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Half of global methane emissions come from highly variable aquatic ecosystem sources

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Atmospheric methane is a potent greenhouse gas that plays a major role in controlling the Earth's climate. The causes of the renewed increase of methane concentration since 2007 are uncertain given the multiple sources and complex biogeochemistry. Here, we present a metadata analysis of methane fluxes from all major natural, impacted and human-made aquatic ecosystems. Our revised bottom-up global aquatic methane emissions combine diffusive, ebullitive and/or plant-mediated fluxes from 15 aquatic ecosystems. We emphasize the high variability of methane fluxes within and between aquatic ecosystems and a positively skewed distribution of empirical data, making global estimates sensitive to statistical assumptions and sampling design. We find aquatic ecosystems contribute (median) 41% or (mean) 53% of total global methane emissions from anthropogenic and natural sources. We show that methane emissions increase from natural to impacted aquatic ecosystems and from coastal to freshwater ecosystems. We argue that aquatic emissions will probably increase due to urbanization, eutrophication and positive climate feedbacks and suggest changes in land-use management as potential mitigation strategies to reduce aquatic methane emissions.

Methane (CH_4) is the second-most important greenhouse gas after carbon dioxide (CO_2), accounting for 16–25% of atmospheric warming to date[1,2]. Atmospheric methane has nearly tripled since pre-industrial times, with a steady rise between 1984 and 1999 (8.4 ± 0.6 ppb yr^{-1}) (ref. [3]), little or no growth between 2000 and 2006 (0.5 ± 0.5 ppb yr^{-1}) (ref. [3]) and renewed growth to present day (2007–2019: 7.3 ± 0.6 ppb yr^{-1}) (refs. [3–6]). Whether the renewed increase is caused by emissions from anthropogenic or natural sources or by a decline in the oxidative capacity of the atmosphere or by a combination of all three factors remains unresolved[7–9]. Depending on the approach used, total methane emissions from natural and anthropogenic sources range between 538 and 884 Tg yr^{-1} (refs. [10,11]). However, top-down versus bottom-up estimates of methane sources and sinks do not match, underscoring the incomplete knowledge of global methane dynamics[10,11].

Reducing the uncertainty in methane emission intensities and partitioning emissions to anthropogenic and natural sources is challenging. At the global scale, bottom-up methane emissions from aquatic ecosystems are not well constrained due to reasons that include the lack of observations, uncertainties associated with surface areas and the risk of 'double counting' of ecosystem types. In particular, methane emissions from small lakes, reservoirs, aquaculture ponds and coastal wetlands were insufficiently assessed in the Intergovernmental Panel on Climate Control Fifth Assessment Report[1] and in the most recent global methane budget[11]. Finally, anthropogenic disturbances such as dam construction[12], eutrophication[13] and wetland modification[14], along with climate feedbacks such as microbial responses to warming[15] and changes in hydrology[16,17], all lead to an alteration of methane fluxes that are currently difficult to account for at the global scale. A better understanding of the aquatic contribution to global methane emissions is therefore critical to a more robust understanding of atmospheric methane dynamics.

Global aquatic methane emissions

In this article, we present a metadata analysis of aquatic methane flux measurements based on inventory, remote sensing and modelling efforts to revise bottom-up estimates of areal methane fluxes (mg CH_4 m^{-2} d^{-1}) (Extended Data Table 1) and global methane emissions (Tg CH_4 yr^{-1}) (Table 1) from rivers and streams, lakes and ponds, reservoirs, estuaries, mangroves, salt marshes, seagrasses, tidal flats, aquaculture ponds and continental shelves, along with recently published estimates of global methane emissions from freshwater wetlands[11], rice paddies[11], continental slope and open ocean[18]. Our global synthesis reveals median (Q1–Q3) methane emissions from aquatic ecosystems of 269 (202–424) Tg CH_4 yr^{-1} or mean (lower–upper

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Table 1 | Annual methane emissions from aquatic ecosystems

Aquatic ecosystem	Bottom-up global methane emission ($\mathrm{Tg\,CH_4\,yr^{-1}}$)		Reference
	Median (Q1–Q3)	**Mean (±c.i.95%)**	
Rivers (ice-corrected)	5.8 (1.8–21.0)	30.5 ± 17.1	This study
Lakes (ice-cover, ice-melt corrected)			
$<0.001\,\mathrm{km^2}$	21.2 (9.1–53.5)	54.5 ± 48.5	This study
0.001–$0.010\,\mathrm{km^2}$	13.2 (5.6–33.1)	31.1 ± 23.7	This study
0.01–$0.10\,\mathrm{km^2}$	4.4 (1.4–16.7)	22.4 ± 18.4	This study
0.1–$1.0\,\mathrm{km^2}$	3.0 (1.1–8.0)	9.9 ± 7.0	This study
$>1\,\mathrm{km^2}$	14.0 (6.0–31.0)	33.0 ± 45.0	This study
All lakes	55.8 (23.3–142.3)	150.9 ± 73.0	This study
Reservoirs (ice-cover, ice-melt corrected)			
$<1\,\mathrm{km^2}$	0.4 (0.1–1.3)	2.4 ± 4.7	This study
$>1\,\mathrm{km^2}$	14.7 (8.7–27.1)	22.0 ± 6.4	This study
All reservoirs	15.1 (8.8–28.4)	24.3 ± 8.0	This study
Freshwater wetlands	150.1 (138.3–164.6)	148.6 ± 15.2	Saunois et al.[11,a]
Freshwater aquaculture ponds	4.4 (0.4–7.9)	14.0 ± 18.8	This study
Rice cultivation	29.9 (24.9–32.1)	29.8 ± 6.7	Saunois et al.[11,b]
Total inland waters	**261.0 (197.5–396.2)**	**398.1 ± 79.4**	**This study**
Estuaries	0.23 (0.02–0.91)	0.90 ± 0.29	This study
Coastal wetlands			
Salt marshes	0.18 (0.02–0.89)	2.00 ± 1.51	This study
Mangroves	0.21 (0.06–0.77)	1.46 ± 0.91	This study
Seagrasses	0.13 (0.07–0.21)	0.18 ± 0.09	This study
Tidal flats	0.17 (0.04–2.70)	4.2 ± 4.9	This study
Coastal aquaculture ponds	0.62 (0.01–1.00)	5.9 ± 15.1	This study
Continental shelves	5.7 (3.6–20.4)	17.2 ± 34.0	This study
Slope (200–2,000 m)	0.30 (0.23–0.40)	0.36 ± 0.93	Weber et al.[18,c]
Open ocean (>2,000 m)	0.91 (0.75–1.12)	1.0 ± 1.7	Weber et al.[18,c]
Total coastal and open ocean	**8.4 (4.8–28.4)**	**33.2 ± 37.6**	**This study**
Total aquatic	**269.4 (202.3–424.6)**	**431.3 ± 87.9**	**This study**

We present median, first (Q1) and third (Q3) quartile, mean and c.i.95% of bottom-up global aquatic methane emissions. Although two decimal places imply more accuracy than the methods provide, this was done to avoid losing the emission estimates from ecosystems with $<1\,\mathrm{Tg\,CH_4\,yr^{-1}}$. [a]Based on 13 biogeochemical models for wetland emissions, bottom-up estimate years 2008–2017. [b]Based on five inventory models for rice cultivation, bottom-up estimate years 2008–2017. [c]Based on two machine-learning models; c.i. is the mean of the lower and upper bound of the 95% level.

confidence interval 95% (c.i.95%)) emissions of 431 (343–519) $\mathrm{Tg\,CH_4\,yr^{-1}}$. Our bottom-up estimates show a larger range with a lower (median) or higher (mean) central tendency than the most recent bottom-up estimate for aquatic ecosystems and wetlands[11] (Table 2). The interquartile range (IQR) ($222\,\mathrm{Tg\,CH_4\,yr^{-1}}$) of our global aquatic emissions is larger than the c.i.95% ($176\,\mathrm{Tg\,CH_4\,yr^{-1}}$), which suggests that methane flux variability is larger than uncertainty. The high variability in data sources is linked to the complexity of how methane is produced, transported and consumed before reaching the atmosphere, with different transport pathways (diffusion, ebullition, plant-mediated), physical interfaces (water–atmosphere, sediment–atmosphere), ecosystem conditions (impacted versus natural), and temporal (diel/tidal, seasonal, inter-annual) and spatial scales involved. We find that the statistical distributions of our datasets are ecosystem-specific and that all aquatic ecosystems have positively skewed distributions (Fig. 1), which greatly affects the results for global upscaling (Fig. 2). If the observational data represent the actual flux distribution, then mean values would be the appropriate measure to scale global emissions. However, our assessment cannot rule out substantial bias in the available flux estimates resulting from limited temporal and spatial coverage and non-random selection of study sites. Under such circumstances, median values provide a more conservative estimate for upscaling.

Methane emissions (Q1–Q3) from freshwater wetlands (138–165 $\mathrm{Tg\,CH_4\,yr^{-1}}$) and lakes (23–142 $\mathrm{Tg\,CH_4\,yr^{-1}}$) are the largest aquatic sources, followed by rice cultivation (25–32 $\mathrm{Tg\,CH_4\,yr^{-1}}$), reservoir (9–28 $\mathrm{Tg\,CH_4\,yr^{-1}}$), coastal ocean (5–28 $\mathrm{Tg\,CH_4\,yr^{-1}}$, <200 m), and river and stream emissions (2–21 $\mathrm{Tg\,yr^{-1}}$). While uncertainties for bottom-up (and top-down) global estimates are still high, natural, impacted and human-made aquatic ecosystems, including wetlands, could be equally important to, or more important than, direct anthropogenic emissions[11,19]. Depending on the approach used (median or mean), we find that 41% or 53% of the global methane emissions can be attributed to aquatic ecosystems, whereas non-aquatic systems contribute the remainder, for example, 8% or 6% to other land sources such as onshore geological, wild animals and termites[11], and 51% or 41% to direct anthropogenic activities such as enteric fermentation and manure, landfill and waste, coal mining, gas and oil industry, transport, and biomass and biofuel burning[11] (Table 2).

Our revised global estimates of aquatic ecosystem emissions are mostly higher than previous estimates (Supplementary Table 1).

Table 2 | Global methane sources and sinks

	Average methane emissions (Tg CH_4 yr^{-1})	Range of methane emissions (Tg CH_4 yr^{-1})	Period of time	Reference
Aquatic sources				
BU[a]	352	253–455	(2008–2017)	Saunois et al.[11]
BU (median, Q1–Q3)	269	202–425	(1978–2019)	This study
BU (mean, lower–upper c.i.95%)	431	343–519	(1978–2019)	This study
Non-aquatic sources				
Natural sources (BU)				
Geological (onshore)	38	13–53	(2008–2017)	Saunois et al.[11]
Wild animals	2	1–3	(2008–2017)	Saunois et al.[11]
Termites	9	3–15	(2008–2017)	Saunois et al.[11]
Anthropogenic sources (BU)				
Agriculture and waste				
Enteric fermentation and manure	111	106–116	(2008–2017)	Saunois et al.[11]
Landfills and waste	65	60–69	(2008–2017)	Saunois et al.[11]
Fossil fuels				
Coal mining	42	29–60	(2008–2017)	Saunois et al.[11]
Oil and gas	79	66–92	(2008–2017)	Saunois et al.[11]
Industry	3	0–7	(2008–2017)	Saunois et al.[11]
Transport	4	1–12	(2008–2017)	Saunois et al.[11]
Biomass and biofuel burning				
Biomass burning	17	14–26	(2008–2017)	Saunois et al.[11]
Biofuel burning	12	10–14	(2008–2017)	Saunois et al.[11]
Total methane sources				
BU[b]	737	594–881	(2008–2017)	Saunois et al.[11]
BU (median, Q1–Q3)	651	505–892	(1978–2019)	This study
BU (mean, lower–upper c.i.95%)	813	646–986	(1978–2019)	This study
Total methane sinks				
BU	625	500–798	(2008–2017)	Saunois et al.[11]
TD	556	501–574	(2008–2017)	Saunois et al.[11]

Bottom-up (BU) global aquatic methane sources compared with other BU natural and anthropogenic methane sources and BU and top-down (TD) methane sinks. [a]Wetlands, freshwater, oceanic sources, permafrost and rice cultivation. [b]Differences of 3 Tg CH_4 yr^{-1} compared with the sum of aquatic and non-aquatic sources (BU) (2008–2017) of 734 Tg CH_4 yr^{-1} in this table are due to rounding errors[11].

