are considered to be upland soil microbial methane oxidation (ca.  
60 10%), and abiotic atmospheric oxidation (ca. 90%). Terrestrial upland vegetation has also been  
61 suggested to be important for atmospheric CH<sub>4</sub> exchange, although not always being mentioned in  
62 global CH<sub>4</sub> budgets (Carmichael et al., 2014).

63  
64 The atmospheric CH<sub>4</sub> levels have sharply increased since pre-industrial times, but in contrast to the  
65 other long-lived GHGs (carbon dioxide and nitrous oxide), the increase has been irregular with  
66 variable growth rates among years and decades for reasons not yet fully understood (Dlugokencky et  
67 al., 2011). Several non-exclusive explanations for this variability have been proposed and one of  
68 them emphasise the potentially important role of wetland emissions (Nisbet et al., 2014; Lan et al.,  
69 2021). Moreover, the recent discovery of large CH<sub>4</sub> emissions from inland waters, including lakes,  
70 ponds, reservoirs, and running water environments, resulted in a situation where the atmospheric  
71 CH<sub>4</sub> growth rates are considerably smaller than expected from global emissions derived by summing  
72 estimated contributions from various sources, referred to as a mismatch between global top-down  
73 and bottom-up CH<sub>4</sub> emission estimates, respectively (Kirschke et al., 2013; Saunio et al., 2020). The  
74 temporal irregularities in atmospheric CH<sub>4</sub> growth rates and the mismatch between top-down and  
75 bottom-up flux estimates jointly highlight the current knowledge gaps regarding CH<sub>4</sub> emission rates  
76 and source attribution. Although emission uncertainties exist for all types of fluxes, the large biogenic  
77 ecosystem CH<sub>4</sub> fluxes, both natural and related with land use, have been considered the most  
78 uncertain (Saunio et al., 2020).

79  
80 It was recently suggested that up to half of the global CH<sub>4</sub> emissions depend on fluxes from wet  
81 ecosystems, including various types of wetlands, lakes, ponds, reservoirs, running water, ocean and  
82 coastal areas, and rice cultivation (Rosentreter et al., 2021). These fluxes are closely linked to  
83 mechanisms controlled by plant communities in or upstream of the aquatic environment. Regardless  
84 of where in the landscape CH<sub>4</sub> fluxes occur, primary production sets the boundaries for overall  
85 carbon cycling, and thereby for the CH<sub>4</sub> production, and plants are the main primary producers in

86 most ecosystems. In other words, the net ecosystem production by plants or other primary  
87 producers is a major indirect factor regulating ecosystem CH<sub>4</sub> production.

88

89 Human land use, including increased anthropogenic input of nutrients to ecosystems, as well as  
90 climate change, profoundly impacts plant communities around the world. There is already evidence  
91 of changes in growing season lengths, net primary productivity, plant biomass stocks, and plant  
92 community composition, exemplified by observations of global greening (Piao et al., 2020). There are  
93 also specific observations of rapid changes of e.g., aquatic macrophyte distribution in the arctic that  
94 can cause large perturbations of ecosystem CH<sub>4</sub> emissions (Andresen et al., 2017). Consequently, a  
95 better understanding of present and future CH<sub>4</sub> emissions is dependent on improved knowledge  
96 about plant community dynamics and particularly of the links between plant communities and  
97 ecosystem CH<sub>4</sub> fluxes.

98

99 This review will first briefly summarize key processes controlling ecosystem CH<sub>4</sub> emissions, which is  
100 needed as a background for the subsequent discussion on how plants influence ecosystem CH<sub>4</sub>  
101 fluxes. The aims are to (1) provide fundamental understanding on how plants play multiple important  
102 roles for ecosystem CH<sub>4</sub> emissions, and (2) give examples from selected ecosystem types. The words  
103 “emission” and “flux” are used in similar contexts to make the language more varied, but with an  
104 important distinction: “Emission” is unidirectional and regards flux to the atmosphere, while “flux” is  
105 omnidirectional and regards transport from one location to another in any direction.

106

107

## 108 **2. Fundamental processes shaping ecosystem CH<sub>4</sub> emissions**

### 109 **2.1 CH<sub>4</sub> production**

110 Biogenic CH<sub>4</sub> is a major final degradation product from anaerobic organic matter decomposition,  
111 formed by methanogenic *Archaea* where or when alternative terminal electron acceptors such as  
112 nitrate, manganese (IV), iron (III), and sulfate are low in abundance (Segers, 1998; Garcia et al.,  
113 2000). Freshwater aquatic systems, and some saline systems where salinity is caused by high  
114 carbonate levels, have low availability of such alternate electron acceptors, and anoxic CH<sub>4</sub>  
115 production can be extensive throughout all parts of the sediment or water saturated soils devoid of  
116 molecular oxygen (O<sub>2</sub>) (Bastviken, 2022). In marine systems, anoxic CH<sub>4</sub> production is dominant  
117 deeper in the sediments, at depths where the alternative electron acceptors have been depleted by  
118 other organic matter degradation processes. CH<sub>4</sub> production in anoxic waters are rarely considered  
119 and substantial anoxic CH<sub>4</sub> production seems largely associated with sediments, soils, or particle-rich  
120 fluids (Bastviken, 2022).

121

122 In addition to the anoxic CH<sub>4</sub> production, CH<sub>4</sub> formation can occur under oxic conditions. Stress on  
123 foliage from incoming light including ultraviolet radiation, rising temperature, and physical injury, has  
124 been reported to trigger oxic CH<sub>4</sub> formation associated with terrestrial vegetation – in many cases  
125 from non-enzymatic processes and with suggested influence from reactive oxygen species and with  
126 variability among plant species (Liu et al., 2015; Martel and Qaderi, 2017; Ernst et al., 2022). In  
127 addition, oxic CH<sub>4</sub> formation in surface water has been attributed to e.g., cyanobacterial  
128 photosynthesis with methylphosphonates and trimethylamine as precursors in surface lake water  
129 (Bižić et al., 2020). Overall, anoxic CH<sub>4</sub> production is believed to dominate while the magnitudes of  
130 the oxic production may be considerable but are still uncertain (Carmichael et al., 2014; Günthel et  
131 al., 2019; Peeters et al., 2019).

132

### 133 **2.2 CH<sub>4</sub> oxidation**

134 The oxidation of CH<sub>4</sub> in ecosystems is primarily performed by microbes, while plants can substantially  
135 influence where conditions are suitable for this microbial CH<sub>4</sub> oxidation and the extent to which CH<sub>4</sub>  
136 can bypass oxidation (discussed in Sections 2.3 and 3 below after describing fundamentals about the  
137 oxidation process here). Microbial oxidation of CH<sub>4</sub> is a source of energy and carbon to  
138 microorganisms in habitats where CH<sub>4</sub>, being the most reduced organic compound, co-exists with  
139 suitable electron acceptors. CH<sub>4</sub> oxidizing bacteria (MOB) are phylogenetically diverse (Smith and  
140 Wrighton, 2019) and are well-known to be able to rapidly consume large amounts of CH<sub>4</sub> in the  
141 presence of O<sub>2</sub> (Bastviken, 2022). Upon oxidation, CH<sub>4</sub> is transformed to CO<sub>2</sub> and H<sub>2</sub>O. Similarly, other  
142 microorganisms, often found to act in syntrophic consortia, can oxidize CH<sub>4</sub> under anaerobic  
143 conditions in the presence of e.g., nitrate, manganese (IV), iron (III), and sulfate (Kallistova et al.,  
144 2017). The oxidation process is often most active where the abundance or re-supply rates of both  
145 CH<sub>4</sub> and suitable electron acceptors are high enough, which is typically at redox transition zones in  
146 sediments, soils, or water. The ecosystem balance between CH<sub>4</sub> production and oxidation sets the  
147 limits for how much CH<sub>4</sub> can be emitted, and zones with microbial CH<sub>4</sub> oxidation can act as an  
148 important biofilter preventing large amounts of emissions. It has been estimated that CH<sub>4</sub> oxidation  
149 removes 45 to almost 100 % of the produced CH<sub>4</sub> in lake ecosystems and 20-40% in wetland soils  
150 before emission (Whalen, 2005; Bastviken et al., 2008; Bastviken, 2022).

151

### 152 **2.3 CH<sub>4</sub> transport processes**

153 The processes controlling CH<sub>4</sub> transport through the ecosystems – from locations of CH<sub>4</sub> production  
154 towards the atmosphere – determine the residence times in different ecosystem habitats (e.g. oxic  
155 and anoxic zones), and thereby the extent to which oxidation can consume CH<sub>4</sub> before it is emitted.

156 Hence, the different transport processes are of great importance for overall ecosystem CH<sub>4</sub>  
157 emissions. This section therefore briefly outlines major transport types because they are important  
158 for the understanding of how plants can influence ecosystem fluxes.

159

160 The movements of dissolved CH<sub>4</sub> in soil, sediment, and surface water can occur in two fundamental  
161 ways. If there is a net water movement over significant distances, dissolved CH<sub>4</sub> follows moving  
162 water, i.e., is transported by advection. If the movement of the water itself is small over larger  
163 distances, the transport can be better described as Fickian transport, i.e., transport of dissolved  
164 compounds from locations with higher concentrations towards locations with lower concentrations  
165 in ways that can be described by Fick's Law (Hemond and Fechner, 2015).

166

167 The Fickian transport includes molecular diffusion and eddy diffusion where turbulence eddies  
168 greatly speed up the transport rates (Hemond and Fechner, 2015). The Fickian transport rates are  
169 determined by the concentration gradient representing the change in concentration with distance,  
170 and the diffusion coefficient describing the transport rate given the physical conditions. In the  
171 absence of turbulence, the slow molecular diffusion limits transport. This can happen in deep  
172 undisturbed sediment pore waters or peats with little subsurface water flow, or across the diffusive  
173 boundary layers, including the water surface diffusive boundary layer at the water-air interface.  
174 Where there is turbulence in the water, the Fickian transport is dominated by the faster eddy  
175 diffusion, often represented by greater diffusion coefficients (Hemond and Fechner, 2015). During  
176 advective transport with the water flow, Fickian transport occur simultaneously and distribute the  
177 solutes within the flowing water volume. In sediments or soils, particles can influence this process by  
178 dispersion (Hemond and Fechner, 2015).

