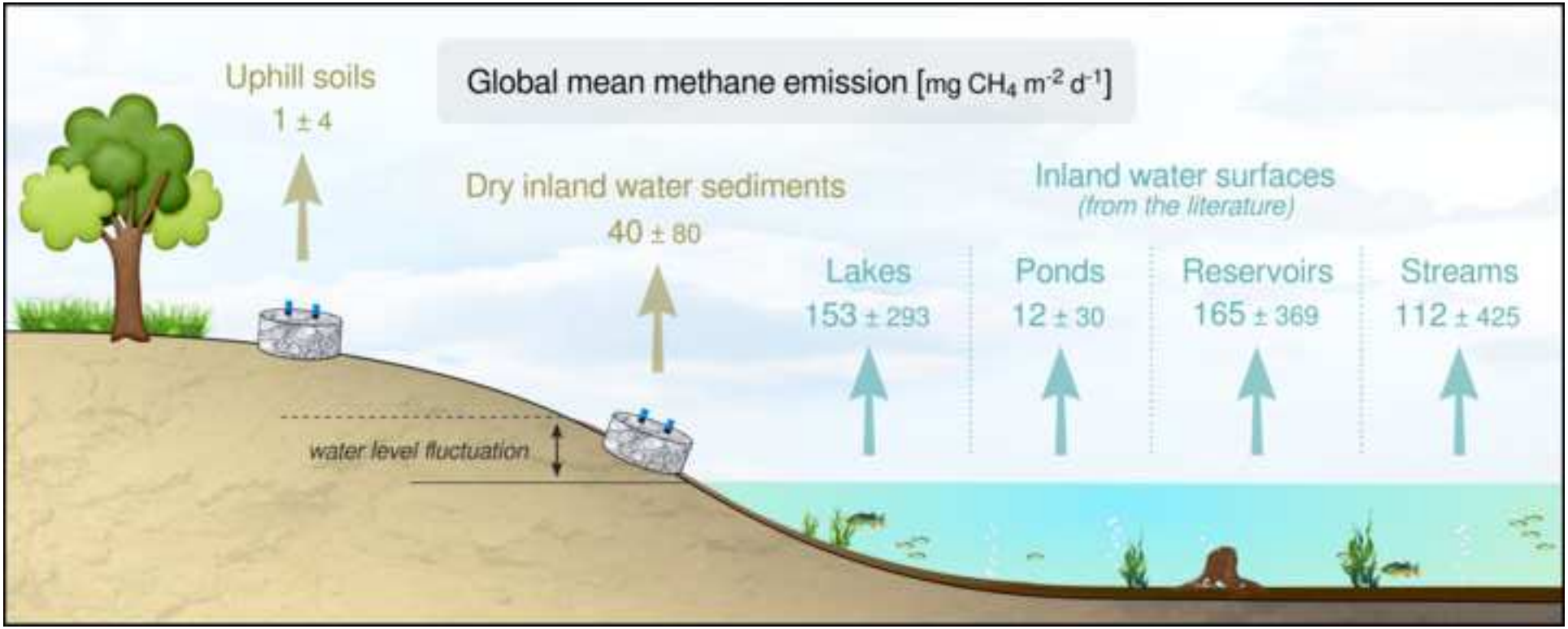
Graphical Abstract



Highlights should be submitted in a separate editable file in the online submission system. Please use 'Highlights' in the file name and include 3 to 5 bullet points (maximum 85 characters, including spaces, per bullet point).

- Dry inland waters are hotspots of C emission to the atmosphere
- CH_4 contributed 10 – 21% to total C emissions (in CO_2-eq) of dry inland waters
- The contribution of CH_4 (total C emissions) did not differ between types of systems
- Globally, dry inland waters emit 2.7 Tg C-CH_4 y^{-1} and emissions are likely rising
- More CH_4 emission data are needed to improve the global GHG budget of inland waters

Cross-continental importance of CH_4 emissions from dry inland-waters

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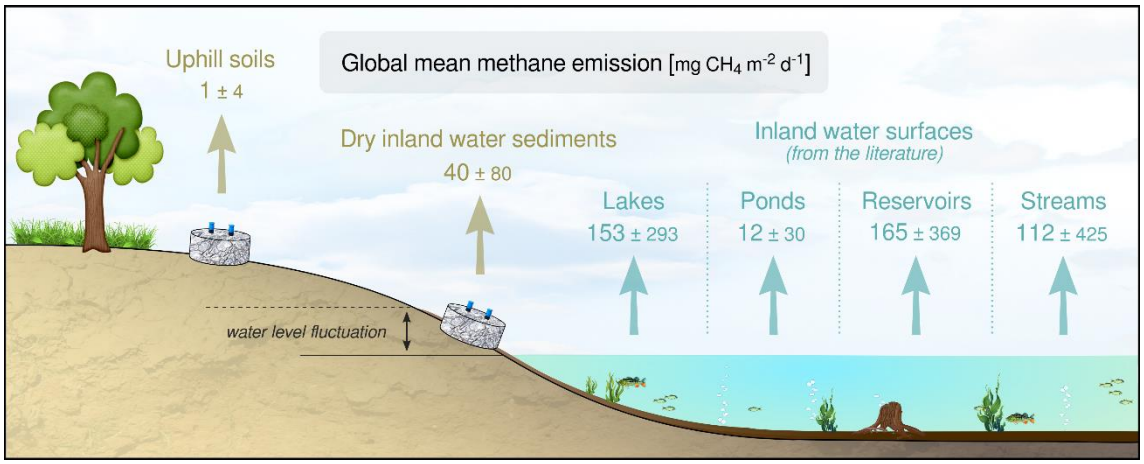
Graphical abstract



Abstract

Despite substantial advances in quantifying greenhouse gas (GHG) emissions from dry inland waters, existing estimates mainly consist of carbon dioxide (CO_2) emissions. However, methane (CH_4) may also be relevant due to its higher Global Warming Potential (GWP). We report CH_4 emissions from dry inland water sediments to i) provide a cross-continental estimate of such emissions for different types of aquatic systems (i.e., lakes, ponds, reservoirs, and streams) and climate zones (i.e., tropical, continental, and temperate); and ii) determine the environmental factors that control these emissions. CH_4 emissions from dry inland waters were consistently higher than emissions observed in adjacent uphill soils, across climate zones and in all aquatic systems except for streams. However, the CH_4 contribution (normalized to CO_2 equivalents; CO_2-eq) to the total GHG emissions of dry inland waters was similar for all types of aquatic systems and varied from 10 – 21%. Although we discuss multiple controlling factors, dry inland water CH_4 emissions were most strongly related to sediment organic matter content and moisture. Summing CO_2 and CH_4 emissions revealed a cross-continental average emission of 9.6 ± 17.4 g CO_2-eq m^{-2} d^{-1} from dry inland waters. We argue that increasing droughts likely expand the worldwide surface area of atmosphere-exposed aquatic sediments, thereby increasing global dry inland water CH_4 emissions. Hence, CH_4 cannot be ignored if we want to fully understand the carbon (C) cycle of dry sediments.