However, the comparison to previous studies is challenging due to the difference in upscaling methods, dissimilar statistical treatment and uncertainties in surface areas. In brief, our combined lake, pond and reservoir emissions are higher than the first mean global estimate for these ecosystems[20], similar to recent estimates based on chlorophyll *a* scaling[21], and lower than recent upscaling from mean values[21]. The relatively lower emissions we present here are largely the result of an 'ice' correction term, which had not previously been implemented in the computation of global lake and reservoir emissions (Supplementary Table 1). Thus, while our mean annual emissions for lakes, ponds and reservoirs are not higher than recent estimates, our mean areal methane fluxes (Extended Data Table 1) are higher than those recently reported[21]. These higher areal fluxes probably result from our inclusion of recent studies that add smaller water bodies and whose methods capture ebullition[22]. The result is a database containing disproportionately more studies from research published since 2015 (205 of 313 lakes or reservoirs; 65%). We find that the smallest lakes are responsible for the largest emission, with ~37% of total lake emission coming from lakes <0.001 km² regardless of mean or median (Table 1).

Our ice-corrected river and stream emissions are substantially higher than the first reported global mean[20], which used a low surface area, only 21 sites for upscaling and no data from the tropics. A more recent review[23], using an updated surface area[24] and 385 sites, reported an average diffusive flux that is higher than our global estimate (Supplementary Table 1). Here we increase the number of sites and include ebullitive fluxes to report fluxes from five latitudinal bands. Approximately 30% of ice-corrected fluxes are from the equatorial latitudes due to the large ice-free surface area of streams and rivers (Supplementary Table 2). However, the data density of total and ebullitive river fluxes is low, particularly for mid to high latitudes.

Our coastal ocean emission estimate is higher than previous mean estimates[11,18,25], which did not include some of the coastal habitats. The large range and uncertainty of coastal methane fluxes that we find in this study are associated with the paucity of data, but also with the high spatial and temporal variability of fluxes in coastal ecosystems driven by, for example, tidal pumping and salinity gradients[26]. More than half of the global coastal ocean emission is attributed to large continental shelf areas, mainly gas seeps (ebullition) and estuarine plumes (Extended Data Fig. 1). However, per area, methane fluxes from continental shelves are much lower compared with those from other coastal ecosystems (Extended Data Table 1). We find particularly high areal mean methane fluxes

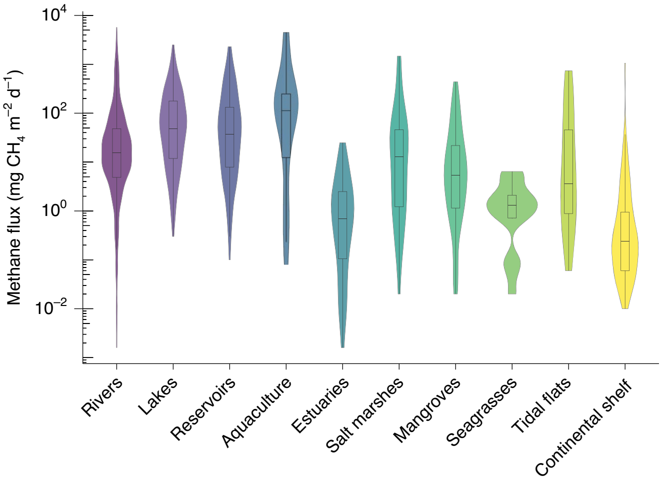

Fig. 1 | Inland water and coastal ocean areal methane fluxes. The violin plots include box plots showing median, lower (Q1) and upper (Q3) quartiles and 1.5 times the length of the interquartile range of methane fluxes from streams and rivers, lakes, reservoirs, aquaculture ponds (coastal and freshwater), estuaries, mangroves, salt marshes, seagrasses, tidal flats and continental shelves compiled in this study. Note the natural-log (ln) scale on the *y*-axis. All datasets (non-log transformed) are positively skewed (skewness coefficient >1, range 1.1–9.8).

from coastal aquaculture ponds that are 7–430 times higher than from non-converted coastal habitats (mangroves, salt marshes, seagrasses, tidal flats) and nearly 70,000 times higher than from the open ocean[18].

Increasing aquatic methane emissions

The renewed increase in atmospheric methane has been attributed to climate feedbacks on wetlands, increased fossil fuel use, methane production by livestock and declining removal of methane by tropospheric OH (sinks)[8,9,19]. Our findings complement this picture by highlighting how human alterations to aquatic ecosystems increase methane emissions. The strongest growth in atmospheric methane since 2007 has been reported in the tropics and subtropics (30° N to 30° S), with fuel burning and both agricultural and ruminant populations as the major sources[8]. Despite the global coverage of our data, we did not detect clear latitudinal trends of methane emissions from aquatic ecosystems, except for the emissions from coastal wetlands peaking at 30° N (Extended Data Fig. 2). Instead of latitudinal patterns, we found methane emissions increasing from rivers to lakes and wetlands, from natural to impacted and eutrophic ecosystems (Extended Data Figs. 3 and 4) and from coastal marine to freshwater ecosystems (Fig. 3). Particularly pronounced is the difference of areal fluxes between aquaculture farms and non-converted coastal and inland water ecosystems (Extended Data Table 1).

As a result of global warming, increased methane emissions are expected across biomes and latitudes because of the higher activities of methanogenic archaea at elevated temperatures relative to methanotrophic microorganisms[27,28]. However, not only archaea but also saprotrophic fungi and cyanobacteria can produce methane under various environmental conditions[29–31]. While the methane flux from these microorganisms is currently poorly constrained, it is intuitive to assume that it increases with increasing eutrophication and temperature. This is indeed supported by a general positive relationship between methane emissions and temperature across biomes[15,27] and the enhanced methane emissions that we found with increasing temperature in coastal wetlands (Extended Data Fig. 5). However, the effect of warming and wetting may have synergistic effects on methane emissions from freshwater wetlands. In fact, when freshwater wetlands dry, both the water-table level and time of inundation drop, which may foster methane oxidation and thereby reduce emissions[32]. Finally, global warming impacts are predicted to be particularly important at high latitudes[33]: therefore, a better understanding of the expected changes in methane emissions from the Arctic[34], from hydrate deposits in the shallow ocean, permafrost soils[35] and melting sea ice[36] and glaciers, for example, would be required.

Human alterations (for example, damming and rice cultivation) increased the surface area of perennial and seasonal freshwater ecosystems by 94,000 km^2 and ~230,000 km^2, respectively, between 1984 and 2014[17]. This areal expansion of inland waters compounds our finding of areal methane fluxes from aquatic ecosystems. It also indicates that total methane fluxes from aquatic ecosystems will probably increase due to habitat expansion and/or transformation.

Uncertainties in aquatic methane sources

Methane emissions from individual sources are challenging to measure given the large spatial and temporal variation in net emissions from production, consumption and transport pathways and due to mixing in the atmosphere[37]. Ebullition often constitutes a substantial, albeit highly variable, fraction of the total aquatic methane flux. While many ecosystems have a large proportion of emissions driven by ebullition (for example, some lakes and reservoirs), other ecosystems may have negligible ebullition rates (for example, seagrasses). Furthermore, different physical interfaces need to be considered when estimating whole-ecosystem emissions, in particular in coastal ecosystems, where methane can be released by exposed (sediment–air flux) or inundated (water–air flux) sediments following the tidal cycle[26]. Plant-mediated methane fluxes can be important in aquatic ecosystems dominated by plants, but the relative contribution of plant-mediated and tree fluxes to total emissions is highly uncertain at a global scale[38]. It is also likely that there is a bias in site selection, but the direction of this bias is unknown.

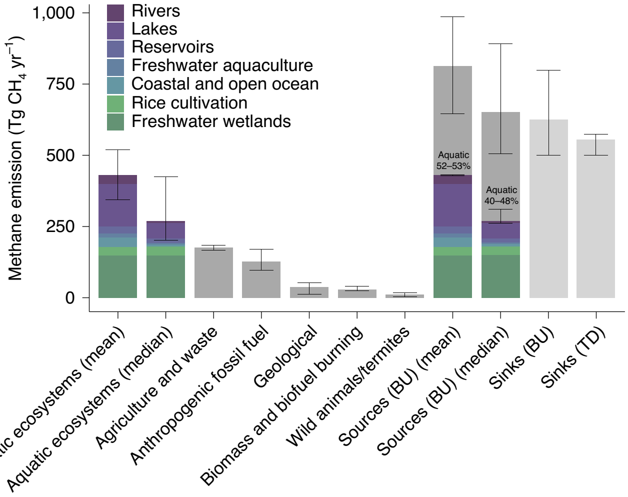

Fig. 2 | Global aquatic methane emissions compared with other global methane sources and sinks. Cumulative BU mean (IQR) and median (±c.i.95%) aquatic methane emissions estimated in this study compared with other BU methane sources versus BU and TD methane sinks from Saunois et al.[11] (Table 2). The coastal and open ocean estimate includes emissions from estuaries, salt marshes, mangroves, seagrasses, tidal flats, coastal aquaculture ponds, continental shelves, continental slopes and the open ocean[18]. Error estimates for freshwater wetland and rice emissions are based on inventory and biogeochemical modelling efforts, therefore showing comparably low variability and uncertainty.

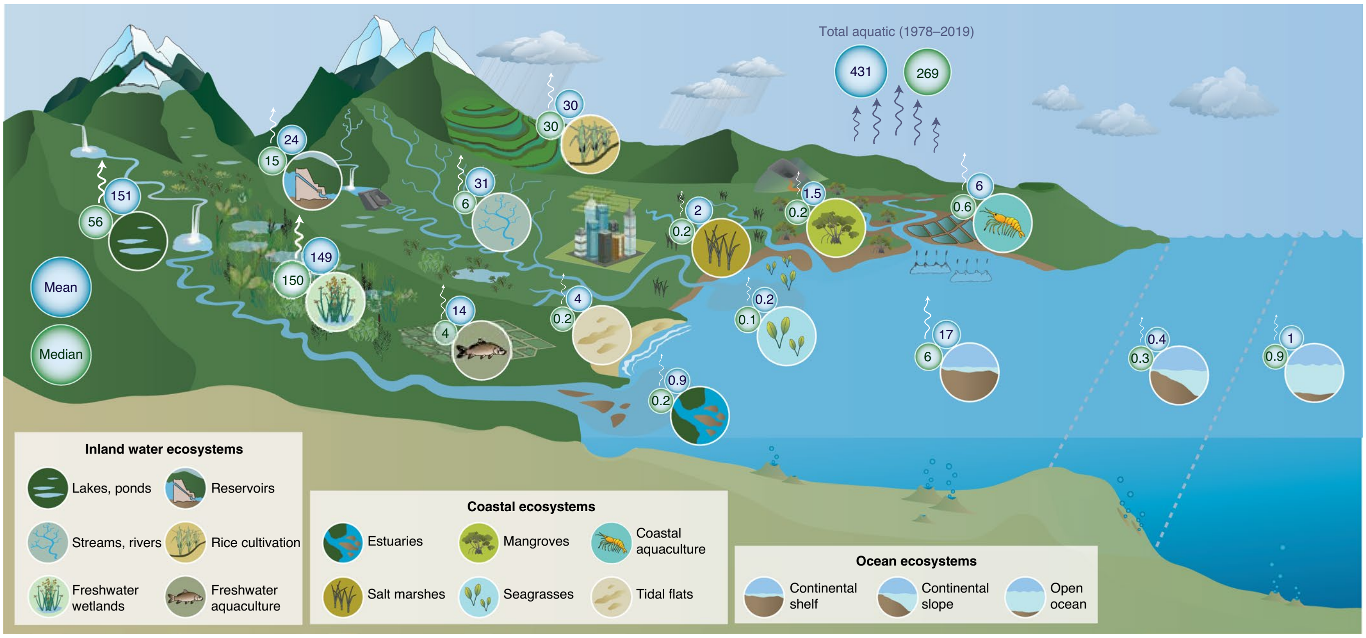

Fig. 3 | Global aquatic methane emissions from headwater streams to the open ocean. Numbers are Tg CH_4 yr^{-1}. Mean emissions are shown in blue circles, and median emissions are shown in green circles. The relative importance of the factors controlling methane distribution and emissions varies along the land–ocean aquatic continuum.