179

180 Accordingly, CH<sub>4</sub> produced in anoxic soils or sediments and dissolved in the pore water may move  
181 slowly by Fickian transport or faster by advection via ground water movement. When reaching the  
182 air-filled pores in soil, gas exchange occurs if the CH<sub>4</sub> concentrations in the water and air are not at  
183 equilibrium. The CH<sub>4</sub> exchanged into the gas phase is further transported by advection or Fickian  
184 transport at rates given by the local air movement or diffusion coefficient. In aquatic environments,  
185 solutes reaching the top of the sediment will be transported through the water column by advective  
186 transport or eddy diffusion depending on local hydrodynamic conditions. Thermo- or halocline  
187 stratifications can greatly reduce the diffusion coefficients and thereby effectively limit transport  
188 rates across such gradients. Finally, when dissolved CH<sub>4</sub> reaches the water surface, the diffusive  
189 boundary layer at the interface between water and air is the final limiting step for the emission of  
190 dissolved CH<sub>4</sub> to the atmosphere – often termed diffusive emission. CH<sub>4</sub> formed under oxic

191 conditions in surface water, an additional source of dissolved CH<sub>4</sub>, can also be emitted via diffusive  
192 emission.

193  
194 The dissolved CH<sub>4</sub> often has a relatively long residence time of CH<sub>4</sub> in the ecosystem (days or more;  
195 (Bastviken et al., 2008) – in turn allowing anaerobic and aerobic CH<sub>4</sub> oxidation to consume large  
196 amounts of the CH<sub>4</sub> before being emitted. However, upon episodes of high turbulence and extensive  
197 mixing, emission by diffusive flux can be rapid. One example is water column turnover in stratified  
198 lakes, where bottom waters developed anoxia during the stratification, and therefore can store and  
199 subsequently release large amounts of CH<sub>4</sub>. In such cases the turnover generates a very steep CH<sub>4</sub>  
200 gradient across the air-water interface that can drive large and rapid emissions (Johnson et al., 2022).

201  
202 Because CH<sub>4</sub> has a low solubility in water, bubbles often form in sediments and where CH<sub>4</sub> formation  
203 rates are high enough. These bubbles will grow and if the sediments are sufficiently loose or have  
204 pore space allowing bubble migration towards the surface, and they are eventually released and  
205 rapidly rise to the atmosphere by ebullition. In many aquatic environments with open water surfaces,  
206 ebullition is a dominant flux pathway (Bastviken et al., 2004; Bastviken et al., 2011). Within such  
207 ecosystems, ebullition seems most prominent at shallow waters and/or where the sediment organic  
208 matter accumulation is high (e.g., accumulation bottoms, river/stream inlet areas, or near littoral  
209 areas with high primary productivity) (DelSontro et al., 2011; Sobek et al., 2012; Natchimuthu et al.,  
210 2016). Ebullition can also be a dominant emission mechanism in peatlands (Christensen et al., 2003).  
211 Ebullition release is too rapid to be directly influenced by CH<sub>4</sub> oxidation as the bubbles pass too  
212 quickly through the oxic sediment zone or water column, but ebullition from deep sediments can  
213 lead to substantial dissolution of CH<sub>4</sub> from the rising bubbles into the water (McGinnis et al., 2006),  
214 and this dissolved CH<sub>4</sub> can be oxidized as described in Section 2.2.

215  
216 Vascular plants represent important conduits for CH<sub>4</sub> from the root zone to the atmosphere (Figure  
217 1). For more details about this topic please see (Vroom et al., 2022). Briefly, many plants with roots  
218 in water-saturated soils or sediments have internal gas transport systems for supplying root cells  
219 with O<sub>2</sub> (Joabsson et al., 1999; Laanbroek, 2010). This is particularly prominent in many aquatic  
220 macrophytes with aerenchyma tissue specially adapted for gas transport. To maintain pressure, the  
221 aerenchyma tissue transports gases both downwards and upward in the plant between roots and  
222 leaf stomata, or stem lenticels on trees, where the gas is exchanged with the atmosphere.  
223 Accordingly, gases entering roots may rapidly be transported via the aerenchyma to the atmosphere  
224 (Yavitt and Knapp, 1998). At least two types of transport via plants have been suggested – molecular  
225 diffusion (passive) and convective flow (active) (Kim et al., 1998). The convective flow is driven by a

226 pressure gradient in the plant and the interplay between molecular flux and convective flux has been  
227 suggested responsible for diel variability in the plant-mediated fluxes (Bendix et al., 1994; Brix et al.,  
228 1996; Whiting and Chanton, 1996; Kim et al., 1998; Kaki et al., 2001; Ding et al., 2004; Juutinen et al.,  
229 2004; Duan et al., 2005). However, some studies over multiple day-night cycles indicate negligible  
230 diel flux variability from areas dominated by vascular plants in high-latitude wetlands (Backstrand et  
231 al., 2008; Milberg et al., 2017). Beyond the explicit diel day-night variability in the plant-mediated  
232 flux, temporal variability in CH<sub>4</sub> flux is linked with multiple factors including temperature, light,  
233 humidity, and plant biomass (Chanton et al., 1993; Brix et al., 1996; Hirota et al., 2004; Juutinen et  
234 al., 2004; Duan et al., 2005; Kankaala et al., 2005; Wang and Han, 2005; Bergstrom et al., 2007;  
235 Milberg et al., 2017). The plant-mediated flux regulation may be strongly dependent on plant species  
236 (Armstrong and Armstrong, 1991; Chanton and Whiting, 1996; Joabsson et al., 1999). However, there  
237 are also observations of similar long-term mean emissions per m<sup>2</sup> from nearby plant species,  
238 suggesting little importance of specific species for long-term mean areal fluxes (Milberg et al., 2017).  
239 Additionally, transport of CH<sub>4</sub> via tree stems has relatively recently been demonstrated to be  
240 important (Barba et al., 2019).

241

242 Overall, plant mediated emissions allow CH<sub>4</sub> formed in sediments to bypass pore water or water  
243 column oxidation before emission. This type of transport can dominate CH<sub>4</sub> emissions in habitats  
244 with emergent aquatic macrophytes (Juutinen et al., 2003; Larmola et al., 2004; Bergstrom et al.,  
245 2007; Pangala et al., 2017). There are indications of a possible trade-off with reduced ebullition from  
246 areas with substantial plant-mediated emission (Noyce et al., 2014; Aben et al., 2022).

247

### 248 **3. Mechanisms by which plants can influence ecosystem CH<sub>4</sub> emission**

249 Terrestrial and aquatic plants and other primary producers can stimulate CH<sub>4</sub> emissions in many ways  
250 at ecosystem scales (Figure 1). Examples include:

- 251 + Primary production provides the primary substrates for both anoxic and oxic CH<sub>4</sub> formation  
252 in most environments. For e.g., wetland and standing water environments, higher CH<sub>4</sub>  
253 emissions are commonly observed under conditions and locations with higher primary  
254 production (see examples in Section 4 below).
- 255 + Plants can provide favourable sites for CH<sub>4</sub> formation inside or on the plants themselves  
256 (Covey and Megonigal, 2019). At the larger scale the foliage of vegetation (both terrestrial  
257 and aquatic) represents a large surface area for abiotic CH<sub>4</sub> production (Keppler et al., 2006;  
258 Carmichael et al., 2014).
- 259 + Plant communities in aquatic environments contribute to trapping of particulate organic  
260 matter to the sediment where stands of plants reduce turbulence (Braskerud, 2001; Duarte



261 et al., 2013; Bodmer et al., 2021; Work et al., 2021) increasing the potential for sediment CH<sub>4</sub>  
262 production

263 + Plant mediated transport by rooted vascular plants substantially enhance emissions by  
264 speeding up transport and reducing exposure to CH<sub>4</sub> oxidation (Vroom et al., 2022).

265

266 Plants can also hamper CH<sub>4</sub> emissions in several ways:

267 – Rooted vascular plants transport O<sub>2</sub> down to the root zone leading to O<sub>2</sub> leakage into the  
268 sediment or soil, which can favour CH<sub>4</sub> oxidation there and reduce emissions (King et al.,  
269 1998).

270 – Plants, including trees and mosses, can offer large surface areas for CH<sub>4</sub> oxidizing  
271 microorganisms in ecosystems (Sundh et al., 1995; Basiliko et al., 2004; Kip et al., 2010;  
272 Sundqvist et al., 2012; Stępniewska et al., 2018).

273 – Dense floating vegetation can also trap bubbles temporarily before they reach the  
274 atmosphere, which increases the CH<sub>4</sub> residence time in the system, favouring CH<sub>4</sub> oxidation  
275 (Bartlett et al., 1988; Kosten et al., 2016; Oliveira Junior et al., 2021).

276 – Dense aquatic vegetation stands can influence turbulence and thereby the transport of  
277 dissolved CH<sub>4</sub> towards and across the atmospheric interface in several ways. Dense floating  
278 macrophyte populations can reduce the wind-induced turbulence in the water, in turn  
279 reducing gas exchange rates, and increasing the potential for oxidation before emission  
280 (Kosten et al., 2016; Oliveira Junior et al., 2021). Diel differences in temperature between  
281 open water and floating plant mats, together with basin scale water movements, can cause  
282 lateral advection so that dissolved gases from vegetated areas are exported and emitted  
283 elsewhere (Amaral et al., 2022). In flooded forests, where winds are also reduced,  
284 turbulence-driven gas exchange rates can be regulated by a combination of shear from wind-  
285 driven water movements induced outside the forest and from convection associated with  
286 nocturnal cooling (MacIntyre et al., 2019). Accordingly, dense aquatic vegetation can not  
287 only influence gas exchange directly, but also the relative importance of different processes  
288 regulating transport and emissions of dissolved CH<sub>4</sub> (Oliveira Junior et al., 2021).

289

290 Other plant effects on fluxes can be logically inferred or hypothesized although hitherto seemingly  
291 not being studied or quantified:

292 ○ Roots of aquatic macrophytes may stabilize sediments, preventing the release of sediment  
293 bubbles and reducing ebullition rates.

294       ○ In dryer environments, transpiration by rooted vegetation can lower the soil water level,  
295           increasing the depth of the aerated CH<sub>4</sub> oxidation zone in the upper soil – reducing  
296           emissions.

297

298 Further studies are needed to fully explore the quantitative importance of these potential plant-  
299 related effects on CH<sub>4</sub> emissions across different ecosystems.