Keywords: Methane; Dry sediments; Aquatic ecosystems; Greenhouse gases;

1. Introduction

Inland waters (e.g., lakes, ponds, reservoirs, rivers) are complex ecosystems that process large amounts of allochthonous and autochthonous organic matter (Attermeyer et al., 2017; Clair and Ehrman, 1996; Friedl and Wüest, 2002; Van Cappellen and Maavara, 2016) and play important roles as sources and sinks within the global C cycle (Cole et al., 2007; Rosentreter et al., 2021; Tranvik et al., 2009). In aquatic ecosystems, organic matter undergoes various biogeochemical processes, including its decomposition into gaseous carbon (C) species (Mattson and Likens, 1992) such as carbon dioxide (CO_2) and methane (CH_4) (Bastviken et al., 2011; DelSontro et al., 2018; Raymond et al., 2013). In addition, part of the organic matter can settle and accumulate in sediments (Heathcote et al., 2015; Mendonça et al., 2017). According to C-budget studies, approximately 0.06 – 0.25 Pg C y^{-1} are estimated to be buried in sediments of inland waters worldwide (Anderson et al., 2020; Mendonça et al., 2017), whereas approximately 3.9 Pg C y^{-1} are emitted from inland waters to the atmosphere as CO_2 and as CH_4 (Drake et al., 2018).

After CO_2, CH_4 is the most important gas contributing to the global greenhouse effect. Considering the Global Warming Potential (GWP) over a 100-year time horizon, one gram of CH_4 exerts an atmospheric heating power equivalent to 34 grams of CO_2 (Myhre et al., 2013). Globally, approximately 0.15 Pg of C are annually emitted from freshwaters to the atmosphere as CH_4 (not considering wetlands, rice paddies and aquaculture ponds). About 0.13 Pg C y^{-1} of these emissions evade to the atmosphere from lentic (non-flowing) aquatic systems such as lakes, ponds and reservoirs, and ~0.02 Pg C y^{-1} from lotic (flowing) systems such as streams and rivers (Rosentreter et al., 2021). A large part of the CH_4 production in aquatic systems occurs in anoxic sediments via microbial degradation of organic matter (Bastviken et al., 2004). The

resulting CH_4 that escapes microbial oxidation at the sediment-water interface and water column (Granéli et al., 1996; Heilman and Carlton, 2001) reaches the atmosphere through diffusion (Bastviken et al., 2004; Cole and Caraco, 1998), ebullition (bubbling) (Bastviken et al., 2004), plant-mediated transport (Abril et al., 2005), and by the passage of deep, CH_4-rich waters through the turbines of hydroelectric reservoirs ("degassing") (Abril et al., 2005; Kemenes et al., 2016). In addition, even after exposure to atmospheric air, sediment CH_4 production can continue in anoxic microhabitats (Dalal et al., 2008; Serrano-Silva et al., 2014). However, a large share of the CH_4 produced in these micro-regions is oxidized to CO_2 by methanotrophic bacteria before evasion to the atmosphere, especially during the first hours or days after atmospheric exposure (Koschorreck, 2000). The remaining CH_4 may directly diffuse to the atmosphere.

Many inland water ecosystems worldwide experience periods of drying (Marcé et al., 2019; Messager et al., 2021). Drying can result from natural (i.e., intermittency of rivers and ponds) or human-induced (i.e., human actions in reservoirs and lakes) water level and flow fluctuations (Beaulieu et al., 2018; Di Baldassarre et al., 2018; Leigh et al., 2016; Wurtsbaugh et al., 2017). During the dry season, considerable areas of marginal aquatic sediments are exposed directly to the atmosphere. Pekel et al. (2016) estimated that ~800,000 km^2 (or 18%) of the global surface area that is covered by inland waters are subject to seasonal atmospheric exposure, especially non-flowing reaches, which dominate the hydrological networks (Messager et al., 2021). Moreover, 15% of the global reservoir surfaces are dry (Keller et al., 2021).

Exposed aquatic sediments may represent a substantial source of GHG to the atmosphere (Keller et al., 2020; Marcé et al., 2019; von Schiller et al., 2014) but are seldom considered in global C emission estimates. Local, regional, and global GHG emission estimates from dry inland waters have emerged and improved considerably in

the last decade (Beaulieu et al., 2018; Gallo et al., 2014; Harrison et al., 2017; Jin et al., 2016; Marcé et al., 2019), especially for CO_2 (Almeida et al., 2019; Catalán et al., 2014; Deshmukh et al., 2018; Keller et al., 2020; Obrador et al., 2018; von Schiller et al., 2014). Keller et al. (2020) found that 0.12 ± 0.13 Pg C y^{-1} are added to recent global inland water C emission estimates when CO_2 emissions from dry inland waters are considered. However, compared to CO_2, other GHGs have been poorly assessed in drying sediments, preventing a complete picture of their role in biogeochemical cycling. Particularly for CH_4, the number of studies on dry inland waters is not sufficient to reliably upscale CH_4 fluxes of these habitats to the global scale (Marcé et al., 2019). Because of this, a recent global estimate of GHG emissions from dry reservoir sediments assumed zero CH_4 emissions (Keller et al., 2021). In addition, the environmental drivers regulating CH_4 fluxes from dry inland waters are not fully understood. Therefore, the contribution of CH_4 emission from exposed sediments to global C emission from inland waters remains to be quantified.

This study aims to assess the importance of CH_4 fluxes from the exposed sediments of different types of aquatic systems (i.e., lakes, ponds, reservoirs, and streams) located in various climate zones across the globe. To achieve this, dry inland water CH_4 fluxes were i) compared to CH_4 fluxes observed in adjacent uphill (natural terrestrial) soils; ii) compared to the CO_2 fluxes obtained at the same locations where CH_4 fluxes were measured; iii) related to physical and chemical sediment properties that were concurrently measured along with CH_4 in order to identify drivers of CH_4 fluxes from exposed sediments; iv) scaled up to the respective dry global surface areas associated with each type of aquatic system studied here, to v) ultimately determine whether dry inland water CH_4 fluxes represent a significant share of the global C emission estimates from inland waters. To the best of our knowledge, this is the first

cross-continental study quantifying the magnitude and environmental controls of CH_4 fluxes from the dry sediments of multiple aquatic system types.

2. Methods

2.1 Studied sites and sampling strategy

This study includes measurements in 89 hydrologically independent aquatic systems (lakes, *n* = 45; ponds, *n* = 16; reservoirs, *n* = 19; and streams, *n* = 9), located in three of the five global climate zones (tropical, *n* = 24; continental, *n* = 11; and temperate, *n* = 54) (Kottek et al., 2006) (Figure 1), which were conducted by 22 research groups from 10 countries. The research groups were classified as levels of a variable named "*research group*", which were used in the analysis of CH_4 flux drivers (see below). The 89 systems are a subset of the 196 aquatic systems included in a recent global study on CO_2 emission from exposed sediments by Keller et al. (2020). The subset was created based on the availability of CH_4 flux data (i.e., not all datasets contained CH_4 data).

At each sampling site, two distinct regions were sampled: i) exposed sediment – hereafter named as "*dry inland water*", which corresponds to an area with air-exposed sediment that experiences periodic and/or recent historical inundation (Marcé et al., 2019); and ii) adjacent uphill soil, which corresponds to the adjacent terrestrial region that is not inundated. At each region, measurements were performed in triplicates that were, if possible, conducted at least 1 meter apart from each other to capture spatial within-region variability.