Very high or very low values can also be related to inadequate sampling methods, incorrect data analysis or reporting.

Another challenge lies within the statistical comparison of different upscaling methods. For example, a recent estimate of global methane emissions from freshwater wetlands was based on an ensemble of 13 biogeochemical models constrained with remote sensing of surface inundation and inventory-based wetland area[39]. These wetland models use standardized climate, atmospheric CO_2 and dynamic wetland area, but to operate at global scales and across multiple wetland types, the models generalize fundamental processes of methane production, oxidation and transport to the atmosphere. By contrast, here, we upscale data-driven methane fluxes from streams, rivers, lakes and reservoirs using a Monte Carlo approach and relationships between methane fluxes and latitudinal band (streams and rivers) (Supplementary Table 2), size bin (lakes and small reservoirs) or chlorophyll *a* concentration (large reservoirs) (Supplementary Table 3). For coastal ecosystems, where fewer data were available, we multiplied rates by surface area.

There are uncertainties associated with surface areas of aquatic ecosystems and the risk of 'double counting' due to issues in clearly identifying different ecosystem types. In particular, small ponds and lakes, streams and rivers, and coastal wetlands are difficult to separate from freshwater wetlands using coarse-to-moderate spatial-resolution optical and radar remote sensing. Recent wetland area mapping aims to reduce the problem of double counting by explicitly removing inland waters from remote-sensing-based surface inundation data[40]. However, there remains a need for finer spatial-resolution approaches that would permit better mapping and counting of both small ponds and streams to partition these from vegetated wetlands.

When we combine our median bottom-up aquatic methane emissions with emissions from thermogenic, pyrogenic and other methane-producing sectors[11], we find a discrepancy of about 26 Tg CH_4 yr^{-1} compared with bottom-up sinks[11], which is similar to the difference of +20 Tg CH_4 yr^{-1} required to account for the change in atmospheric concentrations since 2007 (7.3 ppb yr^{-1})[3] (Table 2). Our median bottom-up total source estimate exceeds the top-down sinks[11] by 95 Tg CH_4 yr^{-1}, which is close to the source–sink imbalance of 112 Tg CH_4 yr^{-1} reported in the global methane budget[11]. However, our mean bottom-up global source estimate exceeds bottom-up and top-down global sinks[11] by 188–257 Tg CH_4 yr^{-1} (Table 2). While we are unable to explain such high source–sink imbalances, they are consistent with the large uncertainties related to bottom-up and top-down global sinks[11,19,41]. In particular, global OH concentrations are difficult to measure, and thus atmospheric chemistry models are used to simulate these concentrations, which vary by 10–20% (refs. [42,43]). The upland soil methanotrophic sink is equally uncertain and known only via numerical modelling estimates and sparse observations made by soil chambers and flux towers[11,44]. Given these uncertainties, there may be room for large aquatic sources of methane to the atmosphere that we identify in our study.

Aquatic methane management interventions

Reducing methane emissions from aquatic ecosystems is an effective pathway to mitigate climate change, particularly those from freshwater wetlands, which account for 35–55% of aquatic emissions (Table 1). Salinities of ~10–15 are an important tipping point for biogeochemical processes in wetlands[45], as sulfate-reducing bacteria, favoured by more saline waters, can outcompete methanogens. Hence, converting freshwater wetlands back to salt marshes by restoring tidal flows is a promising strategy to reduce methane emissions[14] while increasing carbon sequestration. Converting aquaculture ponds and salinized rice paddies back to salt marsh and mangrove habitats may also achieve order-of-magnitude reductions in methane fluxes because mangrove and salt marshes have lower fluxes than aquaculture ponds (Extended Data Table 1). Reducing nutrient inputs to freshwater wetlands, lakes and reservoirs can help reduce methane emissions[13,21] (Extended Data Fig. 4). Reservoirs and constructed ponds can be designed to reduce methane emissions through their placement within the watershed[46] and their depth[47], and in the case of reservoirs, by withdrawing water from depths with lower methane concentrations[48]. In rivers and streams, methane emissions can be reduced if the benthic environments of the streams are restored and organic matter loadings are decreased[49]. In coastal environments, reducing eutrophication should lead to a decrease in methane emissions as suggested by the comparison of fluxes from impacted versus natural sites (Extended Data Fig. 3). Thus, land-use and management choices may substantially reduce methane emissions and lessen the impact on future atmospheric methane.

Because of their prominent contribution to global emissions, actions to reduce aquatic methane emissions through the management of land use, nutrient and organic matter inputs and hydrological flows are a promising avenue to mitigate methane emissions. These actions will be particularly effective when targeting the ecosystems with the greatest contributions to aquatic methane emissions, primarily freshwater wetlands, lakes, reservoirs and rice paddies. This requires an effort to integrate existing knowledge across disciplines, from the microbial processes that cycle methane, to the biogeochemical constraints that favour and inhibit these processes, to spatial and hydrological planning and management to create the conditions conducive to the lowest fluxes, while preserving ecosystem function and biodiversity.

Online content

Any methods, additional references, Nature Research reporting summaries, source data, extended data, supplementary information, acknowledgements, peer review information; details of author contributions and competing interests; and statements of data and code availability are available at https://doi.org/10.1038/s41561-021-00715-2.

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References

1. IPCC *Climate Change 2014: Synthesis Report* (eds Core Writing Team et al.) (IPCC, 2014).
2. Etminan, M., Myhre, G., Highwood, E. J. & Shine, K. P. Radiative forcing of carbon dioxide, methane, and nitrous oxide: a significant revision of the methane radiative forcing. *Geophys. Res. Lett.* **43**, 12614–12623 (2016).
3. Dlugokencky, E. J. *Trends in Atmospheric Methane* (NOAA/GML, 2021); www.esrl.noaa.gov/gmd/ccgg/trends_ch4/
4. Dlugokencky, E. J. Atmospheric methane levels off: temporary pause or a new steady-state? *Geophys. Res. Lett.* **30**, 1992 (2003).
5. Nisbet, E. G. et al. Rising atmospheric methane: 2007–2014 growth and isotopic shift. *Glob. Biogeochem. Cycles* **30**, 1356–1370 (2016).
6. Schaefer, H. et al. A 21st-century shift from fossil-fuel to biogenic methane emissions indicated by $^{13}CH_4$. *Science* **352**, 80–84 (2016).
7. Rigby, M. et al. Role of atmospheric oxidation in recent methane growth. *Proc. Natl Acad. Sci. USA* **114**, 5373–5377 (2017).
8. Nisbet, E. G. et al. Very strong atmospheric methane growth in the 4 years 2014–2017: implications for the Paris Agreement. *Glob. Biogeochem. Cycles* **33**, 318–342 (2019).
9. Turner, A. J., Frankenberg, C. & Kort, E. A. Interpreting contemporary trends in atmospheric methane. *Proc. Natl Acad. Sci. USA* **116**, 2805–2813 (2019).
10. Saunois, M. et al. The global methane budget 2000–2012. *Earth Syst. Sci. Data* **8**, 697–751 (2016).
11. Saunois, M. et al. The global methane budget 2000–2017. *Earth Syst. Sci. Data* **12**, 1561–1623 (2020).
12. Couto, T. B. & Olden, J. D. Global proliferation of small hydropower plants—science and policy. *Front. Ecol. Environ.* **16**, 91–100 (2018).
13. Beaulieu, J. J., DelSontro, T. & Downing, J. A. Eutrophication will increase methane emissions from lakes and impoundments during the 21st century. *Nat. Commun.* **10**, 1375 (2019).
14. Kroeger, K. D., Crooks, S., Moseman-Valtierra, S. & Tang, J. Restoring tides to reduce methane emissions in impounded wetlands: a new and potent blue carbon climate change intervention. *Sci. Rep.* **7**, 11914 (2017).
15. Yvon-Durocher, G. et al. Methane fluxes show consistent temperature dependence across microbial to ecosystem scales. *Nature* **507**, 488–491 (2014).
16. Harrison, J. A., Deemer, B. R., Birchfield, M. K. & O'Malley, M. T. Reservoir water-level drawdowns accelerate and amplify methane emission. *Environ. Sci. Technol.* **51**, 1267–1277 (2017).
17. Pekel, J. F., Cottam, A., Gorelick, N. & Belward, A. S. High-resolution mapping of global surface water and its long-term changes. *Nature* **540**, 418–422 (2016).
18. Weber, T., Wiseman, N. A. & Kock, A. Global ocean methane emissions dominated by shallow coastal waters. *Nat. Commun.* **10**, 4584 (2019).
19. Hmiel, B. et al. Preindustrial $^{14}CH_4$ indicates greater anthropogenic fossil CH_4 emissions. *Nature* **578**, 409–412 (2020).
20. Bastviken, D., Tranvik, L. J., Downing, J. A., Crill, P. M. & Enrich-Prast, A. Freshwater methane emissions offset the continental carbon sink. *Science* **331**, 50 (2011).
21. DelSontro, T., Beaulieu, J. J. & Downing, J. A. Greenhouse gas emissions from lakes and impoundments: upscaling in the face of global change. *Limnol. Oceanogr. Lett.* **3**, 64–75 (2018).
22. Deemer, B. R. et al. Greenhouse gas emissions from reservoir water surfaces: a new global synthesis. *Bioscience* **66**, 949–964 (2016).
23. Stanley, E. H. et al. The ecology of methane in streams and rivers: patterns, controls, and global significance. *Ecol. Monogr.* **86**, 146–171 (2016).
24. Raymond, P. A. et al. Global carbon dioxide emissions from inland waters. *Nature* **503**, 355–359 (2013).
25. Kirschke, S. et al. Three decades of global methane sources and sinks. *Nat. Geosci.* **6**, 813–823 (2013).
26. Rosentreter, J. A., Maher, D. T., Erler, D. V., Murray, R. H. & Eyre, B. D. Methane emissions partially offset "blue carbon" burial in mangroves. *Sci. Adv.* **4**, eaao4985 (2018).
27. Zhu, Y. et al. Disproportionate increase in freshwater methane emissions induced by experimental warming. *Nat. Clim. Change* **10**, 685–690 (2020).
28. Schulz, S., Matsuyama, H. & Conrad, R. Temperature dependence of methane production from different precursors in a profundal sediment (Lake Constance). *FEMS Microbiol. Ecol.* **22**, 207–213 (1997).
29. Schroll, M. et al. The stable carbon isotope signature of methane produced by saprotrophic fungi. *Biogeosciences* **17**, 3891–3901 (2020).
30. Morana, C. et al. Methane paradox in tropical lakes? Sedimentary fluxes rather than pelagic production in oxic conditions sustain methanotrophy and emissions to the atmosphere. *Biogeosciences* **17**, 5209–5221 (2020).
31. Bižić, M. et al. Aquatic and terrestrial cyanobacteria produce methane. *Sci. Adv.* **6**, eaax5343 (2020).
32. Turetsky, M. R. et al. A synthesis of methane emissions from 71 northern, temperate, and subtropical wetlands. *Glob. Change Biol.* **20**, 2183–2197 (2014).
33. Koven, C. D. et al. A simplified, data-constrained approach to estimate the permafrost carbon–climate feedback. *Philos. Trans. R. Soc. A* **373**, 20140423 (2015).
34. Zhang, M., Qiao, F. & Song, Z. Observation of atmospheric methane in the Arctic Ocean up to 87° north. *Sci. China Earth Sci.* **60**, 173–179 (2017).
35. Turetsky, M. R. et al. Carbon release through abrupt permafrost thaw. *Nat. Geosci.* **13**, 138–143 (2020).
36. He, X. et al. Sea ice in the Arctic Ocean: role of shielding and consumption of methane. *Atmos. Environ.* **67**, 8–13 (2013).
37. Ganesan, A. L. et al. Advancing scientific understanding of the global methane budget in support of the Paris Agreement. *Glob. Biogeochem. Cycles* **33**, 1475–1512 (2019).
38. Barba, J. et al. Methane emissions from tree stems: a new frontier in the global carbon cycle. *New Phytol.* **222**, 18–28 (2019).
39. Poulter, B. et al. Global wetland contribution to 2000–2012 atmospheric methane growth rate dynamics. *Environ. Res. Lett.* **12**, 094013 (2017).
40. Zhang, Z. et al. Development of a global dataset of Wetland Area and Dynamics for Methane Modeling (WAD2M). Preprint at *Copernicus* https://doi.org/10.5194/essd-2020-262 (2020).
41. Strode, S. A. et al. Strong sensitivity of the isotopic composition of methane to the plausible range of tropospheric chlorine. *Atmos. Chem. Phys.* **20**, 8405–8419 (2020).
42. Zhao, Y. et al. Inter-model comparison of global hydroxyl radical (OH) distributions and their impact on atmospheric methane over the 2000–2016 period. *Atmos. Chem. Phys.* **19**, 13701–13723 (2019).
43. Zhao, Y. et al. On the role of trend and variability of hydroxyl radical (OH) in the global methane budget. *Atmos. Chem. Phys.* **20**, 13011–13022 (2020).
44. Tian, H. et al. The terrestrial biosphere as a net source of greenhouse gases to the atmosphere. *Nature* **531**, 225–228 (2016).
45. Wang, C., Tong, C., Chambers, L. G. & Liu, X. Identifying the salinity thresholds that impact greenhouse gas production in subtropical tidal freshwater marsh soils. *Wetlands* **37**, 559–571 (2017).
46. Hayes, N. M., Deemer, B. R., Corman, J. R., Razavi, N. R. & Strock, K. E. Key differences between lakes and reservoirs modify climate signals: a case for a new conceptual model. *Limnol. Oceanogr. Lett.* **2**, 47–62 (2017).
47. Gorsky, A. L., Racanelli, G. A., Belvin, A. C. & Chambers, R. M. Greenhouse gas flux from stormwater ponds in southeastern Virginia (USA). *Anthropocene* **28**, 100218 (2019).
48. Guérin, F. et al. Methane and carbon dioxide emissions from tropical reservoirs: significance of downstream rivers. *Geophys. Res. Lett.* **33**, L21407 (2006).
49. Crawford, J. T. & Stanley, E. H. Controls on methane concentrations and fluxes in streams draining human-dominated landscapes. *Ecol. Appl.* **26**, 1581–1591 (2016).