300

301 **\*\*\*\*FIGURE 1 NEAR HERE\*\*\*\***

302

303

#### 304       **4. Interactions between vegetation and CH<sub>4</sub> emission in example ecosystems**

##### 305 *4.1 General primary producer influences on ecosystem CH<sub>4</sub> cycling*

306 Given the many and complex processes by which plants influence ecosystem carbon fluxes as  
307 outlined in Section 3 above and in Figure 1, it is difficult to quantitatively assess the total plant  
308 contributions to total CH<sub>4</sub> flux, and such knowledge is missing in many ecosystems. Accordingly, the  
309 sections below should be seen as attempts to integrate existing conceptual knowledge with available  
310 scattered quantitative information on the importance of plants for CH<sub>4</sub> fluxes in example ecosystems  
311 (some of them illustrated in Figure 2).

312

313 Common to all ecosystems is that primary productivity controls the availability of substrates for CH<sub>4</sub>  
314 production over time. Increasing amounts of evidence indicate that CH<sub>4</sub> production and emissions  
315 are stimulated by the production of labile organic matter and by high primary production (Whiting  
316 and Chanton, 1993; Bellisario et al., 1999; King and Reeburgh, 2002; King et al., 2002; Backstrand et  
317 al., 2008; Bastviken et al., 2008; Davidson et al., 2015; West et al., 2015; Grasset et al., 2018; Kuhn et  
318 al., 2021; Aben et al., 2022). The link between primary production and CH<sub>4</sub> production and emission  
319 can be delayed (example at the end of Section 4.4 below), and for full consideration integration  
320 across long enough time periods is necessary. The indirect influence of plant communities on CH<sub>4</sub>  
321 fluxes has been acknowledged in many ecosystem models where ecosystem primary productivity  
322 proxies are used as an important emission driver (Wania et al., 2013).

323

324 Several links between whole-ecosystem carbon cycling and CH<sub>4</sub> have been made for lakes, ponds, or  
325 wetlands, including:

326       - Anaerobic CH<sub>4</sub> production was estimated to 13% of primary production (Rudd and Taylor, 1980)  
327       and 20-56% of organic matter respiration across multiple ecosystems (Capone and Kiene, 1988;

328 Kuivila et al., 1988; Bédard and Knowles, 1991; Mattson and Likens, 1993; Boon and Mitchell,  
329 1995; Hamilton et al., 1995; Ford et al., 2002).

- 330 - Oxic CH<sub>4</sub> oxidation can be similar to primary production rates during limited time periods in  
331 aquatic ecosystems (Rudd and Taylor, 1980; Kankaala et al., 2006).
- 332 - The production of CH<sub>4</sub> oxidizing bacteria was found to be 0.3 to >10 % of primary productivity  
333 and their biomass constituted 1.4 to 41% of total bacterial biomass in lakes of different types  
334 (Utsumi et al., 1998; Bastviken et al., 2003; Eller et al., 2005; Sundh et al., 2005).
- 335 - CH<sub>4</sub> emissions have been reported to correspond to 24-37% of summer productivity in a small  
336 shallow hypereutrophic lake (Strayer and Tiedje, 1978), and plant-mediated CH<sub>4</sub> fluxes from  
337 stands of *Typha* sp. and *Cladium jamaicense* in the Everglades were 3-14% of net ecosystem  
338 production (Chanton et al., 1993).

339 Collectively, these findings illustrate the large general importance of plant primary production for  
340 CH<sub>4</sub> production, and a large quantitative importance of CH<sub>4</sub> in relation to overall carbon cycling in  
341 aquatic ecosystems.

342

343 Aerobic CH<sub>4</sub> production associated with surfaces of terrestrial upland vegetation or litter has been  
344 comprehensively reviewed (Carmichael et al., 2014; Liu et al., 2015). Experimental studies observed  
345 CH<sub>4</sub> production on upland plants that if extrapolated would result in > 200 Tg CH<sub>4</sub> per year (up to 36%  
346 of the total global CH<sub>4</sub> budget), while other experiments showed much smaller or negligible  
347 production (Carmichael et al., 2014). Most of this information rely on small-scale incubation studies  
348 and field-scale observations of associated fluxes are rare. Given the large vegetation and litter  
349 surface area, potential associated ecosystem fluxes could be important as discussed further in  
350 Section 4.6 below. Other interactions between terrestrial upland vegetation includes the supply  
351 organic substrates for microbial CH<sub>4</sub> production in soil. However, most of this upland soil CH<sub>4</sub> may be  
352 oxidized in aerated top soils (Saunois et al., 2020), unless high soil moisture lead to emissions (Lohila  
353 et al., 2016) or lateral export with soil and ground water lead to emissions in recipient streams  
354 (Natchimuthu et al., 2017; Lupon et al., 2019).

355

356 There can be important, yet complex interactions between plants and temporal variability of CH<sub>4</sub>  
357 emissions. There is growing support for a positive exponential relationship between ecosystem CH<sub>4</sub>  
358 emissions and temperature (Yvon-Durocher et al., 2014; Aben et al., 2017). This temperature  
359 regulation interacts with supply rates of organic substrates for CH<sub>4</sub> production from plant primary  
360 production, and with the other plant effects on CH<sub>4</sub> dynamics, including availability of plant-mediated  
361 transport pathways (Figure1). Accordingly, there can be plant-induced enhancement of ecosystem  
362 CH<sub>4</sub> emissions in synergy with the direct temperature effect, by increased plant productivity,

363 biomass, or prolonged plant growing seasons (Andresen et al., 2017). For example, synergies  
364 between nutrient additions and temperature treatments have been confirmed in experimental  
365 studies with submerged or floating macrophytes (*Elodea canadensis*, *Potamogeton crispus*,  
366 *Ceratophyllum demersum*, *Myriophyllum spicatum*, and *Azolla filiculoides*) (Davidson et al., 2018),  
367 and in some cases plant productivity and composition effects have been found more important for  
368 CH<sub>4</sub> emissions than temperature changes (Davidson et al., 2015; Davidson et al., 2018; Aben et al.,  
369 2022). Another study in less productive nitrogen limited boreal lakes found weak influence of whole  
370 lake nitrogen additions on CH<sub>4</sub> emissions (Klaus et al., 2018), indicating that the importance of plant-  
371 effects versus effects of other factors for CH<sub>4</sub> emissions may differ among ecosystem types.

372

373 \*\*\*\*FIGURE 2 NEAR HERE\*\*\*\*

374

#### 375 **4.2 High latitude wetlands**

376 In high latitude wetlands, the water table position and nutrient status determine the plant  
377 community composition that then affects CH<sub>4</sub> flux through influence on production, oxidation, and  
378 transport as has been comprehensively discussed in earlier reviews on wetland methane emissions  
379 (Bartlett and Harriss, 1993; Bubier and Moore, 1994; Blodau, 2002; Whalen, 2005; Lai, 2009;  
380 Bridgman et al., 2013; Abdalla et al., 2016; Kuhn et al., 2021). Early studies on CH<sub>4</sub> fluxes showed the  
381 correlation between water table position and daily flux, where water tables near the surface had the  
382 highest emissions and correlated with vegetation composition and moss types (Bubier, 1995).  
383 Further research demonstrated the role of vascular plants in controlling CH<sub>4</sub> emissions from high  
384 latitude wetlands by influencing both substrate availability through recent photosynthates, oxidation  
385 and the transport pathways (Joabsson et al., 1999). However, time lags between photosynthesis and  
386 CH<sub>4</sub> production as well as the storage of CH<sub>4</sub> in sediments can mask the relationship between primary  
387 productivity and emissions, which may become clearer when integrated over seasonal to annual time  
388 scales (Blodau, 2002).

389

390 Recent syntheses have shown that broader wetland classes can be used to predict fluxes because  
391 these capture the mean water table position and dominant vegetation types (Olefeldt et al., 2013;  
392 Turetsky et al., 2014; Treat et al., 2018; Kuhn et al., 2021). The major classes have been defined  
393 broadly as freshwater marshes, fens with sedges and mosses, and bogs with *Sphagnum* mosses  
394 (Table 1). CH<sub>4</sub> emissions are variable within and across these classes, with highest emissions from  
395 marshes, followed by fens and bogs, respectively (Table 1). The presence of permafrost is also a key  
396 control on CH<sub>4</sub> emissions; emissions from permafrost wetlands are on average 60% lower than  
397 northern wetlands without permafrost (Treat et al., 2018). Coastal tidal-influenced and saline

398 marshes have generally been considered separately but observations are limited for many northern  
399 regions (Poffenbarger et al., 2011). Other northern ecosystems such as upland tundra and boreal  
400 forests can also emit CH<sub>4</sub> (Lohila et al., 2016; Zona et al., 2016). While these wetland or land cover  
401 classes show considerable variability within each class, likely because these classes include the  
402 variability among the plot and community scale vegetation composition discussed above, these are  
403 useful categories because there are significant differences in CH<sub>4</sub> flux among them (Table 1).  
404 Furthermore, often they can be distinguished with some success from remote sensing observations  
405 or machine learning analysis (Webster et al., 2018; Matthews et al., 2020; Olefeldt et al., 2021). Until  
406 now, uncertainties in the distribution of different wetland types and water bodies have prevented  
407 comparisons between high latitude emissions from models that prescribe wetland emissions based  
408 on area coverage (Melton et al., 2013) and observations (Olefeldt et al., 2013; Turetsky et al., 2014;  
409 Treat et al., 2018; Kuhn et al., 2021).