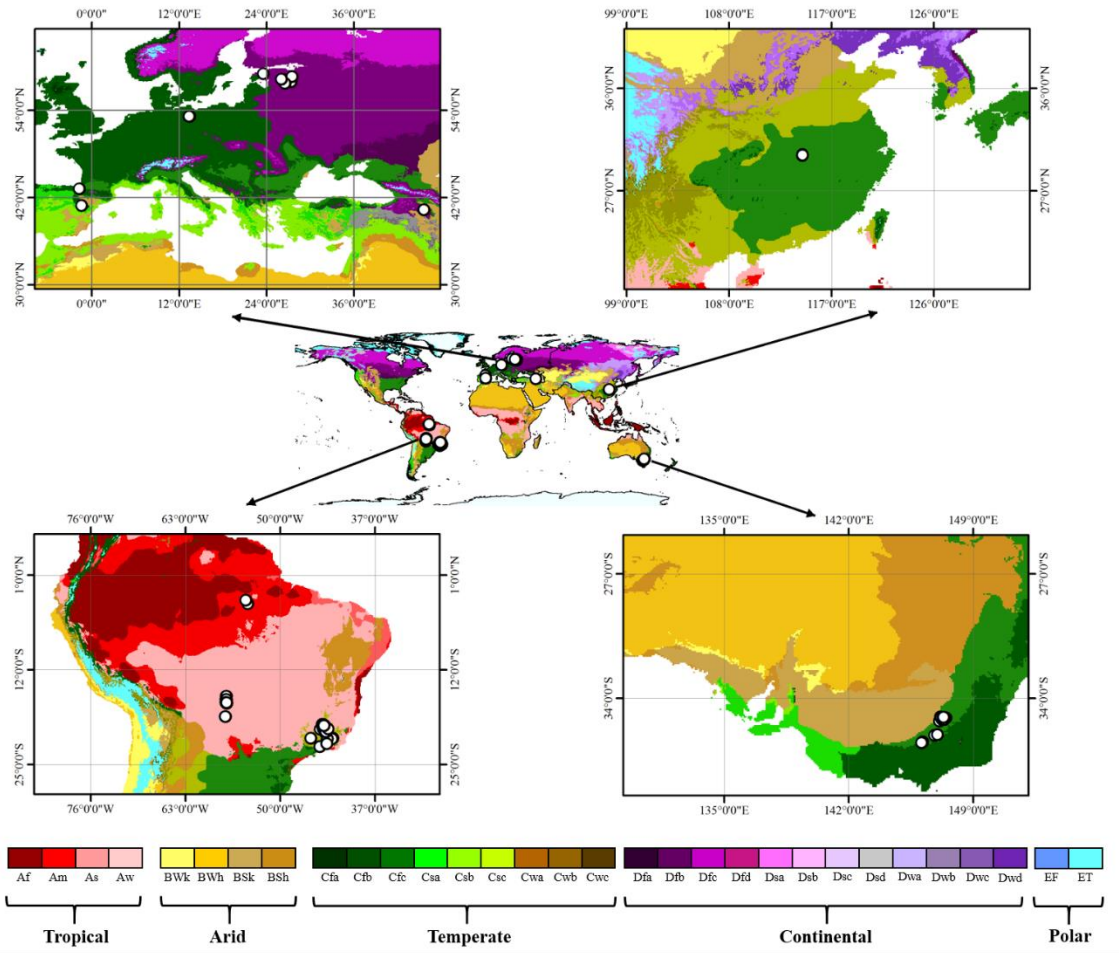


Figure 1 | Cross-continental distribution of the sampling sites (white dots) across the different climate zones according to the Köppen-Geiger climate classification system (Kottek et al., 2006).

2.2 CH_4 flux measurements

Between 2016 and 2017, *in situ* measurements of CH_4 flux (mg CH_4 m^{-2} d^{-1}) were conducted using opaque chambers connected to infrared gas analyzers in closed gas loops. The chambers were gently placed over the sediment/soil surface to avoid disturbance and gas leakage during the measurements, and where necessary, sealed with clay (Lesmeister and Koschorreck, 2017). Changes in CH_4 partial pressure (mCH_4) were

monitored within the chambers over 3-5 minutes, and the fluxes were calculated following:

$$FCH_4 = \left(\frac{dmCH_4}{dt}\right) x \left(\frac{V}{RTA}\right) \quad (1)$$

where $dmCH_4$ is the slope of change in mCH_4 (ppm) over time (dt, given in seconds), V is the volume of the chamber (m^3), R is the gas constant = 8.205746 x 10^{-5} m^3 atm mol^{-1} K^{-1}, T is the air temperature (K), and A is the surface area covered by the chamber (m^2).

Dry inland waters lack CH_4 ebullition as an emission route (Marcé et al., 2019), mainly due to the absence of water overlying the sediments. Therefore, our measurements represent only the diffusion of CH_4 at the sediment/soil-atmosphere interface. Opaque chambers were used in order to minimize temperature changes during measurements, which may affect the gas exchange at the interface between sediment/soil and headspace (Welles et al., 2001). Chamber deployments were performed on top of bare sediment/soil, avoiding vegetated surfaces.

2.3 Sediment/soil characterization

After the flux measurements, surface sediment/soil samples were collected from the plot of the flux measurement, placed in plastic bags and stored in thermal cooler boxes for subsequent laboratory analysis. Air and sediment/soil temperature (°C) were measured *in situ*, and elevation (m.a.s.l., meters above sea level) was either measured *in situ* or read from a map. Sediment/soil texture was determined following a manipulative test developed by the Food and Agriculture Organization of the United Nations (FAO, 2020) and distinguished as clay, light clay, heavy loam, sandy loam, loamy sand, and sand. 10 g of fresh sediment/soil were mixed in 25 mL distilled water for the

determination of electrical conductivity (µS cm^{-1}) and pH by measuring the suspended solution (after 1 h standing) with conventional electrodes (Keller et al., 2020). Moisture content (% weight loss) was determined by drying 5 g of fresh sediment/soil at 105 °C until reaching a constant weight (Keller et al., 2020). Afterward, the samples were combusted at 500 °C until constant weight for the determination of the organic matter content (% weight loss) (Dean, 1974).

2.4 Data analysis and statistical procedures

Each sampling site was assigned to a climate zone according to "The World Maps of Köppen-Geiger Climate Classification" (Kottek et al., 2006). For each sampling site, we then calculated the contribution of dry inland water CH_4 emission to the total (i.e., CO_2 + CH_4) GHG emission in CO_2-equivalents (CO_2-eq; see below how CH_4 was converted to CO_2-eq) for each type of aquatic system (lakes, ponds, reservoirs, and streams). The CO_2 flux data was retrieved from Keller et al. (2020), and each CO_2 flux measurement was associated with the CH_4 flux measurement collected at the same sampling site. For all analyses, triplicate measurements were averaged, and one average value per parameter at each sampling site was used.

To test the relationships between environmental variables and dry inland water CH_4 fluxes, a generalized linear mixed model (GLMM) was performed using the "*glmer*" function in the "*lme4*" package (Bates et al., 2015) in R (v. 4.0.2) (R Core Team, 2018). We used sediment texture, sediment temperature, pH, electrical conductivity, moisture and organic matter content, as well as latitude, elevation, annual mean precipitation, and annual mean air temperature as fixed effects. Given that CH_4 fluxes are primarily driven by the availability and quality of organic matter, moisture,