Methods

We use the term 'natural' to describe less-impacted and less-disturbed study sites or ecosystems, whereas 'impacted' refers to highly impacted, modified, polluted or eutrophied study sites or ecosystems.

Our datasets were compiled from peer-reviewed publications. Temporal (annual, seasonal, diel) or spatial data were averaged to a single flux per study site. If 'site' was not obvious, we set a criterion of 10 km distance to distinguish between sites. An exception was the river and stream dataset, where measurements with the exact same coordinates were treated as one site, and fluxes with different coordinates were treated as many sites to account for variable fluxes of low and high stream orders. Values under detection limit were set to '0' and included in the statistical analysis. Sites were classified as natural or impacted if clearly identified in the literature or on the basis of the authors' knowledge.

Rivers and streams. We compiled peer-reviewed studies until March 2019 using the Boolean search string '(CH_4 OR methane) AND (concentration OR flux OR emission) AND (river OR stream)' in the Web of Science Core Collection (http://isiknowledge.com) and China Knowledge Resource Integrated database (https://www.cnki.net/). In our river and stream database, we included only georeferenced methane concentrations or fluxes. If exact coordinates were not provided but site description was sufficient, we obtained approximate coordinates from Google Maps. We excluded non-river data by either referring to the original site descriptions or by overlying the measurement locations with a map of global open inland waters[50].

Our efforts identified a total of 2,601 records with either a methane concentration or a flux measurement. Our primary analysis showed that methane fluxes calculated from concentration versus gas transfer velocity (k) poorly predicted the literature-reported fluxes. Therefore, we included only reported methane fluxes from publications. This resulted in a collection of 652 methane fluxes from 74 publications, including one unpublished dataset (provided by T.I.B). The total number of records included 187 total fluxes, 590 diffusive fluxes and 126 ebullitive methane fluxes. We refer to the total methane flux as either the sum of diffusive and ebullitive fluxes or the total flux without differentiation between diffusion and ebullition. For example, a properly designed chamber can catch both diffusive and ebullitive methane fluxes[51,52]. If the original studies clearly identified chamber fluxes as diffusive + ebullitive fluxes, we included these as total fluxes. If the original studies identified chamber fluxes as diffusive (for example, because of low observed ebullition) or reported calculated fluxes from concentration and k, we included these as diffusive fluxes. If the original studies measured methane fluxes with bubble traps or invert funnels, we included these as ebullitive fluxes.

We used a Monte Carlo approach to upscale river methane fluxes to the global scale and to estimate uncertainties. We performed simulations for five latitudinal bands (0–10°, 10–25°, 25–40°, 40–60°, 60–90°) and at the global scale for diffusive, ebullitive and total fluxes. Because the data were skewed, we ln-transformed all fluxes before simulations. For each simulation, we generated a total of 1,000 random values from a normal distribution centred around means of the ln methane fluxes and with deviations confined by those of the ln methane fluxes (R package mc2d). Values generated from the simulations were then back-transformed to raw fluxes before calculation of any statistics. Global methane emissions were calculated as the products of the recently developed Global River Widths from Landsat surface area[53] and the post-simulation methane fluxes for each latitudinal band (Supplementary Table 2). Finally, we corrected our latitudinal methane emissions for ice coverage periods by excluding Global River Widths from Landsat surface areas[53] with an atmospheric temperature below −4 °C for each month in each latitudinal band and at the global scale[54].

Lakes and reservoirs. We conducted a literature search until May 2019 using '(CH_4 OR methane) AND (concentration OR flux OR emission) AND (lake OR pond OR reservoir)' in the same search engines used for rivers and streams. Overall, the 84 publications provided 243 and 116 total methane fluxes for 227 lakes and 86 reservoirs, respectively. In our freshwater lakes, ponds and reservoir database, we included studies that provided both diffusive and ebullitive fluxes from the open-water surface either separately (for example, via bubble traps or acoustic surveys for ebullition and via thin-boundary-layer modelling or floating chambers for diffusion) or together (for example, via floating chamber or eddy covariance methods). We categorized 'site' as either a lake or a reservoir, wherein a reservoir was defined as a system whose primary outflow was dammed. The lake category was largely composed of natural lakes and a small subset ($n=23$) of artificial lakes[55,56]. The total methane flux either refers to the total emission estimate (diffusive and ebullitive) of the whole water body reported by the authors or was estimated by us using the mean of all reported areal fluxes (diffusive and ebullitive) or the mean of the range of reported fluxes (diffusive and ebullitive). We excluded studies that estimated only diffusive or ebullitive methane fluxes but not both. We include only studies where both diffusive and ebullitive fluxes were estimated because the extent to which each contributes to total emissions is variable (ranging from negligible to most of the flux)[57]. We further excluded methane fluxes that were made solely during mixing events and fluxes from adjacent marsh and drawdown zones of reservoirs because they should be accounted for in freshwater wetland emissions. Finally, we also excluded methane fluxes from beaver ponds and river reaches upstream of weirs to avoid potential overlap with river and stream emissions. If original studies used an $r^2 > 0.85$ as a cut-off for linear gas accumulation in floating chambers, these fluxes were considered diffusive only and excluded from the dataset (unless accompanied by an independent estimate of ebullition).

Given previous evidence that chlorophyll *a* and ecosystem productivity are predictors of total lentic methane emissions[21,22], we used total phosphorus (TP) to model missing chlorophyll *a* data and assigned trophic statuses[22]. If no estimates of chlorophyll *a* or TP were reported by the primary study, we mined the literature for other studies of the same site that reported TP and/or chlorophyll *a* within a ±five-year time period of the primary study.

We upscaled lake and reservoir methane fluxes separately to a global scale. For each water body type, we used a Monte Carlo analysis (R package mc2d) that allowed for uncertainty in both surface area and areal methane fluxes. Only sites with surface area information were included in the Monte Carlo analysis ($n=198$ lakes, $n=78$ reservoirs). Because the data were skewed, we ln-transformed all total fluxes before Monte Carlo analysis. Our approach for binning Monte Carlo analyses differed for lakes versus reservoirs due to different correlates with methane emissions[57]. In a parallel study, we show that morphometric features better predicted methane emission in lakes, whereas chlorophyll *a* was a better predictor in reservoirs[57].

For small lakes <1 km², we upscaled methane fluxes on the basis of logarithmic size classes. However, for lakes >1 km², our low sample size ($n=20$) precluded this approach, and we lumped together all lakes >1 km². We ran a Monte Carlo analysis with 1,000 iterations for each size class of small lake and for large lakes as one category. Each iteration randomly selected a methane flux from a normal distribution surrounding the mean and standard deviation for that size class. Simulations also selected for a surface area estimate of lakes in each size class using a uniform distribution based on estimates from refs. [58–60]. Because Verpoorter et al.[60] reported combined lake and reservoir surface area, we subtracted reservoir areas using estimates of reservoir surface area for each size class from Lehner et al.[61]. Because surface area estimates for lakes <0.01 km² are highly uncertain, we extrapolated the data from Verpoorter et al.[60] to estimate the lower bound[62].

For reservoirs, we upscaled methane fluxes for small (<1 km²) and large (>1 km²) reservoirs. For small reservoirs, where sample size was low ($n=16$), we used the same scaling approach as with large lakes. For large reservoirs, where estimates of the global distribution of lake and reservoir chlorophyll *a* were available[63], we upscaled methane fluxes on the basis of the positive log-linear relationship between chlorophyll *a* and areal methane fluxes[57] and reservoir surface area estimates[58,61]. We generated 1,000 Monte Carlo simulations of reservoir surface area based on a uniform distribution ranging between the surface area estimates by Downing et al.[58] and those by Lehner et al.[61]. We also allowed for uncertainty in the relationship between chlorophyll *a* and methane flux by generating 1,000 Monte Carlo simulations of slope and intercept terms based on a normal distribution around the standard error of these terms. We then estimated areal methane fluxes by applying reservoir surface areas across 20 chlorophyll *a* bins (with each bin spanning 5 μg l⁻¹ from 0 to 100 μg l⁻¹), then calculating total methane emissions from each bin and finally summing across the 20 bins. The global distributions of chlorophyll *a* concentrations were generated using MERIS OC4 satellite imagery via the Michigan Tech Research Institute method, which is based on 300 m resolution inputs[63].

To account for the impact of ice on lake and reservoir emissions, we excluded surface areas[61] with an average atmospheric temperature of 0 °C or less for each month[54]. For lakes and reservoirs that freeze, we scaled upwards the ice-corrected emissions by 127%[64] to account for an ice–melt pulse in emissions. Both the ice-cover and ice-melt corrections were applied after the Monte Carlo upscaling by adjusting the estimated annual flux by the size-class-specific fraction of emission expected on the basis of both ice cover and ice melt (fractions ranged from 0.60 to 0.98, Supplementary Table 3). Combined corrections for both ice cover and ice melt reduced overall annual methane emissions to 66% of their uncorrected values. We do not account for potential diel effects on lentic methane emissions. A further uncertainty is our small sample size for large lakes (>1 km²) and that half of the large lakes were shallow (≤3 m mean depth) and only 3 were >100 km², suggesting emissions may be overestimated from this size class.