410

411 Temperature provides another broad control on CH<sub>4</sub> flux across high latitude wetlands by controlling  
412 the timing and length of the growing season (also influenced by radiation) and by influencing the soil  
413 temperature. Generally, annual CH<sub>4</sub> fluxes increase with annual temperature in wetlands (Delwiche  
414 et al., 2021), with temperate wetlands having higher annual emissions (median: 13.3 g CH<sub>4</sub> m<sup>-2</sup> yr<sup>-1</sup>)  
415 than similar types of wetlands in boreal (7.2 g CH<sub>4</sub> m<sup>-2</sup> yr<sup>-1</sup>) or Arctic regions (6.2 g CH<sub>4</sub> m<sup>-2</sup> yr<sup>-1</sup>; (Treat  
416 et al., 2018). This is likely due to the direct influence of temperature on rates of microbial CH<sub>4</sub>  
417 production (Dunfield et al., 1993; Yavitt et al., 1997; Treat et al., 2015), but also the indirect effects of  
418 vegetation productivity. In northern soils where freezing is common, peak temperatures in soils lag  
419 peak air temperatures. This causes a delay in peak CH<sub>4</sub> emissions relative to the peak season GPP  
420 that can range from nearly simultaneous to as much as 60 days (Delwiche et al., 2021). Due to these  
421 warm soil temperatures into the fall, as well as CH<sub>4</sub> storage in sediments, emissions outside of the  
422 growing season can account for a substantial portion (13-47%) of annual emissions (Treat et al.,  
423 2018). Thus, even in the absence of vegetation activity, CH<sub>4</sub> emissions can occur in northern wetlands  
424 (Mastepanov et al., 2008; Zona et al., 2016).

425

426 Questions remain about the response of CH<sub>4</sub> flux in northern wetlands to disturbance, including  
427 permafrost thaw, fire, flooding, and other extreme events, such as excessive heat and drought.  
428 However, there are only a few sites with long enough records of CH<sub>4</sub> fluxes to be able to discern  
429 these types of events, and due to lag times between production and emission, measurements should  
430 continue beyond the growing season into the shoulder seasons and winter.

431

432 **4.3 Rice paddies**

433 Rice probably represents the plant genus responsible for most plant-mediated CH<sub>4</sub> emissions. Rice  
434 field emissions are estimated to be 24-40 Tg CH<sub>4</sub> yr<sup>-1</sup> (Bridgham et al., 2013; Sauniois et al., 2020). The  
435 CH<sub>4</sub> production in rice paddies is stimulated by the release of labile organic matter synthesized by  
436 photosynthesis via the roots. More than 50% of the rice CH<sub>4</sub> emission is generated from the root  
437 exudates or decomposed plant material (Lu and Conrad, 2005). Rice production demands the  
438 establishment and maintenance of flooded conditions that reduce the presence of oxygen and other  
439 electron acceptors (e.g., nitrate or sulfate) favouring CH<sub>4</sub> production. The high sediment CH<sub>4</sub>  
440 production rates result in high CH<sub>4</sub> emissions via rice aerenchyma to the atmosphere, bypassing the  
441 sediment oxic-anoxic interface.

442

443 Most of the global production of rice happens at lower latitudes where the temperatures and also  
444 CH<sub>4</sub> production rates are high (Fernando, 1993), and the rice paddies act as landscape emission  
445 hotspots. Considering that CH<sub>4</sub> production is positively correlated with temperatures (Yvon-Durocher  
446 et al., 2014), increasing global temperatures may trigger an increase in overall rice-mediated CH<sub>4</sub>  
447 fluxes. Furthermore, given the predicted increase in global world population from the present 8 to  
448 >10 billion by 2100 (Ezeh et al., 2012), the growing demand for food will likely increase rice paddy  
449 cultivation and increase CH<sub>4</sub> fluxes from rice paddies in the future.

450

451 Several management approaches have been tested in order to minimize the CH<sub>4</sub> emissions from rice  
452 paddies, with the application of gypsum and phosphogypsum, and the application of sulfate with N  
453 fertilizer (e.g., ammonium sulfate) being the most common practices (Liu et al., 2018). Sulfate  
454 reduction is an anaerobic process energetically more favourable than methanogenesis and therefore  
455 sulfate addition decreases CH<sub>4</sub> production and emissions without affecting the rice growth or yield.  
456 Other strategies have focused on management of the flooding regime or straw amendment  
457 (Belenguer-Manzanedo et al., 2022). Genetic modifications have also been successful in regulating  
458 CH<sub>4</sub> emissions, e.g., the addition of a transcription barley gene *SUSIBA2* to experimental rice strains,  
459 promoted a shift in rice carbon flow decreasing its CH<sub>4</sub> emissions (Su et al., 2015). A decrease in 50%  
460 CH<sub>4</sub> emission with the *SUSIBA2 japonica* and *SUSIBA2 indica* rice types have been reported, due to a  
461 decrease in organic carbon to the soil, without decreasing rice yield (Du et al., 2021). We do not  
462 intend to claim that genetic modified rice strains should indiscriminately replace non-modified rice  
463 types, given that this controversial topic is out of the scope of this study. More relevant in the  
464 frameworks of this review is that these findings exemplify how plant physiology and genetic traits of  
465 plant communities can influence ecosystem CH<sub>4</sub> cycling.

466

467 **4.4 Lakes, reservoirs, and ponds**

468 Substrates for CH<sub>4</sub> production in lakes, reservoirs, and ponds (standing water systems collectively  
469 referred to as lentic waters) include input organic matter from plant primary production in upstream  
470 catchments and littoral zones, and from phytoplankton and periphyton production. The catchment  
471 organic matter contributions can fuel substantial CH<sub>4</sub> emission also in systems with low internal  
472 primary production. Positive relationships between in-system primary productivity (aquatic plants,  
473 periphyton, and phytoplankton supplying the most labile organic material) and CH<sub>4</sub> production have  
474 also been suggested (Bastviken et al., 2008; Duc et al., 2010; Davidson et al., 2015; West et al., 2015;  
475 Grasset et al., 2018).

476  
477 Most available CH<sub>4</sub> emission measurements from lentic ecosystems consider fluxes from the open  
478 water surface, where diffusive flux and ebullition dominates. From a mechanistic point of view, such  
479 emissions are not directly linked to primary productivity or CH<sub>4</sub> production rates, and instead  
480 represent a balance between multiple processes, including CH<sub>4</sub> production, different transport  
481 pathways, and CH<sub>4</sub> oxidation. However, for reservoirs, a recent meta-analysis found a clear  
482 relationship between such open water fluxes and chlorophyll-a levels, representing a proxy for in-  
483 system phytoplankton primary productivity (Deemer and Holgerson, 2021). If the recently suggested  
484 oxic surface water CH<sub>4</sub> production is primarily linked with planktonic photosynthesis, this adds a  
485 direct link between phytoplankton metabolism and CH<sub>4</sub> emissions (Bižić et al., 2020; Günthel et al.,  
486 2020). A whole-lake experiment where the primary producers were <sup>13</sup>C-labelled by adding <sup>13</sup>C-  
487 bicarbonate to two lakes provides relevant information to evaluate this possibility. The experiment  
488 showed that the dissolved surface water CH<sub>4</sub> responded most strongly to the <sup>13</sup>C addition  
489 approximately one month after the <sup>13</sup>C signal reached the particulate organic carbon (Bastviken et  
490 al., 2008). This indicates a delayed link between dissolved CH<sub>4</sub> and lake primary production (Figure 3).  
491 Accordingly, this whole-lake C tracer experiment points towards the importance of the longer,  
492 indirect link between primary production and epilimnetic CH<sub>4</sub> via anoxic sediment CH<sub>4</sub> production,  
493 rather than direct, oxic surface water CH<sub>4</sub> production linked to photosynthesis in the studied small  
494 lakes. However, conditions may differ among systems and the debate about the ecosystem  
495 implications of oxic surface water CH<sub>4</sub> production (Günthel et al., 2019; Peeters et al., 2019;  
496 Hartmann et al., 2020) requires additional consideration.

497  
498 **\*\*\*\*FIGURE 3 NEAR HERE\*\*\*\***

499  
500 Littoral zones include areas with submerged, floating-leaved (rooted or non-rooted), and emergent  
501 vegetation. Few field studies have focused on submerged macrophytes but their potential  
502 importance was recently highlighted (Hilt et al., 2022), and experimental studies with submerged

503 plants have indicated high importance for system CH<sub>4</sub> dynamics and emissions in interaction with  
504 nutrient concentrations (see Section 4.1) (Davidson et al., 2015; Davidson et al., 2018; Aben et al.,  
505 2022). Free-floating plants can also have important effects on CH<sub>4</sub> fluxes by providing substrates for  
506 CH<sub>4</sub> production while also influencing CH<sub>4</sub> transport, as outlined in Section 3 and being detailed  
507 elsewhere (Kosten et al., 2016; Oliveira Junior et al., 2021). In a field study of a tropical floodplain  
508 lake, open water fluxes within 0-20 m of dense floating macrophyte populations (*Eichhornia* sp.) was  
509 shown >2-fold greater than from areas being > 45 m away from such vegetation belts with no depth  
510 difference among locations (Peixoto et al., 2015). This indicates substantial local contributions of  
511 decaying plant biomass for ebullition.

512

513 A number of field studies in littoral zones have focused on emissions from emergent vascular aquatic  
514 macrophytes (Juutinen et al., 2003; Larmola et al., 2004; Bergstrom et al., 2007). Littoral flux  
515 measurements and regulation seem largely consistent with wetland observations (see sections 2.3  
516 and 4.2 above). It has been suggested that the littoral zones with plant mediated fluxes can  
517 contribute a large share of the total flux (the sum of vegetated and open water fluxes) if the  
518 vegetated area is extensive enough. Littoral vegetated zones contributed 66-77% of the ice-free  
519 period integrated CH<sub>4</sub> fluxes from three Finnish lakes (Juutinen et al., 2003). In a Canadian lake, a  
520 detailed study showed that 26% of the area covered by emergent macrophytes contributed 80% of  
521 the mean daily CH<sub>4</sub> flux during the ice-free season, and that 34% of the flux from the vegetated area  
522 was emitted via plant mediated flux while 62% was emitted by ebullition among the plants  
523 (Desrosiers et al., 2022). This study also showed that plant community composition was important  
524 for determining the predominant flux pathway.

525 In some cases, littoral plant-mediated CH<sub>4</sub> emissions are large enough to create CH<sub>4</sub> flux gradients  
526 along lake shores (Figure 4). Recent airborne imaging spectroscopy has identified hot spot zones  
527 within 40 m from standing water, possibly indicating the importance of combined emissions from  
528 open water and littoral zones (Elder et al., 2020). Recent mapping of >4500 arctic-boreal lakes  
529 showed that the area with emergent vegetation comprised 16% of the lake area and including CH<sub>4</sub>  
530 fluxes from this area was suggested to increase estimates of total lake CH<sub>4</sub> emissions by 18-25%  
531 (Kyzivat et al., 2022). One challenge is ensuring that regional scaling of CH<sub>4</sub> fluxes does not double-  
532 count lake littoral zones as both a part of the lake CH<sub>4</sub> emission estimate and as a part of the wetland  
533 CH<sub>4</sub> emission estimate.