and temperature (Aben et al., 2017; Grasset et al., 2018; Koschorreck, 2000; Sobek et al., 2012; Yvon-Durocher et al., 2014), the interactions between i) organic matter content and temperature, ii) organic matter and moisture content, and iii) moisture content and temperature of the sediments were also included as fixed effects. The variables research group, type of aquatic system, and climate zone were used as crossed random factors to account for the dependencies in the data. We used GLMM because preliminary analyses showed that the distribution of the residuals of the linear mixed models followed a logarithmic distribution and, therefore, the Gamma family (*link=log*) was applied in the GLMM (Lo and Andrews, 2015). A value of 13 mg m^{-2} d^{-1} was added to the CH_4 flux data (i.e., x + 13) to avoid negative values which would hamper our GLMM analysis since the Gamma family (*link=log*) does not allow negative values in the response variable. The observed negative CH_4 flux values (i.e., influx; see section 3. Results and Discussion) were very small in magnitude compared with emissions – most of the influx data were close to zero and the strongest influx was roughly 7 mg CH_4 m^{-2} d^{-1}, whereas the efflux rates were often two orders of magnitude greater than influx rates. Therefore, the addition of the fixed value aforementioned does not have a relevant impact on the overall driver analysis. Logarithmic and cubic root transformations were adopted for electrical conductivity and organic matter content (x + 1), moisture, and elevation, respectively, to meet the conditions of normality and homoscedasticity of variances. Before analysis, collinearity between predictor variables was assessed using the variance inflation factor (VIF) function in the "*usdm*" package (Naimi et al., 2014) in R. Variables with VIF values > 5 (which is indicative of collinearity) were excluded from the procedures (Akinwande et al., 2015). In the GLMM presented here, the excluded variable was annual precipitation. The model was simplified by removing non-significant predictors. GLMMs were also used to assess

differences in CH_4 fluxes, moisture, and organic matter content among aquatic system types (fixed factor), between sampling regions (fixed factor), and between climate zones (fixed factor), with the variable research group defined as a crossed random factor. Type-III ANOVAs were used to test the significance of the fixed factors, with degrees of freedom and *p* values calculated using the Kenward-Roger approximation (Kenward and Roger, 1997) through the "*lmerTest*" and "*pbkrtest*" packages (Halekoh and Højsgaard, 2014; Kuznetsova et al., 2017). Least-square means (classical Yates contrasts), as well as pairwise differences, were computed by the "*ls_means*" function ("*lmerTest*" package). For all statistical procedures, a p value < 0.05 was adopted as the threshold level of statistical significance.

Finally, to obtain an estimate of cross-continental CH_4 emission from dry inland waters, we multiplied the average CH_4 flux rate of each type of aquatic system by its respective global associated desiccated surface area (for lakes, reservoirs, and ponds: Marcé et al., 2019; for streams: Raymond et al., 2013), and then summed them up. Also, cross-continental CH_4 emissions from dry inland waters were converted into CO_2-eq emissions by using the 100-year time horizon GWP factor of 34 (Myhre et al., 2013).

3. Results and Discussion

3.1 Contrasting CH_4 fluxes from dry inland waters and surrounding terrestrial areas

CH_4 fluxes from dry sediments of inland waters and adjacent uphill (terrestrial) soils ranged from -8 to 352 mg CH_4 m^{-2} d^{-1}, with a median of 0.08 mg CH_4 m^{-2} d^{-1} and an interquartile range (IQR) of 4.1 mg CH_4 m^{-2} d^{-1} (mean ± standard deviation (SD): 20 ± 60 mg CH_4 m^{-2} d^{-1}) (Figure 2). CH_4 uptake was found in 51 uphill soil regions (57%) and 21 dry inland water regions (23%) (Figure 2D – see Figure 2E and F for system

type and climate zones). Variability of CH_4 fluxes was larger among dry inland water sediments than among uphill soils (Figure 2A). Uphill sites tend to be drained/dry and oxic, which represents unfavorable conditions for CH_4 production but favorable conditions for CH_4 consumption (von Fischer and Hedin, 2007). On the other hand, exposed inland-water sediments may sometimes be fully desiccated, showing little or no CH_4 production, or waterlogged with potential anoxia supporting CH_4 production and emission (Koschorreck, 2000). While CO_2 emissions from dry inland waters tend to be lower than those from uphill soils (Almeida et al., 2019; Catalán et al., 2014; Jin et al., 2016; Keller et al., 2020; von Schiller et al., 2014), the pattern we observed for CH_4 was opposite. Average CH_4 emissions from dry inland waters were significantly higher than those from adjacent uphill soils (Figure 2A; Table 1) (mean ± SD and median – IQR, respectively; dry inland water: 40 ± 80 mg CH_4 m^{-2} d^{-1}, and 1 – 28.4 mg CH_4 m^{-2} d^{-1}; uphill soil: 1 ± 4 mg CH_4 m^{-2} d^{-1}, and -0.07 – 1.1 mg CH_4 m^{-2} d^{-1}; GLMM: t = -9.61, p < 0.001). The difference in CH_4 emissions from the two different regions may be attributed to differences in moisture content as well as quality and quantity of organic matter (Dalal et al., 2008; Serça et al., 2016; Serrano-Silva et al., 2014). When air-exposed sediments are still wet, anoxia generally prevails below the upper few millimeters of the sediment (Koschorreck and Darwich, 2003), thereby sustaining CH_4 production. When sediments start to dry out, CH_4 production through organic matter decomposition can still take place in anoxic microhabitats (Dalal et al., 2008; Koschorreck, 2000; Serrano-Silva et al., 2014). As exposed sediments of inland waters dry out further, newly formed fractures ease the contact of deeper sediment layers with atmospheric oxygen (Fromin et al., 2010; Kosten et al., 2018; Paranaíba et al., 2020). The expansion of the oxic layer in the sediment provokes changes in microbial communities and their activity (Borken and Matzner, 2009; Jin et al., 2016; Rodrigo et

al., 1997), favoring aerobic metabolisms (e.g., CH_4 oxidation; Jäckel et al., 2001; Koschorreck, 2000), and eventually leading to a reduction in CH_4 emissions (Kosten et al., 2018; Paranaíba et al., 2020). Furthermore, the microbial community in water-stressed sediments is expected to desiccate (Borken and Matzner, 2009; Jin et al., 2016; Rodrigo et al., 1997), which can be expected to diminish the potential of CH_4 production likely contributing to the wide range in CH_4 fluxes from dry inland-water sediments. The importance of moisture content in regulating CH_4 emission is further exemplified by the mean moisture content being consistently higher in dry inland-water sediments than in uphill soils across all systems globally (mean ± SD; dry inland water: 33.1 ± 21.4%, uphill soil: 17 ± 9.4%; GLMM: t = -7.03, p < 0.001), corresponding with the generally higher CH_4 emissions from the dry inland-water sediments. Mean organic matter content, however, was similar for the two regions (mean ± SD; dry inland water: 7.9 ± 7%, uphill soil: 8.2 ± 7.5%; GLMM: t = 0.19, p = 0.84).

3.2 Dry inland waters CH_4 flux variability across aquatic systems and climate zones

No statistical differences in CH_4 fluxes were found between the different types of dry inland water systems (GLMM, F = 0.63, p = 0.59 – see Table S1 for pairwise comparisons), due to the relatively high variability among sites within each type (Figure 2B; Table 1). Dry inland water sediments were a source of CH_4 in almost all cases, while adjacent uphill soils could be either a source or a sink of CH_4, depending on the site (Figure 2E). Dry inland water CH_4 fluxes were, on average (± SD), 48 ± 91 mg CH_4 m^{-2} d^{-1} (n = 45; median – IQR: 2.3 – 48.2 mg CH_4 m^{-2} d^{-1}) in lakes, 38 ± 63 mg CH_4 m^{-2} d^{-1} (n = 16; median – IQR: 0.7 – 84 mg CH_4 m^{-2} d^{-1}) in ponds, 36 ± 78 mg CH_4 m^{-2} d^{-1} (n = 19; median – IQR: 0.08 – 13.9 mg CH_4 m^{-2} d^{-1}) in reservoirs, and 7 ± 17 mg CH_4 m^{-2} d^{-1} (n = 9; median – IQR: 0.1 – 3.5 mg CH_4 m^{-2} d^{-1}) in streams (Figure 2B; Table 1).