Freshwater aquaculture ponds. We conducted a literature search using '(CH_4 OR methane) AND (aquaculture pond OR aquaculture farm) AND (shrimp OR fish)'. For freshwater aquaculture ponds, we built on the database from Yuan et al.[65] and added three new studies of diffusive and ebullitive methane fluxes since 2018. Total freshwater aquaculture pond fluxes in the database were derived mainly from carp and mixed shrimp–fish ponds. We scaled areal freshwater aquaculture methane fluxes to global emissions using the surface area estimated by Verdegem and Bosma[66] (Supplementary Table 4), which is likely an underestimate, assuming an increase of freshwater aquaculture farms since 2009.

Coastal ocean. For each coastal ocean ecosystem, we performed a literature review until December 2019 using Scopus by Elsevier (https://www.scopus.com/) and Google Scholar (https://scholar.google.com/) databases. In addition, we scanned the reference lists of publications. When methane fluxes were presented only in figures, we used a manual data extraction tool (WebPlotDigitizer) to estimate the values. We included methane fluxes with identifiable coordinates (latitude/longitude) derived from the original studies or from Google Earth on the basis of site description. Coastal wetlands were distinguished from inner estuaries by accounting for methane fluxes solely from studies that were conducted in clearly vegetation-dominated salt marsh, seagrass or mangrove sites in opposition to spatial surveys over salinity gradients in estuarine open waters. For each coastal ocean ecosystem, we upscaled combined spatial and temporal methane fluxes to a global scale using recent surface area estimates (Supplementary Table 4).

Estuaries. We conducted a literature search using '(CH_4 OR methane) AND estuary', which resulted in 53 publications containing 137 averaged water–air methane fluxes for 124 sites. In our estuary database, we included methane fluxes over full salinity gradients. We excluded methane fluxes from coastal wetlands and from incomplete coverage of salinity gradients. Most studies reported diffusive methane fluxes computed from concentration gradients and k parameterizations. A minority ($n=3$) of the studies measured diffusive fluxes with floating chambers, and only one study reported measurements with eddy covariance. If the original studies estimated fluxes using several k parameterizations, we chose the value corresponding to the parameterization most accepted (for example, we chose the Wanninkhof[67] over the Liss and Merlivat[68] model).

Salt marshes. We conducted a literature search using '(CH_4 OR methane) AND (saltmarsh OR salt-marsh OR tidal marsh)', which resulted in 75 publications containing 89 averaged methane fluxes for 60 sites. In our salt marsh database, we included methane flux estimates and measurements for salt marsh and tidal marsh. We excluded methane fluxes from freshwater marsh (salinity <0.5) that should be accounted for in freshwater wetland emissions. Salt marsh methane fluxes were grouped into three salinity classes: oligohaline (0.5–5), mesohaline (5–18) and polyhaline (>18) (ref. [69]). Most studies ($n=49$) reported diffusive methane fluxes from the sediment–air interface during low tide using static chambers. Several other studies ($n=33$) reported sediment–water–air fluxes during exposed and inundated periods using either static dynamic chambers or eddy covariance. Few studies ($n=7$) were available that estimated the water–air methane flux, computed either on the basis of k parameterization or using the floating chamber approach.

Mangroves. We conducted a literature search using '(CH_4 OR methane) AND (mangroves OR mangrove forest)', which resulted in 56 publications containing 79 averaged methane fluxes for 59 sites. Our global mangrove methane emission estimate is an update of the review by Rosentreter et al.[26]. In our mangrove database, we included sediment–water fluxes from core incubations ($n=2$), sediment–air ($n=45$) and sediment–water–air fluxes ($n=8$) using static chambers, and water–air fluxes ($n=22$) using floating chambers or based on k parameterizations. Our revised global estimate includes mainly diffusive sediment–air and water–air fluxes, but also plant-mediated fluxes (through pneumatophores, roots, stems, leaves) and fluxes over sediments with crab burrows. No estimates of ebullitive fluxes from mangroves were available. We excluded fluxes estimated from methane concentrations in gas bubbles that were actively stirred up from mangrove sediments as they cannot be accounted for in in situ ebullition.

Seagrasses. We conducted a literature search using '(CH_4 OR methane) AND (seagrasses OR seagrass beds OR seagrass meadows)', which resulted in 11 publications containing 18 averaged methane fluxes for 18 sites. In our seagrass database, we included plant-mediated and diffusive sediment–water fluxes ($n=14$) from submerged seagrass meadows and few available water–air methane fluxes ($n=4$) over seagrass meadows. The majority of studies reported sediment–water fluxes from core incubation and benthic chambers. One study used a dynamic flux chamber, which allowed flux measurements during exposed and submersed conditions, and hence includes sediment–air fluxes[70]. No estimates of ebullitive fluxes from seagrass sites were available.

Tidal flats. We conducted a literature search using '(CH_4 OR methane) AND (tidal flat OR mud flat OR sand flat)', which resulted in 23 publications containing 25 averaged methane fluxes for 16 sites. Tidal flat ecosystems were classified as tidal mudflats, tidal sand flats or wide tidal rock platforms[71] and distinguished from coastal wetlands through the absence of vegetation. Because tidal flats comprise at least a global distribution of 127,921 km^2 (ref. [71]), which is similar to that of mangrove forests, and are characterized by frequent tidal inundation, we included tidal flats in our coastal ocean emission estimate. Our tidal flat database is biased towards tidal mudflats in China, with a few data from North America and Europe. We included diffusive and ebullitive fluxes from coastal bare sediments of the inter-tidal zone (salinity >0.5) measured with static chambers or core incubations, which resulted in 16 sediment–air fluxes, 8 sediment–water–air fluxes and one water–air flux. We excluded freshwater bare sediments and sites where the salinity region was unclear.

Coastal aquaculture ponds. We conducted a literature search using '(CH_4 OR methane) AND (aquaculture pond OR aquaculture farm) AND (shrimp OR fish)', which resulted in 10 publications containing 18 methane fluxes for 5 sites. Most methane fluxes ($n=10$) were from coastal aquaculture ponds near the Min River estuary in China. In our coastal aquaculture database, we included diffusive and ebullitive fluxes mainly from shrimp ponds, with the residual measurements from mixed fish–shrimp, mixed shrimp–sea cucumber, drained and undrained coastal aquaculture farms.

Continental shelves. Continental shelves were subdivided into estuarine plumes, seep areas and upwelling areas if identified as such in the literature or on the basis of the authors' knowledge. We conducted a literature search using '(CH_4 OR methane) AND (shelf OR coastal) AND (Arctic ocean OR upwelling OR river plume)', which resulted in 77 publications providing 9 methane fluxes for estuarine plumes, 19 for seep areas (diffusion), 3 for seep areas (ebullition), 12 for upwelling areas and 57 for other continental shelf areas. In our continental shelf database, we included methane water–air flux estimates or measurements for continental shelf environments. We excluded studies that reported only the dissolved methane concentrations without computing fluxes. We summed our upscaled emissions from estuarine plumes, seep areas (diffusion + ebullition), upwelling areas, the East Siberian Arctic Shelf and other continental shelves to total global continental shelf methane emissions.

Statistical analysis. We use the IQR to describe methane flux variability and the c.i.95% (using the population standard deviation (σ) and sample size (n) assuming Student's t distribution and a confidence level of $\alpha=1-0.95=0.05$) to estimate uncertainties of mean methane fluxes. For global estimates, we combined the confidence intervals by taking the square root of the sum of the variances. To compute the skewness coefficient of each dataset, we applied the function 'skewness' from the R package e1071 (ref. [72]). We did not conduct an assessment for publication bias.

Reporting Summary. Further information on research design is available in the Nature Research Reporting Summary linked to this article.

Data availability

The datasets that support the findings of this study are available in the *Figshare* repository: https://doi.org/10.6084/m9.figshare.13611296. Source data are provided with this paper.

References

50. Lehner, B. & Döll, P. Development and validation of a global database of lakes, reservoirs and wetlands. *J. Hydrol.* **296**, 1–22 (2004).
51. Cole, J. J., Bade, D. L., Bastviken, D., Pace, M. L. & Van de Bogert, M. Multiple approaches to estimating air–water gas exchange in small lakes. *Limnol. Oceanogr. Methods* **8**, 285–293 (2010).
52. Gålfalk, M., Bastviken, D., Fredriksson, S. & Arneborg, L. Determination of the piston velocity for water–air interfaces using flux chambers, acoustic Doppler velocimetry, and IR imaging of the water surface. *J. Geophys. Res. Biogeosci.* **118**, 770–782 (2013).
53. Allen, G. H. & Pavelsky, T. Global extent of rivers and streams. *Science* **361**, 585–588 (2018).
54. Fick, S. E. & Hijmans, R. J. WorldClim 2: new 1-km spatial resolution climate surfaces for global land areas. *Int. J. Climatol.* **37**, 4302–4315 (2017).
55. Grinham, A. et al. The importance of small artificial water bodies as sources of methane emissions in Queensland, Australia. *Hydrol. Earth Syst. Sci.* **22**, 5281–5298 (2018).
56. van Bergen, T. J. H. M. et al. Seasonal and diel variation in greenhouse gas emissions from an urban pond and its major drivers. *Limnol. Oceanogr.* **64**, 2129–2139 (2019).
57. Deemer, B. R. & Holgerson, M. A. Drivers of methane flux differ between lakes and reservoirs, complicating global upscaling efforts. *J. Geophys. Res. Biogeosci.* **126**, https://doi.org/10.1029/2019JG005600 (2021).
58. Downing, J. A. et al. The global abundance and size distribution of lakes, ponds, and impoundments. *Limnol. Oceanogr.* **51**, 2388–2397 (2006).
59. Downing, J. A. Emerging global role of small lakes and ponds: little things mean a lot. *Limnetica* **29**, 9–24 (2010).
60. Verpoorter, C., Kutser, T., Seekell, D. A. & Tranvik, L. J. A global inventory of lakes based on high-resolution satellite imagery. *Geophys. Res. Lett.* **41**, 6396–6402 (2014).
61. Lehner, B. et al. High-resolution mapping of the world's reservoirs and dams for sustainable river-flow management. *Front. Ecol. Environ.* **9**, 494–502 (2011).
62. Holgerson, M. A. & Raymond, P. A. Large contribution to inland water CO_2 and CH_4 emissions from very small ponds. *Nat. Geosci.* **9**, 222–226 (2016).
63. Sayers, M. J. et al. A new method to generate a high-resolution global distribution map of lake chlorophyll. *Int. J. Remote Sens.* **36**, 1942–1964 (2015).
64. Denfeld, B. A., Baulch, H. M., del Giorgio, P. A., Hampton, S. E. & Karlsson, J. A synthesis of carbon dioxide and methane dynamics during the ice-covered period of northern lakes. *Limnol. Oceanogr. Lett.* **3**, 117–131 (2018).
65. Yuan, J. et al. Rapid growth in greenhouse gas emissions from the adoption of industrial-scale aquaculture. *Nat. Clim. Change* **9**, 318–322 (2019).

66. Verdegem, M. C. J. & Bosma, R. H. Water withdrawal for brackish and inland aquaculture, and options to produce more fish in ponds with present water use. *Water Policy* **11**, 52–68 (2009).
67. Wanninkhof, R. Relationship between wind speed and gas exchange over the ocean. *J. Geophys. Res.* **97**, 7373–7382 (1992).
68. Liss, P. S. & Merlivat, L. in *The Role of Air–Sea Exchange in Geochemical Cycling* (ed. Buat-Ménard, P.) 113–127 (Springer, 1986).
69. Poffenbarger, H. J., Needelman, B. A. & Megonigal, J. P. Salinity influence on methane emissions from tidal marshes. *Wetlands* **31**, 831–842 (2011).
70. Bahlmann, E. et al. Tidal controls on trace gas dynamics in a seagrass meadow of the Ria Formosa lagoon (southern Portugal). *Biogeosciences* **12**, 1683–1696 (2015).
71. Murray, N. J. et al. The global distribution and trajectory of tidal flats. *Nature* **565**, 222–225 (2018).
72. R Core Team *R: A Language and Environment for Statistical Computing* (R Foundation, 2020); https://www.R-project.org/

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Author contributions

J.A.R. did the synthesis for mangroves, salt marshes, seagrasses and tidal flats and produced all figures in the main manuscript; A.V.B. did the synthesis for estuaries and continental shelves; A.V.B. and J.A.R. did the synthesis for aquaculture ponds; C.S. compiled the data for streams, rivers, lakes and reservoirs with help from S.L.; B.R.D. and M.A.H. updated the compiled data for lakes and reservoirs and analysed the data with input from J.M.; C.S., S.L., G.H.A. and P.A.R. analysed the data for streams and rivers; G.H.A. determined zonal estimates of river surface area and stream and lake ice corrections; B.D.E. and J.A.R. conceived the project; J.A.R. drafted the first manuscript, and all authors reviewed and edited the manuscript and approved the final version.