534

535 The issue of double-counting CH<sub>4</sub> emissions from lakes and wetlands are further discussed elsewhere  
536 (Thornton et al., 2016). Fundamentally, this is a question about matching land cover categories with  
537 flux measurements. There may be a mismatch between the traditional definition of lakes including



538 their littoral zones versus a more “methanocentric” land cover categorization based on underlying  
539 mechanisms and regulation. The latter leads to a potential conclusion that all vegetated aquatic  
540 environments – also in lakes, ponds, and reservoirs – are better categorized as wetlands of different  
541 types, while open water, being more easily distinguished by remote sensing and being dominated by  
542 other CH<sub>4</sub> flux pathways and other flux regulation, represents another main land cover category.  
543 Such a methanocentric land cover categorization may have many advantages for CH<sub>4</sub> emission  
544 extrapolation but require replacing traditional ecosystem definitions with land cover categories  
545 based on predominant biogeochemical processes. Overall, littoral zones require additional attention  
546 to properly quantify lentic CH<sub>4</sub> emissions, and efforts developing a clear distinction of how all CH<sub>4</sub>  
547 emitting land cover types are classified and combined with the most relevant flux observations are  
548 critically needed (Kuhn et al., 2021; Olefeldt et al., 2021).

549

550 **\*\*\*\*FIGURE 4 NEAR HERE\*\*\*\***

551

552 Most examples above from lentic systems indicates that presence of plants increases CH<sub>4</sub> emissions.  
553 However, in hypereutrophic aquatic systems which emit large amounts of CH<sub>4</sub>, such as agricultural  
554 dams (Grinham et al., 2018; Ollivier et al., 2019), there are observations that increased presence of  
555 vegetation can result in less nitrogen and phosphorous in the water, more dissolved oxygen, and  
556 lower methane emissions (Malerba et al., 2022). Speculated reasons could include combinations of  
557 factors mentioned above such as root zone oxygenation and trapping of bubbles along with more  
558 surfaces suitable for CH<sub>4</sub> oxidisers, and possibly also reduced phytoplankton production if there was  
559 light competition.

560

#### 561 ***4.5 Amazon floodplain forests***

562 The Amazonian lowland basin forest is an example of a vast tropical floodplain forest (Melack and  
563 Hess, 2011; Hess et al., 2015). It represents a highly diverse, yet unique environment constituted by a  
564 rich mosaic of terrestrial, aquatic and transitional ecosystems subjected to seasonal and permanent  
565 waterlogging (Junk et al., 2011). The Amazon River flows 4000 km from the Andes to the Atlantic,  
566 carrying more water than any other river. The basin includes an extensive system of riverine flooded  
567 forests, which in some cases are flooded on a seasonal basis and in other cases are flooded all  
568 through the year. Hot tropical temperatures, extensive tree cover with continuous supply of fresh  
569 carbon substrates and anoxia due to flooding create favourable conditions for CH<sub>4</sub> production and  
570 emission (Wassmann et al., 1992). Therefore, it is not surprising when this region alone is responsible  
571 for emitting ~8% (46.2±10.3 Tg CH<sub>4</sub> yr<sup>-1</sup>) (Basso et al., 2021) of the global CH<sub>4</sub> emissions estimated to  
572 576 Tg CH<sub>4</sub> yr<sup>-1</sup> (Saunois et al., 2020).

573

574 The floodplain forests experience extensive flooding, and the flooding depth and duration is linked to  
575 the type of forest (low várzea, high várzea or chavascal), location (upstream or downstream of the  
576 river) and draining catchment characteristics (Junk et al., 2011). Since the late 1980s, attempts have  
577 been made to quantify different CH<sub>4</sub> sources of tropical floodplain forests and significant CH<sub>4</sub>  
578 emissions are reported from the flooded forest soils, floating and rooted macrophytes, aquatic  
579 sources within the flooded forest and adjoining open waters of lakes and rivers (example data in  
580 Table 1) (Bartlett et al., 1988; Devol et al., 1988; Bastviken et al., 2010; Sawakuchi et al., 2014;  
581 Barbosa et al., 2020; Barbosa et al., 2021). The trees are adapted to anoxic environment through  
582 morphological and physiological traits, including gas transport to supply root cells with O<sub>2</sub>, to survive  
583 flooding (Junk et al., 2010; Parolin and Wittmann, 2010). As other woody plants experiencing  
584 flooding, they have lenticels on the stems for such gas exchange and the gas exchange contribute to  
585 an extensive recently discovered plant mediated CH<sub>4</sub> flux from tree stems (Gauci et al., 2010).

586

587 Large seasonal variation in inundation period and areas is a key challenge to identifying the variability  
588 in space and time of CH<sub>4</sub> emissions from the Amazon flooded forests (Barbosa et al., 2021). This is  
589 further complicated when new CH<sub>4</sub> emissions pathways such as those from flooded trees are  
590 discovered, when regionalization of emissions from previously known CH<sub>4</sub> sources in the Amazon  
591 basin is already a challenging task (Melack et al., 2022). In recent years, flooded trees are not only  
592 known to influence CH<sub>4</sub> dynamics through their fresh carbon supply stimulating methanogenesis and  
593 root-zone O<sub>2</sub> leakage stimulating CH<sub>4</sub> oxidation - they are also known to emit CH<sub>4</sub> (Pangala et al.,  
594 2017). Further, stem flux from flooded trees were estimated to contribute nearly half the regional  
595 Amazon basin CH<sub>4</sub> emissions (Pangala et al., 2017). Apart from the tree-mediated flux of CH<sub>4</sub> from  
596 the root zone to the atmosphere, enhanced by morphological adaptations in flooded trees, recent  
597 studies now suggest that trees themselves can produce CH<sub>4</sub> within their tree stems albeit at lower  
598 rates (Covey et al., 2012; Covey and Megonigal, 2019).

599

600 CH<sub>4</sub> emissions from 13 forested floodplains along the Amazon River in Brazil was measured,  
601 attempting to capture spatial variability (Pangala et al., 2017). The measurements were made during  
602 a single high-water event leading to uncertainty in extrapolations over time. In a recent study, tree  
603 stem CH<sub>4</sub> emissions were reported to continue throughout all four hydrological distinct seasons  
604 (rising, flooded, receding and low water period), albeit at lower rates (Gauci et al., 2022). The study  
605 also found a strong relationship between water table depth below the surface and tree CH<sub>4</sub> emission  
606 and highlighted that riparian floodplain margins with water table below-ground contribute an  
607 additional 2.3-3.9 Tg CH<sub>4</sub> yr<sup>-1</sup> to the atmosphere. Applying this to global tropical wetlands yield a non-

608 flooded riparian tree CH<sub>4</sub> emission estimate of 6.4 Tg CH<sub>4</sub> yr<sup>-1</sup> with recognition that the area-related  
609 extrapolation is uncertain (Gauci et al., 2022).

610  
611 While studies so far suggest CH<sub>4</sub> emissions from the floodplain forest are significant, the variability  
612 and regulation remains largely unknown, including the extent to which the spatial variability is driven  
613 by soil dynamics, climate, flooding regime, or tree species traits. For instance, white-water (carrying  
614 sediments from the Andes), clear-water (draining the ancient shields) and black-water (draining  
615 white sand areas and soils with humic substances) are known to emit different quantities of CH<sub>4</sub>  
616 (Pangala et al., 2017), thereby greatly influencing the rates and overall regional annual CH<sub>4</sub> estimates  
617 in synergy with ecosystem processes including plant influences on CH<sub>4</sub> fluxes (Figure 1). The nutrients  
618 associated with water types strongly determine the floodplain forest ecology and species  
619 composition. While studies in other forested wetlands highlight a link between tree traits and tree  
620 CH<sub>4</sub> flux (Barba et al., 2019; Covey and Megonigal, 2019), the Amazonian flooded forest tree species  
621 influence on CH<sub>4</sub> flux remains unclear.

622  
623 In recent years there has been a renewed threat to Amazon forests from the expansion of cattle  
624 ranching, low-productivity agriculture, dams, mining, fire, deforestation and intensified flooding and  
625 prolonged dry period, changing the face of the flooded forests at an alarming rate. How CH<sub>4</sub>  
626 emissions, particularly from flooded trees, respond to such change is still unclear. Amazonian tree  
627 mortality rates are already increasing in many intact forests and Amazonian forest species  
628 composition has been affected by flooding and recent droughts. The mortality of wet-affiliated  
629 Amazonian tree genera has increased in places where the dry season has intensified (Aleixo et al.,  
630 2019) or where the hydrology was changed by damming (Assahira et al., 2017). Such changes may  
631 have profound impact on the CH<sub>4</sub> dynamics from flooded forests and on future tropical CH<sub>4</sub>  
632 emissions.

633

#### 634 **4.6 Vegetation-related CH<sub>4</sub> emissions in other forests**

635 Beyond the Amazon floodplain, the number of CH<sub>4</sub> flux measurements from tree stems growing on  
636 temperate and tropical peatlands, in upland forest ecosystems and in riparian forests has been  
637 increasing. Temperate ecosystems growing in both riparian lowland ecosystems and peatlands have  
638 demonstrated CH<sub>4</sub> emissions from both ash trees (*Fraxinus mandschurica*; (Terazawa et al., 2007),  
639 alder (*Alnus glutinosa*; (Gauci et al., 2010; Pangala et al., 2015) and birch (*Betula pubescens*; (Pangala  
640 et al., 2015). All trees tended to demonstrate a decrease in stem emissions with distance from the  
641 forest floor as found in many other studies of wetland tree emissions. The two species birch and  
642 alder measured in a UK alder carr ecosystem, tended to operate differently in terms of their seasonal

643 CH<sub>4</sub> emissions with birch giving a large range of emissions depending on season of up to ~200 μg m<sup>-2</sup>  
644 hr<sup>-1</sup> in summer and as low as ~50 μg m<sup>-2</sup> hr<sup>-1</sup> in winter. This is in contrast to alder, where emissions  
645 ranged between ~100 μg m<sup>-2</sup>hr<sup>-1</sup> in winter and around ~180 μg m<sup>-2</sup> hr<sup>-1</sup> in summer (Pangala et al.,  
646 2015) suggesting differences in the CH<sub>4</sub> transport mechanisms from soil to emission, between the  
647 tree species. More controlled mesocosm experiments with alder saplings gave further insights into  
648 factors controlling the size of emissions (Pangala et al., 2014) with pore water CH<sub>4</sub> concentrations  
649 and stem lenticel density exhibiting a major control over emissions.