The lower CH_4 flux rate from dry streams corresponded with their significantly lower mean (± SD) moisture and organic matter content when compared to lakes, ponds and reservoirs (moisture content: streams: 20 ± 27%, lakes: 31 ± 20%, ponds: 52 ± 21%, reservoirs: 27 ± 10%; GLMM, $F = 6.25$, $p = 0.0006$ – see Table S2 for pairwise comparisons; organic matter content: streams: 1 ± 1%, lakes: 9 ± 8%, ponds: 8 ± 4%, reservoirs: 9 ± 6%; GLMM, $F = 3.48$, $p = 0.01$ – see Table S3 for pairwise comparisons). In fact, dry sediments of rivers and streams tend to have less organic matter content than dry sediments of lentic water bodies (Gómez-gener et al., 2015). Rivers and streams are more sensitive to variations in hydrological cycles (i.e., are subject to high and recurrent water stress). In addition, water flow erodes fine-grained sediment, which hinders organic matter accumulation at the margins of these systems (Boix-Fayos et al., 2015; Gómez-Gener et al., 2016).

The CH_4 fluxes presented here were higher than values reported for individual dry inland water CH_4-emission in earlier studies conducted in different aquatic systems (Table 1). We can only speculate about the underlying reason, which may be related to drier conditions or low (quality) organic matter content found in the systems from earlier studies. For instance, the mean ± SD of organic matter content found in 16 ephemeral streams by Gallo et al. (2014) was 3 ± 2.7%, and mean ± SD dry CH_4 emission was 0.4 ± 0.5 mg CH_4 m^{-2} d^{-1}, which is both considerably lower than the values we found.

The CH_4 fluxes per square meter from dry inland waters were lower than those from surface waters reported in the literature (Table 1). This may be related to lower oxygen availability in submerged sediments possibly leading to higher CH_4 production and lower CH_4 consumption. In addition, the littoral regions of streams and reservoirs tend to be depleted in labile organic matter due to frequent water level changes, which

hampers the production of CH_4 in these regions (Dalal et al., 2008; Serrano-Silva et al., 2014).

No statistical differences in dry inland water CH_4 fluxes were found between climate zones (GLMM, $F = 1.41$, $p = 0.22$ – see Table S4 for pairwise comparisons), again likely due to the substantial variation in fluxes within climate zones. CH_4 efflux prevailed in dry inland-water sediments across climate zones, while CH_4 influx was more evident in adjacent uphill soils (except for soils from tropical zones) (Figure 2F). Mean (± SD) dry inland water CH_4 fluxes were 96 ± 128 mg CH_4 m^{-2} d^{-1} ($n = 11$; median – IQR: 0.5 – 232.1 mg CH_4 m^{-2} d^{-1}) in continental zones, 54 ± 77 mg CH_4 m^{-2} d^{-1} ($n = 24$; median – IQR: 0.08 – 87.5 mg CH_4 m^{-2} d^{-1}) in tropical zones, and 22 ± 58 mg CH_4 m^{-2} d^{-1} ($n = 54$; median – IQR: -0.03 – 3.7 mg CH_4 m^{-2} d^{-1}) in temperate zones (Figure 2C). Interestingly, the highest emissions obtained in our study were observed at sampling sites located in the continental zone (mean ± SD: 352 ± 150 mg CH_4 m^{-2} d^{-1}; 293 ± 351 mg CH_4 m^{-2} d^{-1}; and 232 ± 201 mg CH_4 m^{-2} d^{-1}), which ended up determining the higher mean CH_4 emission attributed to continental zones. In addition, local characteristics not captured in our sampling design (e.g., surrounding land use, trophic state, microbial community structure, timing of atmospheric exposure) rather than regional characteristics (e.g., mean annual temperature) may be responsible for both the high CH_4 emission rates and the high variability observed in our measurements. Mean sediment moisture content was similar among climate zones (GLMM, $F = 2.50$, $p = 0.09$; see Table S5 for pairwise comparisons). The mean moisture content (± SD) in dry sediments was 37 ± 22% in temperate zones, 32 ± 27% in continental zones, and 25 ± 14% in tropical zones. The highest mean (± SD) organic matter content was observed in dry sediments of tropical zones (11 ± 9%), followed by those in temperate (7 ± 5%) and

continental zones (4 ± 5%) (GLMM, F = 5.37, p = 0.006 – see Table S6 for pairwise comparisons).