Competing interests

The authors declare no competing interests.

Additional information

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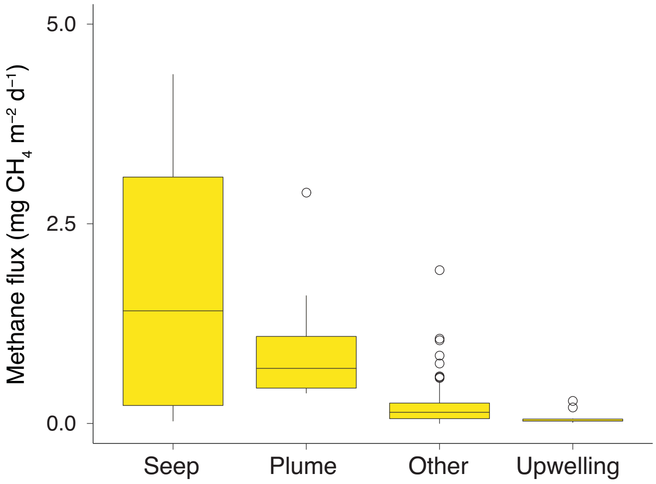
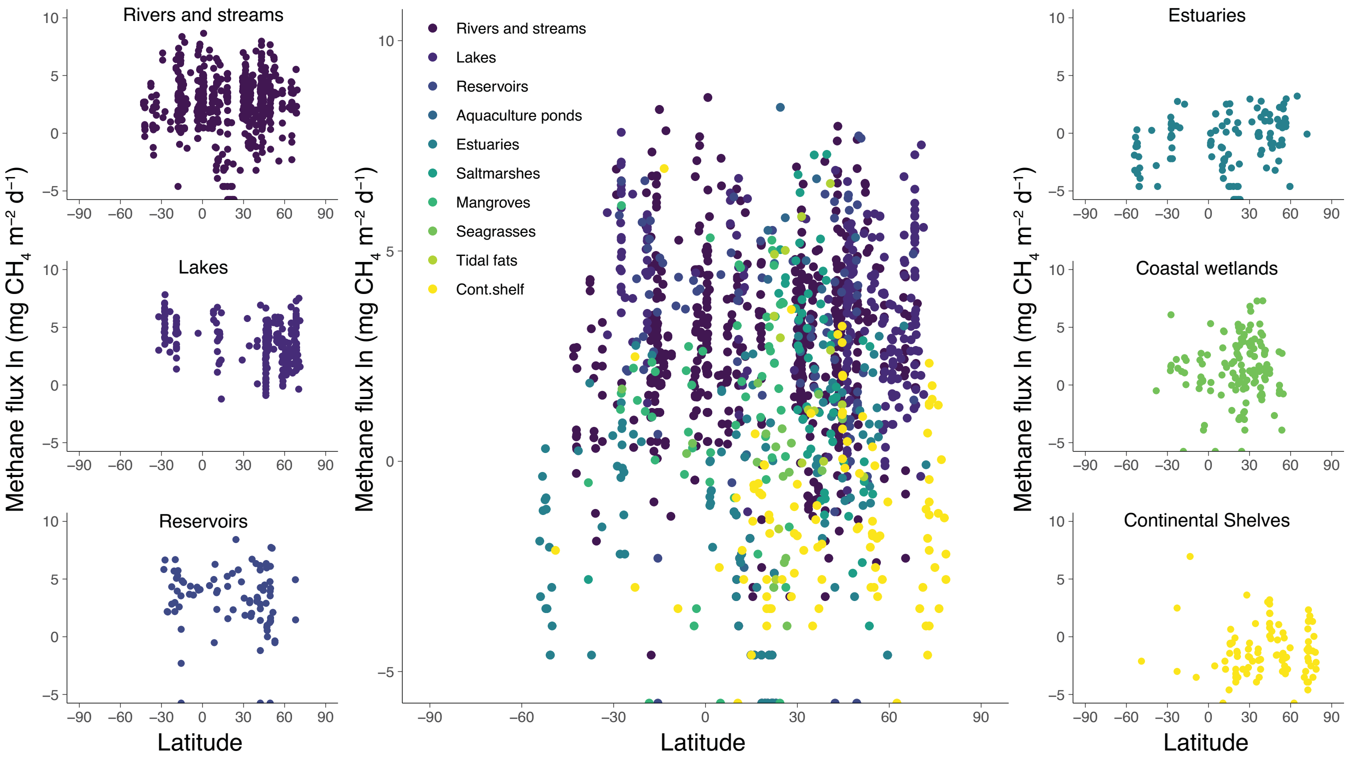
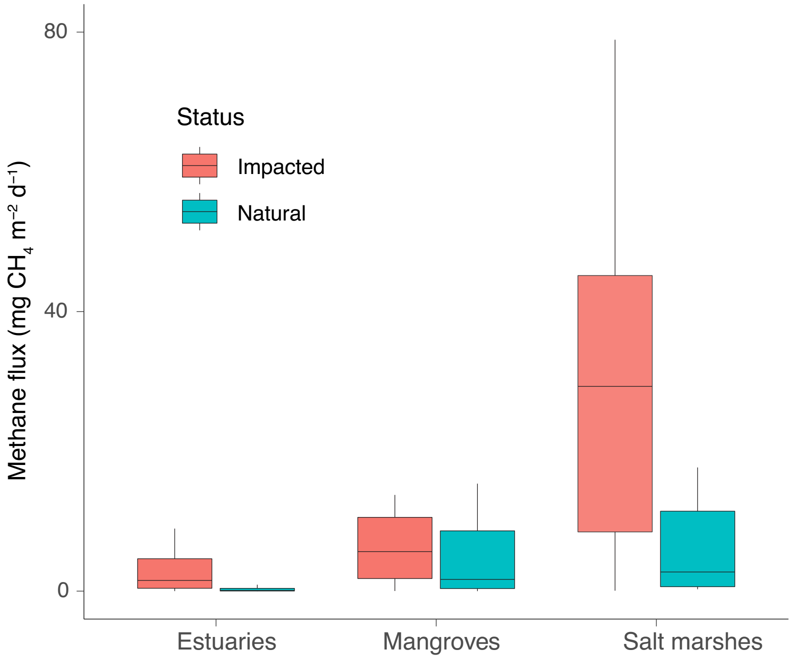


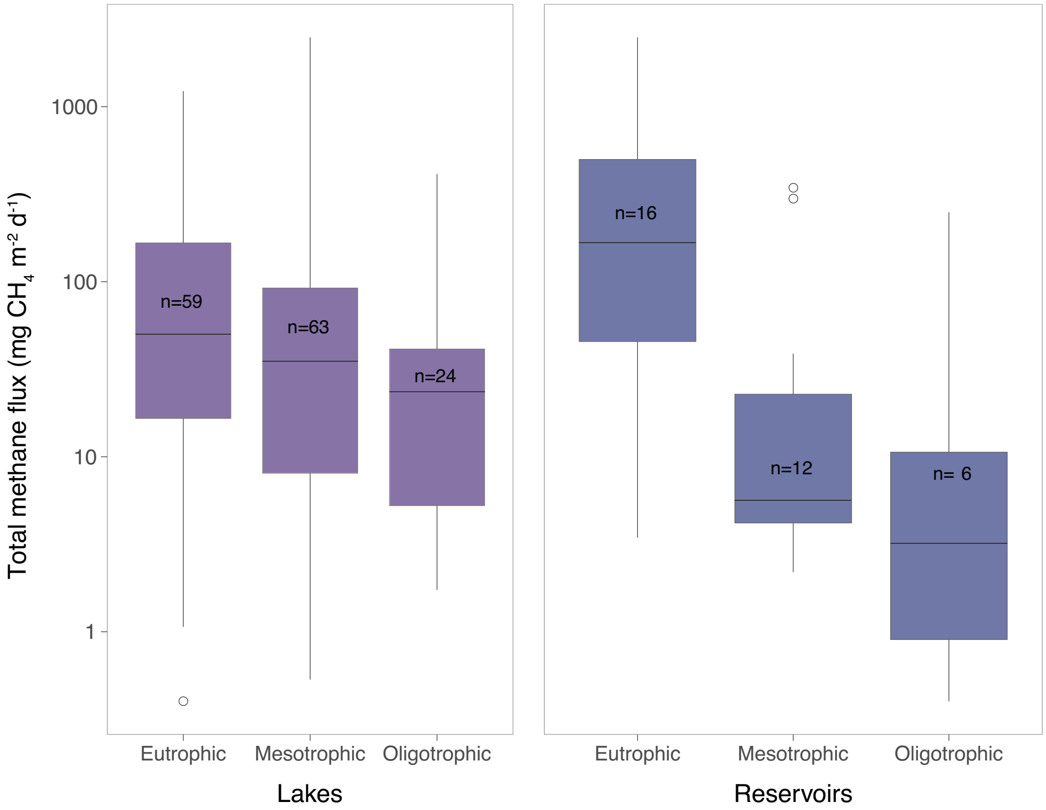
Extended Data Fig. 1 | Areal methane fluxes from continental shelf regions. Boxplot showing median, lower (Q1), upper (Q3) quartiles and 1.5 times the length of the interquartile range of diffusive methane fluxes in areas with natural gas seeps, estuarine plumes, upwelling areas and the remaining (other) continental shelves. Differences are statistically significant (Kruskal-Wallis test, $p<0.0001$).