650

651 Further controls over tree stem emissions have been found for Southeast Asian peat swamp forests  
652 where a large range of CH<sub>4</sub> fluxes measured from 10 peatland tree species (zero to ~200 μg m<sup>-2</sup> hr<sup>-1</sup>)  
653 seemed to be controlled by wood specific density (with the higher the wood density, the lower the  
654 emission), soil pore water CH<sub>4</sub> concentrations and stem diameter (Pangala et al., 2014). Cumulatively,  
655 emissions from tree stems in these ecosystems, as with those from the Amazon floodplain,  
656 dominated ecosystem emissions when scaled. This is in contrast to emissions from trees in  
657 neotropical peatlands in Panama where trees contributed ~30% of total ecosystem emissions where  
658 factors such as species identity, stem diameter, water level and soil temperature explained much of  
659 the observed variance in tree stem emission (Sjögersten et al., 2020). Fluxes, were, however larger  
660 than those from SE Asian peat swamps with individual stem fluxes, particularly near the stem base in  
661 the range 1-30 mg m<sup>-2</sup> d<sup>-1</sup>. While palm emissions in these Panamanian peat swamps tended to be  
662 negligible, confining tree-stem emissions solely to hard wood trees, in Peruvian peatlands palm  
663 stems tended to emit substantial quantities of CH<sub>4</sub> (Soosaar et al., 2022).

664

665 In upland ecosystems, trees inhabit areas of lower water availability given free draining soils and  
666 substrates and so there is less soil CH<sub>4</sub> being produced in relatively sparse anaerobic microsites. That  
667 said, emissions are still observed, particularly at the stem bases (30 cm above the forest floor) in  
668 Panamanian upland trees where emissions at around ~100 μg m<sup>-2</sup> hr<sup>-1</sup> were comparable to those  
669 observed in Borneo peat swamps and temperate alder carr. Other results, tend to conflict with some  
670 trees demonstrating some emission, but with no clear vertical pattern of exchange and with high  
671 variability (Pitz et al., 2018; Barba et al., 2019; Barba et al., 2021) though net uptake has been  
672 observed in other studies (Machacova et al., 2021; Gauci et al., 2022).

673

674 While trees are clearly capable of emitting soil-derived CH<sub>4</sub> at their stem bases, uptake of CH<sub>4</sub> further  
675 up the tree stem has been suggested (Jeffrey et al., 2020; Gauci et al., 2022). In parallel, there is a  
676 growing literature regarding abiotic oxic CH<sub>4</sub> production at plant and litter surfaces generating  
677 emissions (reviewed by (Carmichael et al., 2014; Liu et al., 2015). This literature is based on

678 observations of CH<sub>4</sub> release from plant tissue enclosed in CH<sub>4</sub>-free vials or chambers. Mechanisms  
679 are discussed and plant produced molecules with detachable methyl groups are potential precursors.  
680 The CH<sub>4</sub> release seem enhanced by UV-light, increasing temperature, reactive oxygen species and  
681 other types of plant stress. Measured CH<sub>4</sub> production rates are often low in absolute numbers in the  
682 experimental settings but scaling to large plant surface areas results in global emission estimates in  
683 the order of 8 – 176 Tg CH<sub>4</sub> yr<sup>-1</sup> (Carmichael et al., 2014; Liu et al., 2015) to a large extent from  
684 forests, or 1-31% of the global CH<sub>4</sub> emissions (using a global top-down estimate of 576 Tg CH<sub>4</sub> yr<sup>-1</sup>;  
685 Table 1). Because of the high uncertainty in extrapolation of small-scale incubation studies and  
686 limited field scale observations, this flux was not yet specifically considered in recent global CH<sub>4</sub>  
687 budgets (Saunois et al., 2020), and large emissions from aerobic CH<sub>4</sub> production on plants and forests  
688 are challenging to reconcile with *in-situ* observations at present. There may be some bias in *in-situ*  
689 flux measurements if not properly capturing UV- effects, but top-down inversion estimates based on  
690 atmospheric concentration gradients in space and time should capture all emissions. Hence, overall  
691 tree and vegetation emissions at ecosystem scales remain enigmatic and represent an important  
692 challenge to constrain and predict the global CH<sub>4</sub> budget.

693

#### 694 **4.7 Coastal ecosystems**

695 Globally, vegetated coastal areas including salt marshes, mangroves and seagrass meadows are  
696 estimated to emit 3.6 to 6.2 Tg CH<sub>4</sub> yr<sup>-1</sup>, with the highest fluxes observed in salt marshes followed by  
697 mangroves and seagrass meadows (Table 1) (Al-Haj and Fulweiler, 2020; Rosentreter et al., 2021). As  
698 previously described in other environments, the roots can transport CH<sub>4</sub> from the sediments directly  
699 to the atmosphere bypassing the CH<sub>4</sub> oxidation in the sediments. In an Australian mangrove, tree  
700 emissions from pneumatophores (roots growing upwards into the air for gas exchange increasing  
701 root system O<sub>2</sub> access) accounted for ~ 26% of the mangrove emissions (Jeffrey et al., 2019).  
702 Although no direct evidence of plant-mediated emissions from seagrass have been found in the  
703 literature, it has been suggested that dead seagrass or detached parts deposited in the sediment can  
704 provide methylated compounds that can sustain CH<sub>4</sub> production for a long time (Schorn et al., 2022).  
705 As in other freshwater environments, plants and cyanobacteria have a key role as suppliers of  
706 organic matter. A main difference from freshwater environments is that coastal environments tend  
707 to be sulfate-rich areas, and sulfate-reducing microorganisms outcompete methanogens for organic  
708 substrates limiting CH<sub>4</sub> production (Oremland and Polcin, 1982; Schorn et al., 2022). Zhuang et al  
709 (2018) observed that methylotropic methanogenesis contributed to 43-87% of the total CH<sub>4</sub>  
710 production in the sulfate reduction zone at the top layer of the sediment, and the remaining  
711 produced by hydrogenotrophic methanogenesis. The lower layers of the sediment, where sulfate  
712 was depleted, 67-98% of the CH<sub>4</sub> was produced by hydrogenotrophic methanogenesis. Acetoclastic

713 methanogenesis contributed a maximum of 31% of the CH<sub>4</sub> production in organic-rich sediment  
714 (Zhuang et al., 2018). Due to the thicker sediment redox gradient where sulfate metabolism  
715 dominates, CH<sub>4</sub> production is confined to deeper sediment layers than in freshwaters. Therefore,  
716 plant mediated CH<sub>4</sub> emissions in coastal areas may be more extensive via plants with deeper roots.  
717 Despite this limitation, methylotropic methanogenesis can still maintain significant CH<sub>4</sub> production,  
718 sustaining a sediment-water flux of approximately 1.7 mg CH<sub>4</sub> m<sup>-2</sup> d<sup>-1</sup> in seagrass sediments (Schorn  
719 et al., 2022). Coastal environments are estimated to account for up to ~1% of the global CH<sub>4</sub> budget  
720 and contribute more than 60% of the marine CH<sub>4</sub> emission (Al-Haj and Fulweiler, 2020).

721  
722 Sulfate reduction is associated with anaerobic oxidation of CH<sub>4</sub> (AOM), which can significantly  
723 influence the fluxes of CH<sub>4</sub> from the sediment to the water column in coastal areas (Egger et al.,  
724 2018). In addition to AOM, rooted plants transport oxygen to the root zone and sediment, where  
725 aerobic methane oxidation can occur. Fluxes from deforested mangroves and cut seagrass indicate  
726 an increase in CH<sub>4</sub> emissions that was attributed to cessation of the O<sub>2</sub> transport and oxidation in the  
727 sediment (Giani et al., 1996).

728  
729 As in any other aquatic ecosystem, plants have a major role as source of organic substrates.  
730 Therefore, CH<sub>4</sub> emissions from coastal environments may increase with intensified land-use and  
731 eutrophication of coastal areas leading to greater primary production and organic matter sediment  
732 load (Rosentreter et al., 2021).

733

734

## 735 **5. Conclusions and need for future studies**

736 Overall, primary production is indirectly the foundation for all contemporary non-fossil CH<sub>4</sub>  
737 emissions, corresponding to approximately 80 % of the annual atmospheric CH<sub>4</sub> budget, or 431-671  
738 Tg CH<sub>4</sub> yr<sup>-1</sup> including fluxes from agriculture, forestry, other land use, biomass burning, and from the  
739 waste sector (Saunois et al., 2020; bottom-up fluxes 2008-2017 used). In addition, plants can  
740 influence the extent and dynamics of ecosystem CH<sub>4</sub> fluxes in many ways (Figure 1). Importantly,  
741 plant communities respond rapidly to environmental change. Therefore, adequate understanding  
742 and predictions of relevant plant community features are key to adequate assessments of future  
743 landscape CH<sub>4</sub> emissions. To approach such understanding, improved quantitative knowledge on CH<sub>4</sub>  
744 fluxes from plant habitats under varying conditions are needed. This leads to several demands on  
745 future ecosystem-level research of vegetation-related CH<sub>4</sub> fluxes including:

- 746 • All CH<sub>4</sub> sources and sinks associated with vegetation need to be properly identified and  
747 quantified, and fluxes with different regulation need to be distinguished.

- 748 • Flux variability should be examined across spatial and temporal scales of relevance for local  
749 habitat/vegetation communities to distinguish short-term local variability from long-term  
750 large-scale trends.
- 751 • Comprehensive long-term ecosystem CH<sub>4</sub> flux assessments are needed, simultaneously  
752 quantifying plant-related emissions and other major types of emissions, along with careful  
753 characterization of properties and processes in studied ecosystems that can provide  
754 regulatory or predictive understanding. This should be done at sites representative of  
755 different vegetation types, to support dynamic ecosystem scale modelling of CH<sub>4</sub> flux.
- 756 • Tropical ecosystems need increased scientific attention, given their great importance for  
757 contemporary and future CH<sub>4</sub> emissions.
- 758 • For flux extrapolation, more accurate areal distributions of key ecosystems and habitats  
759 based on criteria optimized for estimating CH<sub>4</sub> emissions is needed. This includes, e.g.,  
760 distinguishing different types of vegetated wetlands, such as the respective areas of bogs,  
761 fens and marshes in precise and dynamic ways that capture changes over time (Melack and  
762 Hess, 2022).