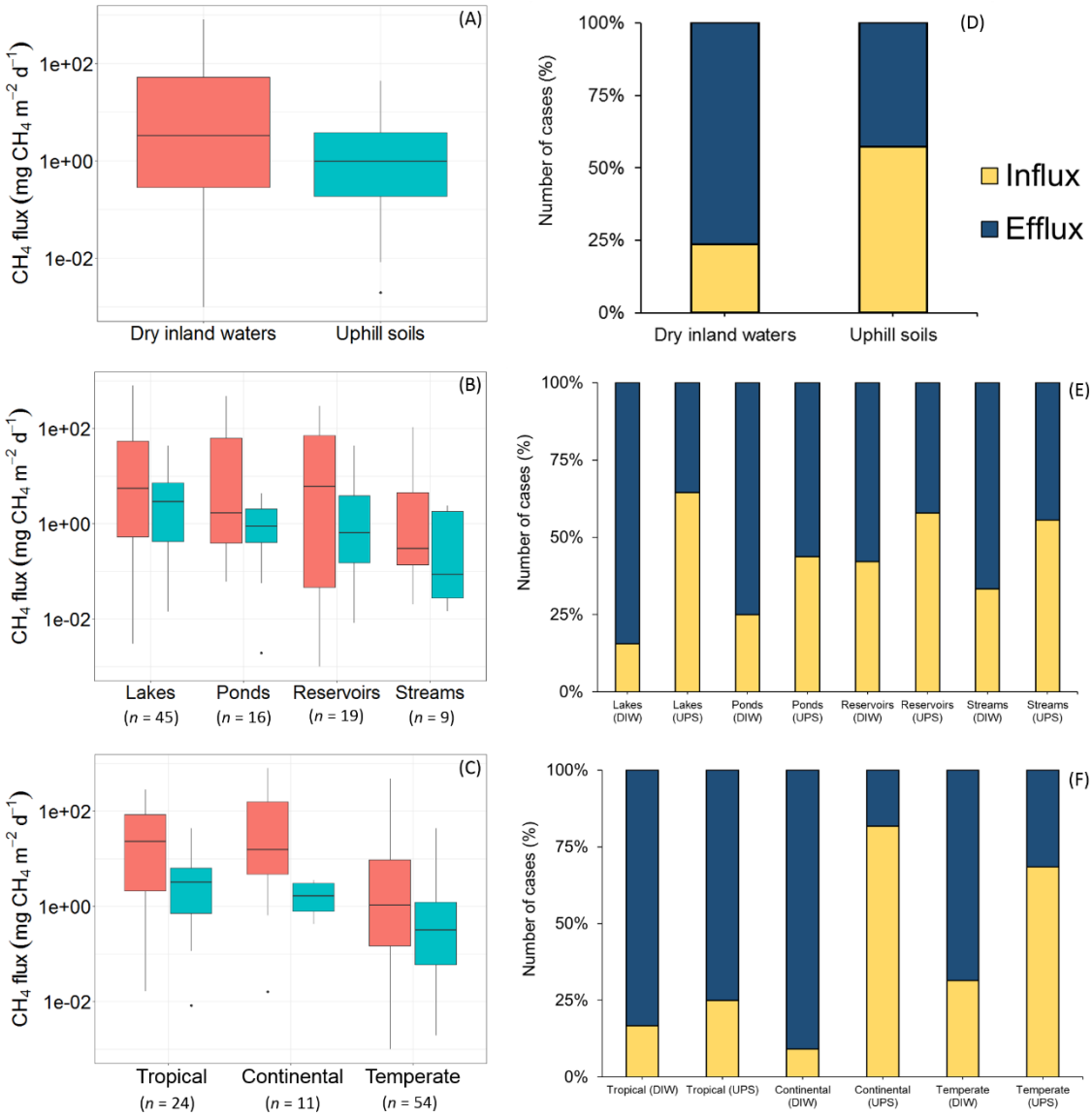


Figure 2 | Boxplot of CH_4 fluxes (mg CH_4 m^{-2} d^{-1}) from dry inland waters (red boxes) and adjacent uphill soils (cyan boxes) (*A*); in different types of aquatic systems (*B*); and different climate zones (*C*). Number of cases of CH_4 influx (yellow bars) and efflux (blue bars) from dry inland waters (DIW) and adjacent uphill soils (UPS) (*D*); in different types of aquatic systems (*E*); and different climate zones (*F*). In *A*, *B* and *C*,

the y-axes are presented as logarithmic scale (log_{10}), the lines within the boxes indicate the median, the boxes delimit the 25th and 75th percentiles, and the whiskers delimit the 5th and 95th percentiles.

Table 1 | Upper part: Mean ± standard deviation of CH_4 fluxes (mg CH_4 m^{-2} d^{-1}) from dry inland waters (dry sediments) and adjacent uphill soils among lakes, ponds, reservoirs, and streams. **Middle part:** Mean ± standard deviation of CH_4 fluxes (mg CH_4 m^{-2} d^{-1}) from other dry inland waters (documented in the literature). **Bottom part:** Global mean ± standard deviation of CH_4 fluxes (mg CH_4 m^{-2} d^{-1}) from surface waters of lakes, ponds, reservoirs, and streams (documented in the literature).

System type	**CH_4 flux (mg CH_4 m^{-2} d^{-1})**	**Reference**
Lakes *(n = 45)*		
Dry sediment	48 ± 91	
Uphill soil	1 ± 5	
Ponds *(n = 16)*		
Dry sediment	38 ± 63	
Uphill soil	0.3 ± 1	
Reservoirs *(n = 19)*		
Dry sediment	36 ± 78	This study
Uphill soil	2 ± 4	
Streams *(n = 9)*		
Dry sediment	7 ± 17	
Uphill soil	0.2 ± 0.7	
All systems *(n = 89)*		
Dry sediment	40 ± 80	
Uphill soil	1 ± 4	
Lake (Brazil)	1.4 ± 0.15 (Amazonian floodplain)	Koschorreck, 2000
Ponds (Spain)	4.8 ± 3.8 (Dry bed)	Obrador et al. 2018
Reservoir (Brazil)	0.9 ± 6.9 (Drawdown)	Amorim et al. 2019
Reservoir (China)	7 ± 8.9 (Drawdown)	Chen et al. 2011
Reservoir (China)	4 ± 1.5 (Drawdown)	Yang et al. 2012
Reservoir (China)	7.7 ± 5 (Drawdown)	Hao et al. 2019
Reservoir (Laos)	27 ± 36 (Drawdown)	Serça et al. 2016
Reservoir (Germany)	4.1[a] (Drawdown)	Marcé et al. 2019
Reservoir (Germany)	7.2[a] (Drawdown)	Marcé et al. 2019
Reservoir (Spain)	0 (Drawdown)	Marcé et al. 2019
Reservoir (Spain)	4.1[a] (Drawdown)	Marcé et al. 2019
Reservoir (Spain)	0.3[a] (Drawdown)	Marcé et al. 2019
Streams (United States)	0.4 ± 0.5 (Dry river bed)	Gallo et al. 2014
Streams (Spain)	3.2 ± 0.9 (Dry river and impoundment beds)	Gómez-Gener et al. 2015
Global CH_4 flux rates from surface waters (mg CH_4 m^{-2} d^{-1})		

Lakes	153 ± 293	Rosentreter et al. 2021
Ponds	12 ± 30	Holgerson and Raymond 2016
Reservoirs	165 ± 369	Rosentreter et al. 2021
Streams	112 ± 425	Rosentreter et al. 2021

[a] *Mean values*

3.3 Drivers of CH_4 fluxes

The fixed effects resulting from the GLMM modeling on dry inland water CH_4 fluxes explained 23% of the total variance (marginal R squared, R^2m), and fixed and random effects together explained 57% of the total variance (conditional R squared, R^2c) (Table 2). Organic matter content and the interaction between organic matter content and sediment temperature were the strongest predictors of CH_4 fluxes from dry inland waters ($p < 0.001$; Figure S1; Table 2), followed by moisture, conductivity ($p < 0.01$; Figure S1; Table 2), elevation and the interaction between moisture and organic matter content ($p < 0.05$; Figure S1; Table 2). This suggests that local sediment characteristics rather than regional characteristics such as annual mean temperature drive CH_4 emissions, which agrees with findings for dry inland-water CO_2 emissions (Keller et al., 2020) (Figure S1; Table 2). However, the particular drivers of CO_2 and CH_4 emissions differed. Most pronounced was the positive relationship between organic matter content and CO_2 emission (Keller et al., 2020) and the negative relationship between CH_4 and organic matter content reported here. The relationship between organic matter content and CH_4 emission was more complex than the negative GLMM coefficient may suggest, given that high CH_4 emissions were measured along the entire organic matter gradient, particularly at intermediate moisture contents (Figure 3). Although not investigated here, the quality of available organic matter may likely be the controlling factor of CH_4 production in our dry inland water sediments (Dalal et al., 2008; Serça et al., 2016; Serrano-Silva et al., 2014; Strom et al., 2003). The quality of organic matter depends on its origin and may be of particular importance in the context

of this study regarding the frequency of sediment exposure to the atmosphere. The more frequently a sediment is exposed to the atmosphere, the less labile its organic matter tends to be (Dalal et al., 2008; Serrano-Silva et al., 2014). This might suggest that lower CH_4 production rates can be expected from exposed sediments in aquatic systems that experience frequent water level fluctuations than from those with a generally more constant water level (e.g., reservoirs and lakes, respectively; Table 1). The transition from wet to drying stage triggers microbial processes responsible for organic matter breakdown (Fromin et al., 2010; Jin et al., 2016) that in turn boost CH_4 emissions, mainly in the first hours and/or days after the transition (Jin et al., 2016; Koschorreck, 2000; Kosten et al., 2018; Paranaíba et al., 2020). The drying-rewetting history of the sediments in our study may therefore have influenced the observed relationships between bulk organic matter content and CH_4 fluxes.

We found a positive effect of moisture on dry inland water CH_4 fluxes (Figure S1; Table 2), which may be related to the fact that the moisture content regulates microbial activity in these water-stressed marginal regions (Baldwin and Mitchell, 2000; Manzoni et al., 2012; Sponseller, 2007). CH_4-producing microorganisms thrive in anoxic conditions. Moisture permits anoxic microhabitats and reduces the depth to which oxygen penetrates the sediments. Increased sediment moisture content therefore favors the presence and maintenance of methanogenic (i.e., CH_4-producing) microbial communities and likely reduces CH_4 oxidation, which may help to explain our finding that moisture content and CH_4 emissions were positively correlated (Dalal et al., 2008; Koschorreck, 2000; Serrano-Silva et al., 2014). Ultimately, the positive effect of sediment conductivity and land elevation on dry inland water CH_4 fluxes may be associated with the influence of regional-to-local underlying characteristics that are not explicitly included in our analysis. For example, a water body's trophic status, type of

surrounding land cover (e.g., natural vegetation, crops, urbanization), and a sediment's organic matter quality, microbial community structure and timing and history of its exposure to the atmosphere may affect CH_4 dynamics (Atekwana et al., 2004; Dalal et al., 2008; Datry et al., 2018; Lischeid and Kalettka, 2012; Onandia et al., 2021; Serrano-Silva et al., 2014).