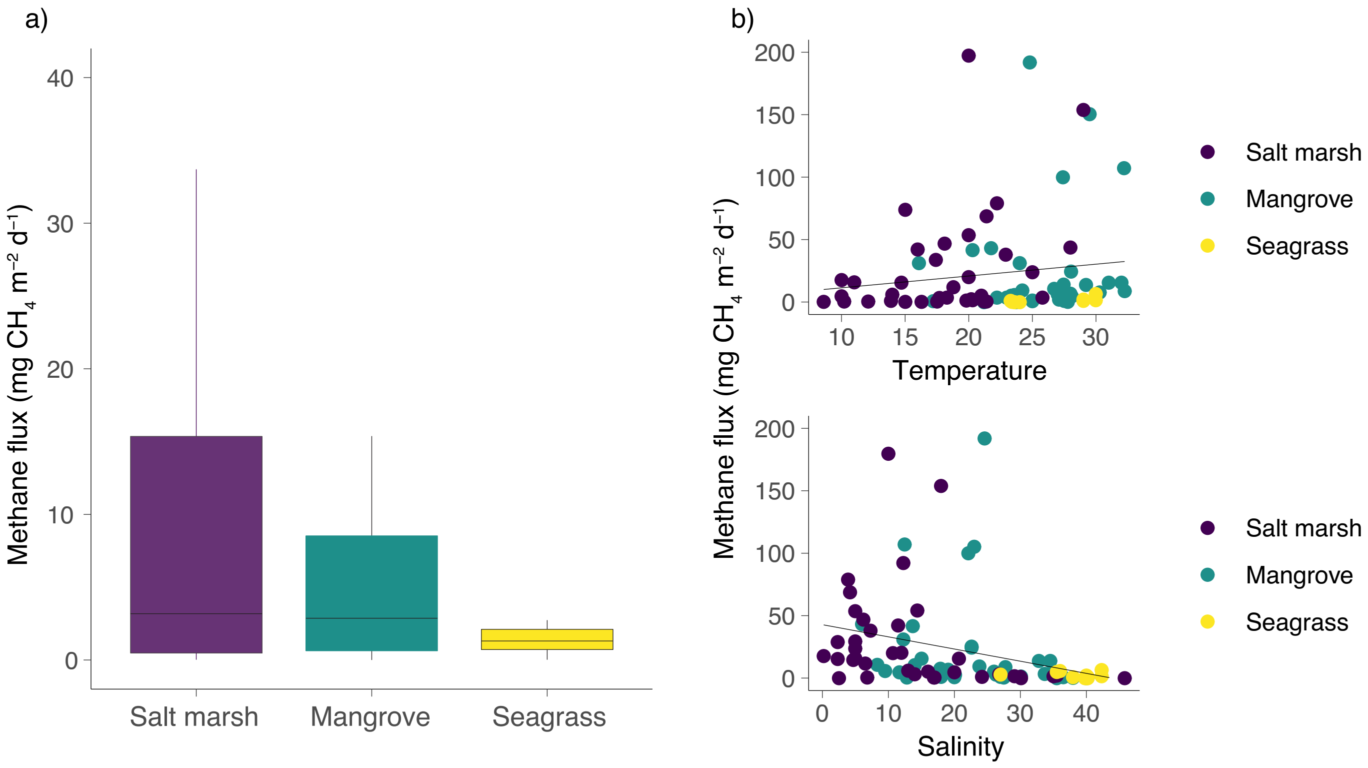
Extended Data Fig. 2 | Areal methane fluxes from aquatic ecosystems over latitudes. Natural log (ln) transformed methane fluxes over latitudes of all aquatic ecosystems compiled in this study, and individual plots for rivers and streams, lakes, reservoirs, estuaries, coastal wetlands (mangroves, salt marshes, seagrasses), and continental shelves.



Extended Data Fig. 3 | Areal methane fluxes from natural and impacted estuaries, mangroves, and salt marshes. Boxplots showing median, lower (Q1), upper (Q3) quartiles and 1.5 times the length of the interquartile range of methane fluxes from impacted and more natural (low disturbed) estuaries, mangroves and salt marshes. Several sites that could not be classified as 'impacted' or 'natural' were excluded from this plot.



Extended Data Fig. 4 | Areal methane fluxes from eutrophic, mesotrophic and oligotrophic lakes and reservoirs. Boxplots showing median, lower (Q1), upper (Q3) quartiles and 1.5 times the length of the interquartile range of total (diffusive and ebullitive) methane fluxes from eutrophic, mesotrophic and oligotrophic lakes and reservoirs.



Extended Data Fig. 5 | Areal methane fluxes from coastal wetlands and relationships of methane fluxes versus temperature and salinity. a) Boxplots showing median, lower (Q1), upper (Q3) quartiles and 1.5 times the length of the interquartile range of methane fluxes from salt marshes, mangroves and seagrasses. **b**) Linear relationships of coastal wetland methane fluxes and temperature ($r^2 = 0.04$, $p = 0.07$) and salinity ($r^2 = 0.02$, $p = 0.1$). Salt marsh extreme methane flux values ($n = 2$) are not shown.

Extended Data Table 1 | Areal methane fluxes from inland and coastal ocean ecosystems

Aquatic ecosystem	Total methane flux (mg CH_4 m^{-2} d^{-1})					
Inland waters	Mean ± C.I.95%	Median	IQR	Q1 lower quartile	Q3 upper quartile	n
Rivers and streams	182.4 ± 93.2	21.6	73.2	7.9	81.1	652
Lakes						
< 0.001 km^2	407.6 ± 238.0	265.3	277.8	90.1	367.9	24
0.001 – 0.01 km^2	228.8 ± 114.6	112.2	151.9	59.6	211.5	27
0.01 – 0.1 km^2	98.3 ± 39.3	40.7	82.3	12.2	94.4	69
0.1 – 1 km^2	62.5 ± 37.8	20.8	50.1	6.9	57.0	58
> 1 km^2	144.8 ± 191.6	13.7	83.6	5.0	88.7	20
All lakes	148.0 ± 42.4	46.4	117.4	11.7	129.0	198
Reservoirs						
< 1 km^2	119.6 ± 116.5	26.1	74.9	3.9	78.8	16
> 1 km^2	188.9 ± 105.6	46.4	144.8	8.6	153.4	62
All reservoirs	174.7 ± 86.5	36.2	127.7	7.6	135.3	78
Freshwater aquaculture ponds	439.2 ± 589.7	136.1	234.8	12.7	247.5	16
Coastal ocean						
Estuaries	2.4 ± 0.8	0.6	2.4	0.06	2.4	124
Coastal wetlands						
Saltmarshes	99.5 ± 75.5	8.8	43.4	1.0	44.4	60
Mangroves	29.0 ± 18.2	4.2	14.2	1.1	15.4	59
Seagrasses	1.8 ± 1.0	1.3	1.4	0.7	2.1	18
Tidal flats	90.2 ± 104.3	3.6	56.9	0.9	57.8	16
Coastal aquaculture ponds	686.8 ± 1,774.5	73.2	116.7	1.2	117.8	5
Continental shelves	12.1 ± 19.9	0.2	0.9	0.06	0.9	100 (A)

(A) n refers to flux measurements of continental shelf regions

The different transport pathways and interfaces that are included in the total methane flux of each aquatic ecosystem are reported in Supplementary Table 5. n refers to the number of sites.

nature research

Corresponding author(s): Judith Rosentreter

Last updated by author(s): 2021-01-21

Reporting Summary

✓

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Statistics

For all statistical analyses, confirm that the following items are present in the figure legend, table legend, main text, or Methods section.

n/a	Confirmed	
☐	☑	The exact sample size (*n*) for each experimental group/condition, given as a discrete number and unit of measurement
☑	☐	A statement on whether measurements were taken from distinct samples or whether the same sample was measured repeatedly
☐	☑	The statistical test(s) used AND whether they are one- or two-sided *Only common tests should be described solely by name; describe more complex techniques in the Methods section.*
☑	☐	A description of all covariates tested
☐	☑	A description of any assumptions or corrections, such as tests of normality and adjustment for multiple comparisons
☐	☑	A full description of the statistical parameters including central tendency (e.g. means) or other basic estimates (e.g. regression coefficient) AND variation (e.g. standard deviation) or associated estimates of uncertainty (e.g. confidence intervals)
☐	☑	For null hypothesis testing, the test statistic (e.g. *F*, *t*, *r*) with confidence intervals, effect sizes, degrees of freedom and *P* value noted *Give P values as exact values whenever suitable.*
☑	☐	For Bayesian analysis, information on the choice of priors and Markov chain Monte Carlo settings
☑	☐	For hierarchical and complex designs, identification of the appropriate level for tests and full reporting of outcomes
☐	☑	Estimates of effect sizes (e.g. Cohen's *d*, Pearson's *r*), indicating how they were calculated

Our web collection on statistics for biologists contains articles on many of the points above.

Software and code

Policy information about availability of computer code

Data collection	Data were extracted from peer-reviewed publications searching in the databases Web of Science Core Collection, China Knowledge Resource Integrated Database for rivers, lakes and reservoirs, and Scopus by Elsevier and Google Scholar for coastal ocean ecosystems, using Microsoft Excel. We used the manual data extraction tool WebPlotDigitizer to estimate values that were only presented in figures in studies. We combined our datasets with wetland and rice cultivation model outputs (Saunois et al. 2020)) and slope and open ocean model outputs from Web
Data analysis	Data analysis was performed using R (R Core Team, RStudio, version 1.3.1093). Plots were generated using the ggplot2 package. Skewness coefficients were calculated using the R package e1071. For the Monte Carlo analysis, we used the R package mc2d.

For manuscripts utilizing custom algorithms or software that are central to the research but not yet described in published literature, software must be made available to editors and reviewers. We strongly encourage code deposition in a community repository (e.g. GitHub). See the Nature Research guidelines for submitting code & software for further information.

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Policy information about availability of data

All manuscripts must include a data availability statement. This statement should provide the following information, where applicable:

- Accession codes, unique identifiers, or web links for publicly available datasets
- A list of figures that have associated raw data
- A description of any restrictions on data availability

Provide your data availability statement here.

Field-specific reporting

Please select the one below that is the best fit for your research. If you are not sure, read the appropriate sections before making your selection.

☐ Life sciences ☐ Behavioural & social sciences ☑ Ecological, evolutionary & environmental sciences

For a reference copy of the document with all sections, see nature.com/documents/nr-reporting-summary-flat.pdf

Life sciences study design

All studies must disclose on these points even when the disclosure is negative.

Sample size	*Describe how sample size was determined, detailing any statistical methods used to predetermine sample size OR if no sample-size calculation was performed, describe how sample sizes were chosen and provide a rationale for why these sample sizes are sufficient.*
Data exclusions	*Describe any data exclusions. If no data were excluded from the analyses, state so OR if data were excluded, describe the exclusions and the rationale behind them, indicating whether exclusion criteria were pre-established.*
Replication	*Describe the measures taken to verify the reproducibility of the experimental findings. If all attempts at replication were successful, confirm this OR if there are any findings that were not replicated or cannot be reproduced, note this and describe why.*
Randomization	*Describe how samples/organisms/participants were allocated into experimental groups. If allocation was not random, describe how covariates were controlled OR if this is not relevant to your study, explain why.*
Blinding	*Describe whether the investigators were blinded to group allocation during data collection and/or analysis. If blinding was not possible, describe why OR explain why blinding was not relevant to your study.*

Behavioural & social sciences study design

All studies must disclose on these points even when the disclosure is negative.

Study description	*Briefly describe the study type including whether data are quantitative, qualitative, or mixed-methods (e.g. qualitative cross-sectional, quantitative experimental, mixed-methods case study).*
Research sample	*State the research sample (e.g. Harvard university undergraduates, villagers in rural India) and provide relevant demographic information (e.g. age, sex) and indicate whether the sample is representative. Provide a rationale for the study sample chosen. For studies involving existing datasets, please describe the dataset and source.*
Sampling strategy	*Describe the sampling procedure (e.g. random, snowball, stratified, convenience). Describe the statistical methods that were used to predetermine sample size OR if no sample-size calculation was performed, describe how sample sizes were chosen and provide a rationale for why these sample sizes are sufficient. For qualitative data, please indicate whether data saturation was considered, and what criteria were used to decide that no further sampling was needed.*
Data collection	*Provide details about the data collection procedure, including the instruments or devices used to record the data (e.g. pen and paper, computer, eye tracker, video or audio equipment) whether anyone was present besides the participant(s) and the researcher, and whether the researcher was blind to experimental condition and/or the study hypothesis during data collection.*
Timing	*Indicate the start and stop dates of data collection. If there is a gap between collection periods, state the dates for each sample cohort.*
Data exclusions	*If no data were excluded from the analyses, state so OR if data were excluded, provide the exact number of exclusions and the rationale behind them, indicating whether exclusion criteria were pre-established.*
Non-participation	*State how many participants dropped out/declined participation and the reason(s) given OR provide response rate OR state that no participants dropped out/declined participation.*
Randomization	*If participants were not allocated into experimental groups, state so OR describe how participants were allocated to groups, and if allocation was not random, describe how covariates were controlled.*

Ecological, evolutionary & environmental sciences study design

All studies must disclose on these points even when the disclosure is negative.