763

764 Addressing these key knowledge gaps effectively would greatly benefit from improvements in the  
765 methodologies to assess greenhouse gas emissions, vegetation dynamics, and potential driver  
766 variables at high resolution across landscapes (Bastviken et al., 2022). Because plant communities  
767 can change quickly in response to land use, hydrology, and climate, an appropriate understanding of  
768 present and future plant community dynamics are essential to predict CH<sub>4</sub> emissions in a rapidly  
769 changing world.

770

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780

## 781 **7. Author Statement**

782 DB: Conceptualization; Data curation; Formal analysis; Investigation; Methodology; Project  
783 administration; Resources; Supervision; Validation; Visualization; Writing - original draft; Writing -  
784 review & editing. CT, SRP, VG, AEP: Data curation; Investigation; Formal analysis; Writing - original  
785 draft; Writing - review & editing. MK: Investigation; Validation; Writing - review & editing. MG:  
786 Software; Formal analysis; Visualization. MBR: Formal analysis; Visualization. HOS: Data curation;  
787 Investigation; Formal analysis; Methodology; Validation; Visualization; Writing - original draft;  
788 Writing - review & editing.

789

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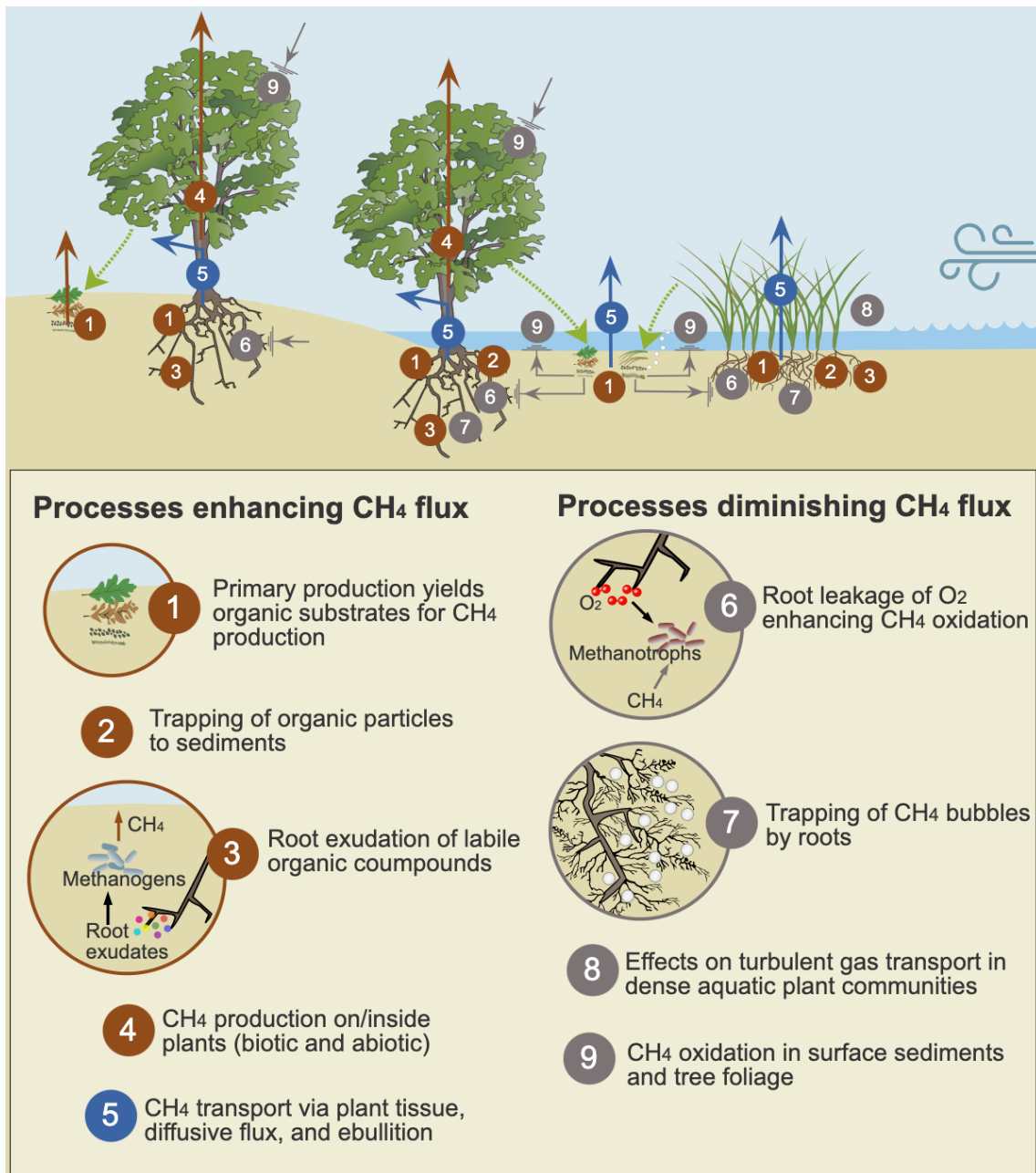
**Table 1.** Examples of net CH<sub>4</sub> emission ranges observed in ecosystem habitats with different primary producer communities. Flux denotes range as measured by min-max or IQR (interquartile range). Global CH<sub>4</sub> budget estimates are provided at the lower part of the Table to enable easy comparisons.

| Biome and ecosystem          | Habitat                                                                                                                                                                                                           | Flux range (mg CH <sub>4</sub> m <sup>-2</sup> d <sup>-1</sup> ) | Global flux (Tg CH <sub>4</sub> yr <sup>-1</sup> ) (seasonally integrated) | References                                                                                                                    |
|------------------------------|-------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------|------------------------------------------------------------------|----------------------------------------------------------------------------|-------------------------------------------------------------------------------------------------------------------------------|
| High-latitude wetlands       | Bog <sup>1</sup>                                                                                                                                                                                                  | -4.3 - 278; 7 - 57 (IQR)                                         | 9 (permafrost region)                                                      | (Bao et al., 2021; Kuhn et al., 2021; Treat et al., 2021)                                                                     |
|                              | Fen <sup>2</sup>                                                                                                                                                                                                  | -30 - 371; 20 - 107 (IQR)                                        | 21.5 (permafrost region)                                                   |                                                                                                                               |
|                              | Marsh <sup>3</sup>                                                                                                                                                                                                | -38 - 761; 71 - 200 (IQR)                                        | 2.6 (permafrost region)                                                    |                                                                                                                               |
| Rice fields                  |                                                                                                                                                                                                                   |                                                                  | 25-38                                                                      | (Saunois et al., 2020)                                                                                                        |
| Lakes, reservoirs, and ponds | Open water emission                                                                                                                                                                                               | 0.1 - 2497; 9 - 153 (IQR)                                        | 31 - 73                                                                    | Measured fluxes: (Rosentreter et al., 2021). Seasonally integrated global flux; (Johnson et al., 2021; Johnson et al., 2022). |
|                              | Littoral with emergent plants                                                                                                                                                                                     | 8 - 1392                                                         | 6 - 15 <sup>4</sup>                                                        |                                                                                                                               |
| Tropical floodplain forests  | Global flooded tree flux                                                                                                                                                                                          |                                                                  | 37.1 (stem flux)                                                           | (Pangala et al., 2017; Gauci et al., 2022)                                                                                    |
|                              | Non-flooded tree flux                                                                                                                                                                                             |                                                                  | 6.4 (stem flux)                                                            | (Gauci et al., 2022) (Gauci et al., 2022)                                                                                     |
|                              | Amazonian flooded forest                                                                                                                                                                                          | 1 - 6504 (stem m <sup>2</sup> )                                  | 12.7 - 21.1 (stem flux)                                                    | (Pangala et al., 2017; Gauci et al., 2022) (Gauci et al., 2022)                                                               |
|                              | Aquatic diffusive flux                                                                                                                                                                                            | 2.5 - 50.5                                                       |                                                                            | (Barbosa et al., 2020) (data from flooded forest only)                                                                        |
|                              | Aquatic ebullition                                                                                                                                                                                                | 45 - 168                                                         |                                                                            | (Barbosa et al., 2021) (data from flooded forest only) (Barbosa et al., 2020)                                                 |
| (Barbosa et al., 2021)       | Amazon aquatic total flux                                                                                                                                                                                         | 36 - 617                                                         | 9.7 ± 5.2                                                                  | (Pangala et al., 2017) (Amazon flooded forest)                                                                                |
| Global forests               | Stem flux in upland and wetland forests                                                                                                                                                                           | -14 - 6504 (stem m <sup>2</sup> )                                | 60                                                                         | (Covey and Megonigal, 2019)                                                                                                   |
|                              | Abiotic CH <sub>4</sub> production on plant and litter surfaces                                                                                                                                                   |                                                                  | 8-176                                                                      | (Carmichael et al., 2014; Liu et al., 2015)                                                                                   |
| Coastal vegetation           | Mangroves                                                                                                                                                                                                         | -1.1 - 1169                                                      | 1.5 - 4.0                                                                  | (Al-Haj and Fulweiler, 2020; Rosentreter et al., 2021).                                                                       |
|                              | Salt marshes                                                                                                                                                                                                      | -1.5 - 1510                                                      | 1.1 - 2.0                                                                  |                                                                                                                               |
|                              | Seagrass meadows                                                                                                                                                                                                  | 0.02 - 6.4                                                       | 0.5 - 1.0                                                                  |                                                                                                                               |
| <b>Flux category</b>         | <b>Global CH<sub>4</sub> flux estimates for 2008-2017 extracted from Saunois et al. (2020) for comparison</b><br>Tg CH <sub>4</sub> yr <sup>-1</sup> (mean and range; bottom-up estimates unless otherwise noted) |                                                                  |                                                                            |                                                                                                                               |