Table 2 | Results from the GLMM describing CH_4 flux from dry inland waters. Standardized coefficients (β), standard error (SE), *t*-values, 95% confidence intervals (CI), marginal R squared (R^2m), and conditional R squared (R^2c) are reported. Moisture and elevation data were transformed by cubic root, organic matter content and conductivity were log_{10}-transformed, and all predictor variables were z-transformed before analysis. The colon indicates interaction between the respective variables.

Input variable	**CH_4 flux**			
	β	***SE***	***t-value***	***CI***
(Intercept)	3.53	0.30	11.64	2.93 – 4.12
Interaction (Organic matter:Sediment temperature)	0.39	0.10	3.69	0.18 – 0.59
Organic matter	-0.54	0.15	-3.55	-0.85 – -0.24
Moisture	0.49	0.15	3.20	0.19 – 0.79
Conductivity	0.37	0.12	3.01	0.12 – 0.61
Elevation	0.35	0.17	1.98	0.004 – 0.7
Interaction (Moisture:Organic matter)	-0.20	0.10	-2.01	-0.41– -0.006
R^2m	0.23			
R^2c	0.57			

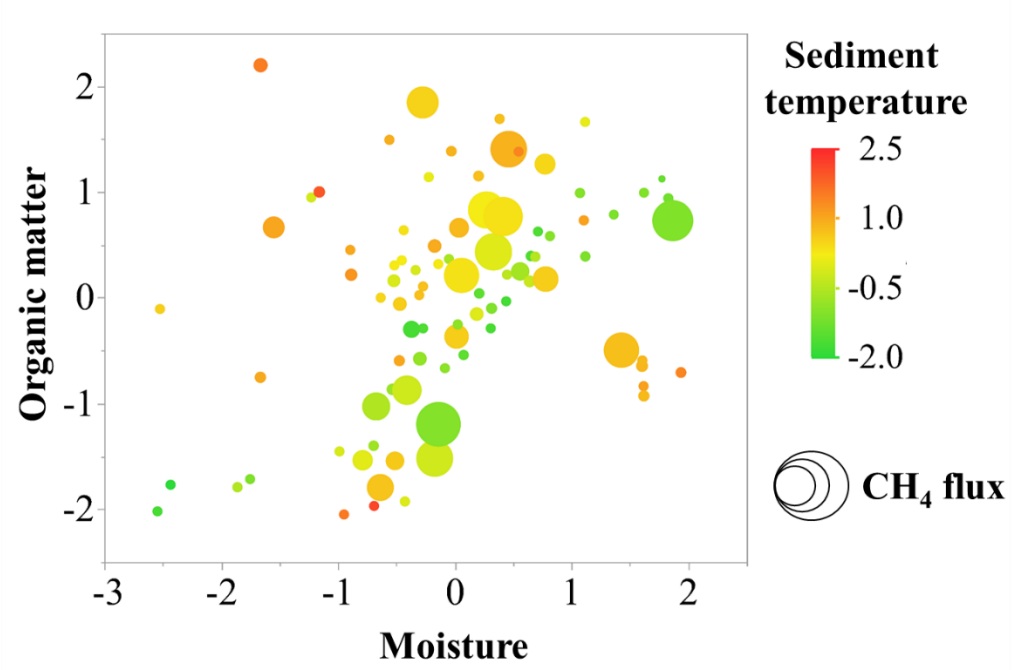


Figure 3 | Response of dry inland water CH_4 fluxes (mg CH_4 m^{-2} d^{-1}) to the interaction between organic matter (%), moisture (%) and sediment temperature (°C) (all z-transformed) arising from the GLMM. Larger circles represent higher CH_4 flux values.

3.4 Contribution of CH_4 to the CO_2-equivalent cross-continental inland water fluxes

Summing dry inland water CO_2 fluxes (Keller et al., 2020) with the CH_4 fluxes presented here (as CO_2-eq; assuming a GWP of 34 for CH_4 compared to CO_2; Myhre et al., 2013) resulted in a cross-continental mean (± SD) emission rate of 9.6 ± 17.4 g CO_2-eq m^{-2} d^{-1} (Figure 4), of which ~14% are attributed to CH_4. This estimate represents about 2.6 ± 4.7 (± SD) g C m^{-2} d^{-1}, which is about one order of magnitude higher than the global organic C burial rate related to lakes, ponds, and reservoirs (~0.1 g C m^{-2} d^{-1}; Mendonça et al., 2017). We found no statistical differences in CH_4 contribution to the total CO_2-eq emission between types of aquatic systems (mean ± SD; lakes = 9.2 ± 13 g CO_2-eq m^{-2} d^{-1}; ponds = 12.3 ± 11 g CO_2-eq m^{-2} d^{-1}; reservoirs = 12.4 ± 29 g CO_2-eq m^{-2} d^{-1}; and streams = 1.1 ± 0.8 g CO_2-eq m^{-2} d^{-1}; GLMM, F = 1.01, p = 0.39 – see Table

S7 for pairwise comparisons) (Figure 4). This can likely be explained by the large variability in climate conditions, trophic state, sediment type and water level fluctuations, within and between the different types of systems. Therefore, other factors likely outplay differences raising from the type of aquatic system. As a consequence, the contribution of CH_4 to the total GHG emission estimate did not significantly vary among systems either; it ranged from 10% to 21% contribution to the total CO_2-eq emission from dry inland waters (Figure 4).

Upscaling the mean dry inland water CH_4 flux rates from lakes, reservoirs, ponds and streams according to their respective global surface areas revealed that 3.6 ± 0.4 (± standard error of the mean; SEM) Tg CH_4 evade from the dry sediments of inland waters to the atmosphere annually (Table 3). This represents approximately 2.4% (± 0.2%; SEM) of the global CH_4 emission estimate attributed to water surfaces of lentic and lotic inland water ecosystems (0.15 Pg CH_4 y^{-1}; Rosentreter et al., 2021). Converting our cross-continental CH_4 emission from dry inland waters to C emission indicates that CH_4 adds ~2.7 (± 0.3; SEM) Tg C y^{-1} (or 0.07%) to the current global C emission estimate from inland waters (3.9 Pg C y^{-1}; Drake et al., 2018) (Table 3).