Study description	Meta-analysis of aquatic methane flux measurements based on inventroy, remote sensing and modelling efforts
Research sample	Literature search of peer-reviewed publications

Research sample	
Sampling strategy	Boolean search string to search for publications in databases. Aditonally, we scanned the reference lists of publications
Data collection	Data were extracted using Microsoft Excel, J.A.R. did the synthesis for mangroves, saltmarshes, seagrasses and tidal flats; A.V.B. did the synthesis for estuaries and continental shelves; A.V.B. and J.A.R. did the synthesis for aquaculture ponds; C.S. compiled the data for streams, rivers, lakes, and reservoirs with help from S. L.
Timing and spatial scale	Start of literature search: 2018, end of literature search: Dec 2019, database includes studies published in the years 1978-2019
Data exclusions	See methods for details on data inclusion and exclusion criteria for each aquatic ecosystem database
Reproducibility	The database containing all compiled aquatic ecosystem data sets is accessible via figshare. Data Sources are available for Fig1 and 2
Randomization	No experimental groups
Blinding	No blinding strategy

Did the study involve field work? ☐ Yes ☑ No

Field work, collection and transport

Field conditions	*Describe the study conditions for field work, providing relevant parameters (e.g. temperature, rainfall).*
Location	*State the location of the sampling or experiment, providing relevant parameters (e.g. latitude and longitude, elevation, water depth).*
Access & import/export	*Describe the efforts you have made to access habitats and to collect and import/export your samples in a responsible manner and in compliance with local, national and international laws, noting any permits that were obtained (give the name of the issuing authority, the date of issue, and any identifying information).*
Disturbance	*Describe any disturbance caused by the study and how it was minimized.*

Reporting for specific materials, systems and methods

We require information from authors about some types of materials, experimental systems and methods used in many studies. Here, indicate whether each material, system or method listed is relevant to your study. If you are not sure if a list item applies to your research, read the appropriate section before selecting a response.

Materials & experimental systems

n/a	Involved in the study
☑	☐ Antibodies
☑	☐ Eukaryotic cell lines
☑	☐ Palaeontology and archaeology
☑	☐ Animals and other organisms
☑	☐ Human research participants
☑	☐ Clinical data
☑	☐ Dual use research of concern

Methods

n/a	Involved in the study
☑	☐ ChIP-seq
☑	☐ Flow cytometry
☑	☐ MRI-based neuroimaging

Antibodies

Antibodies used	*Describe all antibodies used in the study; as applicable, provide supplier name, catalog number, clone name, and lot number.*
Validation	*Describe the validation of each primary antibody for the species and application, noting any validation statements on the manufacturer's website, relevant citations, antibody profiles in online databases, or data provided in the manuscript.*

Eukaryotic cell lines

Policy information about cell lines

Cell line source(s)	*State the source of each cell line used.*

Authentication	*Describe the authentication procedures for each cell line used OR declare that none of the cell lines used were authenticated.*
Mycoplasma contamination	*Confirm that all cell lines tested negative for mycoplasma contamination OR describe the results of the testing for mycoplasma contamination OR declare that the cell lines were not tested for mycoplasma contamination.*
Commonly misidentified lines (See ICLAC register)	*Name any commonly misidentified cell lines used in the study and provide a rationale for their use.*

Palaeontology and Archaeology

Specimen provenance	*Provide provenance information for specimens and describe permits that were obtained for the work (including the name of the issuing authority, the date of issue, and any identifying information).*
Specimen deposition	*Indicate where the specimens have been deposited to permit free access by other researchers.*
Dating methods	*If new dates are provided, describe how they were obtained (e.g. collection, storage, sample pretreatment and measurement), where they were obtained (i.e. lab name), the calibration program and the protocol for quality assurance OR state that no new dates are provided.*

☐ Tick this box to confirm that the raw and calibrated dates are available in the paper or in Supplementary Information.

Ethics oversight	*Identify the organization(s) that approved or provided guidance on the study protocol, OR state that no ethical approval or guidance was required and explain why not.*

Note that full information on the approval of the study protocol must also be provided in the manuscript.

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Policy information about studies involving animals; ARRIVE guidelines recommended for reporting animal research

Laboratory animals	*For laboratory animals, report species, strain, sex and age OR state that the study did not involve laboratory animals.*
Wild animals	*Provide details on animals observed in or captured in the field; report species, sex and age where possible. Describe how animals were caught and transported and what happened to captive animals after the study (if killed, explain why and describe method; if released, say where and when) OR state that the study did not involve wild animals.*
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Ethics oversight	*Identify the organization(s) that approved or provided guidance on the study protocol, OR state that no ethical approval or guidance was required and explain why not.*

Note that full information on the approval of the study protocol must also be provided in the manuscript.

Human research participants

Policy information about studies involving human research participants

Population characteristics	*Describe the covariate-relevant population characteristics of the human research participants (e.g. age, gender, genotypic information, past and current diagnosis and treatment categories). If you filled out the behavioural & social sciences study design questions and have nothing to add here, write "See above."*
Recruitment	*Describe how participants were recruited. Outline any potential self-selection bias or other biases that may be present and how these are likely to impact results.*
Ethics oversight	*Identify the organization(s) that approved the study protocol.*

Note that full information on the approval of the study protocol must also be provided in the manuscript.

Clinical data

Policy information about clinical studies

All manuscripts should comply with the ICMJE guidelines for publication of clinical research and a completed CONSORT checklist must be included with all submissions.

Clinical trial registration	*Provide the trial registration number from ClinicalTrials.gov or an equivalent agency.*
Study protocol	*Note where the full trial protocol can be accessed OR if not available, explain why.*
Data collection	*Describe the settings and locales of data collection, noting the time periods of recruitment and data collection.*
Outcomes	*Describe how you pre-defined primary and secondary outcome measures and how you assessed these measures.*

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Policy information about dual use research of concern

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Could the accidental, deliberate or reckless misuse of agents or technologies generated in the work, or the application of information presented in the manuscript, pose a threat to:

No	Yes	
☐	☐	Public health
☐	☐	National security
☐	☐	Crops and/or livestock
☐	☐	Ecosystems
☐	☐	Any other significant area

Other impacts	*Describe any other significant impacts.*
Hazards	*Please describe the agents/technologies/information that may pose a threat, including any agents subject to oversight for dual use research of concern.*

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☐	☐	Enhance the virulence of a pathogen or render a nonpathogen virulent
☐	☐	Increase transmissibility of a pathogen
☐	☐	Alter the host range of a pathogen
☐	☐	Enable evasion of diagnostic/detection modalities
☐	☐	Enable the weaponization of a biological agent or toxin
☐	☐	Any other potentially harmful combination of experiments and agents

Other combinations	*Describe any other potentially harmful combination(s) of experiments and agents.*

Precautions and benefits

Biosecurity precautions	*Describe the precautions that were taken during the design and conduct of this research, or will be required in the communication and application of the research, to minimise biosecurity risks. These may include bio-containment facilities, changes to the study design/ methodology or redaction of details from the manuscript.*
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ChIP-seq

Data deposition

☐ Confirm that both raw and final processed data have been deposited in a public database such as GEO.

☐ Confirm that you have deposited or provided access to graph files (e.g. BED files) for the called peaks.

Data access links *May remain private before publication.*	*For "Initial submission" or "Revised version" documents, provide reviewer access links. For your "Final submission" document, provide a link to the deposited data.*
Files in database submission	*Provide a list of all files available in the database submission.*

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Methodology

Replicates	*Describe the experimental replicates, specifying number, type and replicate agreement.*
Sequencing depth	*Describe the sequencing depth for each experiment, providing the total number of reads, uniquely mapped reads, length of reads and whether they were paired- or single-end.*
Antibodies	*Describe the antibodies used for the ChIP-seq experiments; as applicable, provide supplier name, catalog number, clone name, and lot number.*
Peak calling parameters	*Specify the command line program and parameters used for read mapping and peak calling, including the ChIP, control and index files used.*
Data quality	*Describe the methods used to ensure data quality in full detail, including how many peaks are at FDR 5% and above 5-fold enrichment.*
Software	*Describe the software used to collect and analyze the ChIP-seq data. For custom code that has been deposited into a community repository, provide accession details.*

Flow Cytometry

Plots

Confirm that:

☐ The axis labels state the marker and fluorochrome used (e.g. CD4-FITC).

☐ The axis scales are clearly visible. Include numbers along axes only for bottom left plot of group (a 'group' is an analysis of identical markers).

☐ All plots are contour plots with outliers or pseudocolor plots.

☐ A numerical value for number of cells or percentage (with statistics) is provided.

Methodology

Sample preparation	*Describe the sample preparation, detailing the biological source of the cells and any tissue processing steps used.*
Instrument	*Identify the instrument used for data collection, specifying make and model number.*
Software	*Describe the software used to collect and analyze the flow cytometry data. For custom code that has been deposited into a community repository, provide accession details.*
Cell population abundance	*Describe the abundance of the relevant cell populations within post-sort fractions, providing details on the purity of the samples and how it was determined.*
Gating strategy	*Describe the gating strategy used for all relevant experiments, specifying the preliminary FSC/SSC gates of the starting cell population, indicating where boundaries between "positive" and "negative" staining cell populations are defined.*

☐ Tick this box to confirm that a figure exemplifying the gating strategy is provided in the Supplementary Information.

Magnetic resonance imaging

Experimental design

Design type	*Indicate task or resting state; event-related or block design.*
Design specifications	*Specify the number of blocks, trials or experimental units per session and/or subject, and specify the length of each trial or block (if trials are blocked) and interval between trials.*
Behavioral performance measures	*State number and/or type of variables recorded (e.g. correct button press, response time) and what statistics were used to establish that the subjects were performing the task as expected (e.g. mean, range, and/or standard deviation across subjects).*

Acquisition

Imaging type(s)	*Specify: functional, structural, diffusion, perfusion.*
Field strength	*Specify in Tesla*
Sequence & imaging parameters	*Specify the pulse sequence type (gradient echo, spin echo, etc.), imaging type (EPI, spiral, etc.), field of view, matrix size, slice thickness, orientation and TE/TR/flip angle.*
Area of acquisition	*State whether a whole brain scan was used OR define the area of acquisition, describing how the region was determined.*

Diffusion MRI ☐ Used ☐ Not used

Parameters *Specify # of directions, b-values, whether single shell or multi-shell, and if cardiac gating was used.*

Preprocessing

Preprocessing software	*Provide detail on software version and revision number and on specific parameters (model/functions, brain extraction, segmentation, smoothing kernel size, etc.).*
Normalization	*If data were normalized/standardized, describe the approach(es): specify linear or non-linear and define image types used for transformation OR indicate that data were not normalized and explain rationale for lack of normalization.*
Normalization template	*Describe the template used for normalization/transformation, specifying subject space or group standardized space (e.g. original Talairach, MNI305, ICBM152) OR indicate that the data were not normalized.*
Noise and artifact removal	*Describe your procedure(s) for artifact and structured noise removal, specifying motion parameters, tissue signals and physiological signals (heart rate, respiration).*
Volume censoring	*Define your software and/or method and criteria for volume censoring, and state the extent of such censoring.*

Statistical modeling & inference

Model type and settings	*Specify type (mass univariate, multivariate, RSA, predictive, etc.) and describe essential details of the model at the first and second levels (e.g. fixed, random or mixed effects; drift or auto-correlation).*
Effect(s) tested	*Define precise effect in terms of the task or stimulus conditions instead of psychological concepts and indicate whether ANOVA or factorial designs were used.*

Specify type of analysis: ☐ Whole brain ☐ ROI-based ☐ Both

Anatomical location(s) *Describe how anatomical locations were determined (e.g. specify whether automated labeling algorithms or probabilistic atlases were used).*

Statistic type for inference (See Eklund et al. 2016)	*Specify voxel-wise or cluster-wise and report all relevant parameters for cluster-wise methods.*
Correction	*Describe the type of correction and how it is obtained for multiple comparisons (e.g. FWE, FDR, permutation or Monte Carlo).*

Models & analysis

n/a	Involved in the study
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☐	☐ Graph analysis
☐	☐ Multivariate modeling or predictive analysis

Functional and/or effective connectivity	*Report the measures of dependence used and the model details (e.g. Pearson correlation, partial correlation, mutual information).*
Graph analysis	*Report the dependent variable and connectivity measure, specifying weighted graph or binarized graph, subject- or group-level, and the global and/or node summaries used (e.g. clustering coefficient, efficiency, etc.).*
Multivariate modeling and predictive analysis	*Specify independent variables, features extraction and dimension reduction, model, training and evaluation metrics.*