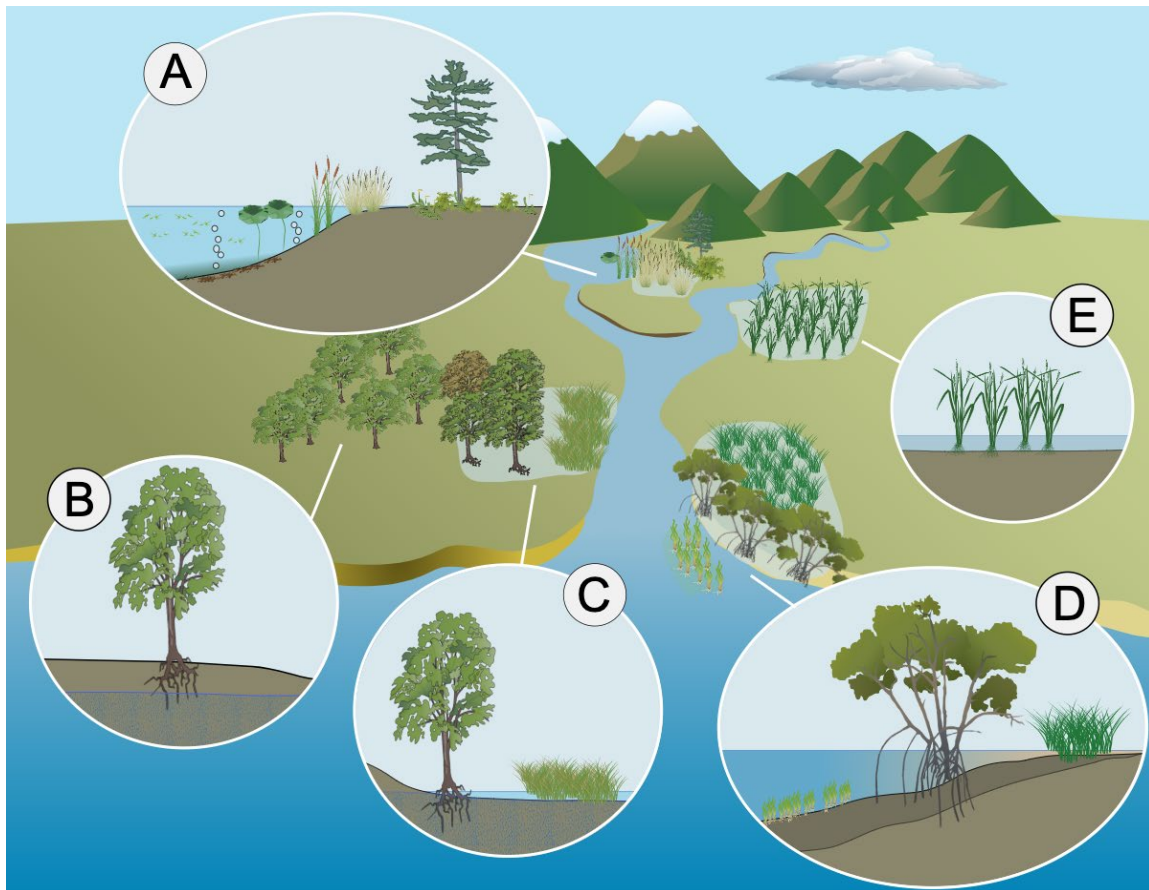
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|-------------------------------------------|----------------------|-------------------------------|
| <i>Total global emissions (top-down)</i>  | <i>576 [550–594]</i> | <i>(Saunois et al., 2020)</i> |
| <i>Total global emissions (bottom-up)</i> | <i>737 [594–881]</i> |                               |
| <i>- Fossil fuel production and use</i>   | <i>128 [113–154]</i> |                               |
| <i>- Agriculture and waste</i>            | <i>206 [191–223]</i> |                               |
| <i>- Biomass and biofuel burning</i>      | <i>30 [26–40]</i>    |                               |
| <i>- Wetlands</i>                         | <i>149 [102–182]</i> |                               |
| <i>- Other natural emissions (total)</i>  | <i>222 [143–306]</i> |                               |
| <i>Freshwater</i>                         | <i>159 [117–212]</i> |                               |
| <i>Biogenic open ocean and coastal</i>    | <i>6 [4–10]</i>      |                               |

<sup>1</sup>Ombrotrophic; low productivity; Sphagnum-dominated. <sup>2</sup>Variable hydrological connectivity and productivity; Sphagnum, sedges, shrubs. <sup>3</sup>Minerotrophic, high productivity; emergent macrophytes, sedges, often in standing water. <sup>4</sup>Based on estimates of 10 Tg CH<sub>4</sub> yr<sup>-1</sup> or 21% of open water emissions (see references).

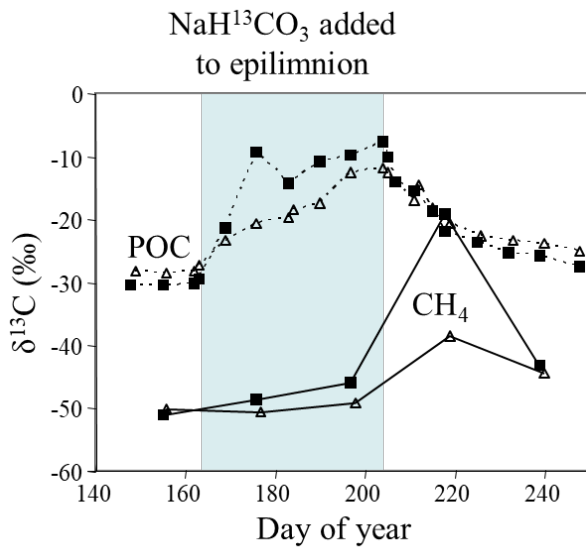




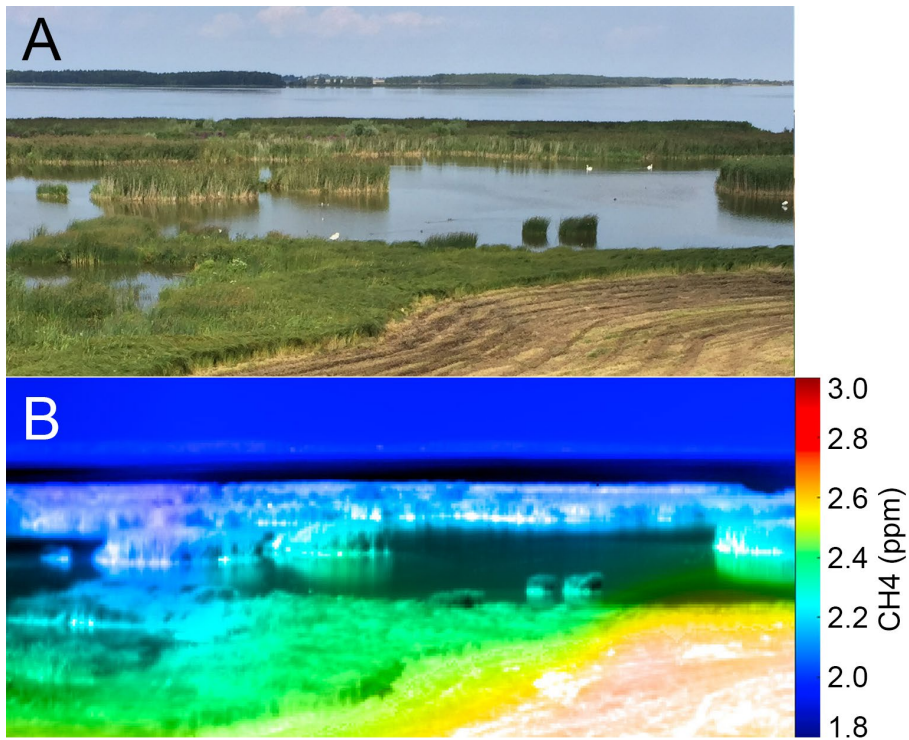
**Figure 1.** Examples of how plants and other primary producers can influence terrestrial and aquatic ecosystem CH<sub>4</sub> fluxes. The colours on numbers and arrows represent CH<sub>4</sub> production (brown), transport (blue), oxidation (grey), and source of organic substrate (green). Plant drawings are generic to vascular non-woody and woody plants but are intended to represent all primary producers, although not all illustrated mechanisms are relevant for non-vascular plants. This figure represents a simplification (for a more extensive list of mechanisms and their global implications please see e.g., Carmichael et al., 2014; Liu et al., 2015; Bodmer et al., 2021).



**Figure 2.** Examples of ecosystems where plant influences are important for total net CH<sub>4</sub> emissions: A) Lentic open water (lakes, ponds, and reservoirs) and freshwater marsh, bog, and fen ecosystems along a hydrological gradient characteristic of higher latitudes; B) upland forests; C) floodplain forests and wetlands exemplifying lower latitudes; D) coastal vegetated areas (salt marshes, mangroves, and seagrass meadows); E) rice fields. See Figure 1 and text for illustration of mechanisms by which the plant communities influence CH<sub>4</sub> fluxes in the respective ecosystems.



**Figure 3.** Results from a whole-lake experiment where <sup>13</sup>C-labelled sodium bicarbonate were added to the epilimnion to act as <sup>13</sup>C tracer of primary production in the ecosystem (Pace et al., 2004). The shaded area denotes the time period of <sup>13</sup>C addition. The response of epilimnetic particulate organic carbon (POC; including phytoplankton) and CH<sub>4</sub> is shown and were offset in time. Black squares and open triangles are Paul and Peter Lake, respectively, Wisconsin, USA. Results illustrate a clear but delayed link between recent primary production and dissolved CH<sub>4</sub> in a whole-lake context. (Modified from Bastviken et al., 2008.)



**Figure 4.** Image of a lake shore with a hyperspectral camera optimized for sensitive detection of  $\text{CH}_4$  (Gålfalk et al., 2016). Panel A shows the visible light image of the scene and Panel B shows mean  $\text{CH}_4$  mixing ratio along each line of sight from the camera to the background. The wind comes from the lake towards the shore which moves emitted  $\text{CH}_4$  towards the lower parts of the image. Some  $\text{CH}_4$  emissions from the outer reed belts (*Phragmites australis*) are visible via slightly elevated nearby mixing ratio with a somewhat patchy appearance depending on local wind mixing. Larger  $\text{CH}_4$  emissions from the near-shore sedge vegetation are clearly visible. For methods behind the imaging, see Gålfalk et al., (2017).