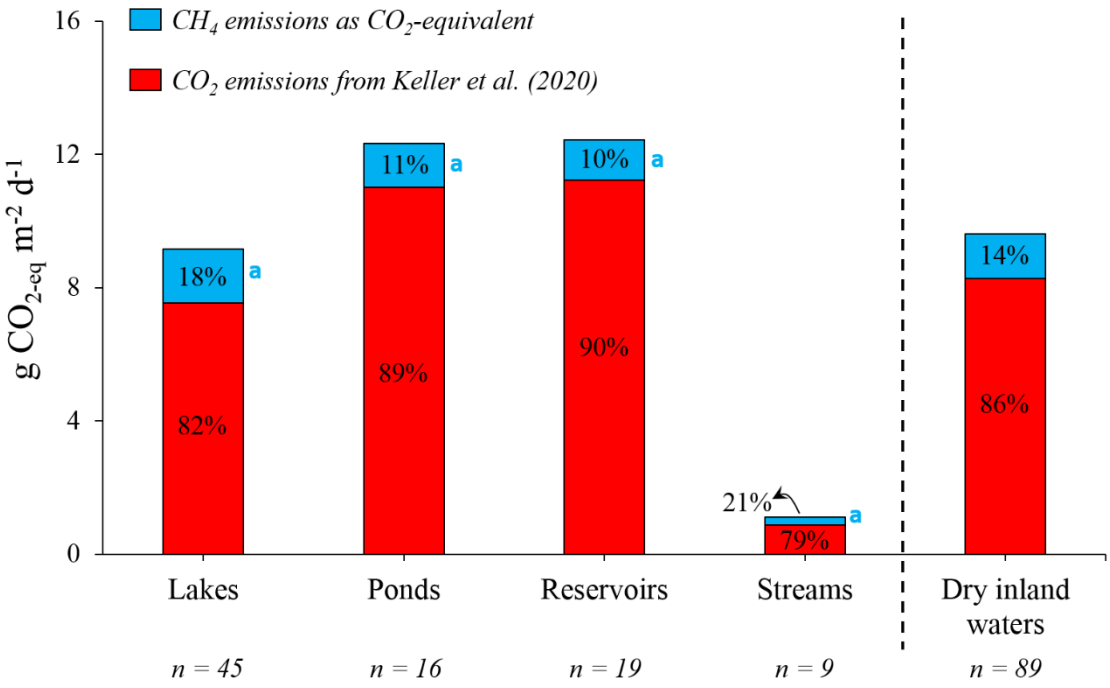


Figure 4 | Cross-continental mean CO_2-equivalent emission rates (CH_4 – blue; CO_2 – red; g CO_2-eq m^{-2} d^{-1}) from dry inland waters (far-right bar) divided by the different types of aquatic systems (lakes, ponds, reservoirs, and streams). CO_2 flux measurements were obtained from Keller et al. (2020) and were associated with the CH_4 flux measurements collected at the same sampling sites. CH_4 fluxes were converted into CO_2-equivalents by multiplying the mass-based CH_4 flux by 34, according to the 100-year GWP (Myhre et al., 2013). Percentage values represent the contribution of each gas to the cross-continental average emission rate in each type of aquatic system. Letter "a" indicates no statistical difference in CH_4 contribution between the types of aquatic systems.

Table 3 | Cross-continental mean fluxes (± standard error of the mean; mg CH_4 m^{-2} d^{-1}) and cross-continental estimates of dry inland water CH_4 emissions (Tg CH_4 y^{-1}, Pg CO_2-eq y^{-1}, and Tg C y^{-1}) by different types of aquatic systems.

System type	Area of exposed aquatic sediments during one year [a] (km^2)	CH_4 emission rate (mg CH_4 m^{-2} d^{-1})	Cross-continental CH_4 emission (Tg CH_4 y^{-1})	Cross-continental CH_4 emission in CO_2 equivalents (Pg CO_2-eq y^{-1})	Cross-continental CH_4 emission as C emission (Tg C y^{-1})
Lakes and reservoirs	187,542 (Marcé et al., 2019)	44 ± 10.9	3.1 ± 0.7	0.1 ± 0.02	2.3 ± 0.5
Ponds	18,390 (Marcé et al., 2019)	38 ± 15.7	0.26 ± 0.1	0.009 ± 0.003	0.2 ± 0.08
Streams and rivers	84,461 (Raymond et al., 2013)	7 ± 5.6	0.21 ± 0.1	0.007 ± 0.006	0.16 ± 0.13
Total	290,393		3.6 ± 0.4	0.11 ± 0.01	2.7 ± 0.3

[a] ***Seasonal and permanent exposure***

4. Conclusions, implications and future perspectives

This study provides the first cross-continental assessment of CH_4 fluxes from dry inland waters based on *in situ* measurements. We found that 14% of the cross-continental CO_2-eq emissions from dry inland waters can be attributed to CH_4. Our estimate comes with uncertainties as the number of aquatic systems and climate zones included in this study were non-uniformly represented (i.e., arid and polar regions were not represented at all, and temperate zones were overrepresented), and given the large variation in dry inland water CH_4 fluxes observed within the different types of aquatic systems and climate zones studied here. Moreover, our estimates are solely related to gaseous C species (CH_4 and CO_2) emissions and do not account for nitrous oxide (N_2O) emissions which is an important GHG in these systems as well (Arce et al., 2018). In addition, our global estimate of CH_4 emissions from dry inland waters may be an underestimation because we likely underestimated the global surface area of dry inland waters. While we used a surface area of 290,393 km^2 for our upscaling exercise, another study that does not differentiate between types of aquatic systems and included wetlands concluded that this area is considerably higher (806,321 km^2 – Pekel et al. (2016)). Also, during our sampling, we likely generally missed emission peaks (i.e., hot moments of emission) that can occur at the onset of drying (Jin et al., 2016; Koschorreck, 2000; Kosten et al., 2018; Paranaíba et al., 2020). Ultimately, while our estimates account for a good portion of the variability related to weather conditions (since we sampled CH_4 fluxes and environmental parameters across a wide range of locations and climate zones), our estimates do not consider CH_4 fluxes occurring under extreme weather events (e.g., rainy days, snowy days), which therefore represents a knowledge gap in this area of research and certainly deserves further research.

While the global CH_4 emission from dry inland waters may be small compared to total aquatic (wet and dry, CO_2 and CH_4) emissions, for individual systems, CH_4 emission from dry sediments can be important (Jin et al., 2016). Dry inland-water sediments occupy a temporally varying fraction of aquatic systems due to cycles of rising and falling water levels. Hence, the contribution of dry-sediment CH_4, CO_2 and N_2O emissions to the total emission also varies through time (Almeida et al., 2019; Arce et al., 2018; Keller et al., 2021; Kosten et al., 2018; Paranaíba et al., 2020). The time-integrated contribution of dry sediment to total inland water emissions is likely to increase in the future as drought events are becoming more frequent and more intense. As a result of this and ongoing widespread direct consumptive water uses, large areas of marginal sediments from aquatic systems worldwide will be exposed to the atmosphere (Pekel et al., 2016; Steward et al., 2012; Wurtsbaugh et al., 2017). We argue that future work on aquatic GHG emissions needs to take CH_4, CO_2 and N_2O emissions from these dynamic wet-dry regions into account in order to further improve our estimates of the global GHG budget of inland waters. Such gained insights into the environmental processes that produce and consume GHGs will enable improved predictions of changes in atmospheric GHG concentrations under varying climate change scenarios.

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The authors declare no competing interests.

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System type	CH_4 flux (mg CH_4 m^{-2} d^{-1})	Reference
Lakes *(n = 45)*		
Dry sediment	*48 ± 91*	
Uphill soil	*1 ± 5*	
Ponds *(n = 16)*		
Dry sediment	*38 ± 63*	
Uphill soil	*0.3 ± 1*	
Reservoirs *(n = 19)*		
Dry sediment	*36 ± 78*	This study
Uphill soil	*2 ± 4*	
Streams *(n = 9)*		
Dry sediment	*7 ± 17*	
Uphill soil	*0.2 ± 0.7*	
All systems *(n = 89)*		
Dry sediment	*40 ± 80*	
Uphill soil	*1 ± 4*	
Lake (Brazil)	*1.4 ± 0.15 (Amazonian floodplain)*	Koschorreck, 2000
Ponds (Spain)	*4.8 ± 3.8 (Dry bed)*	Obrador et al. 2018
Reservoir (Brazil)	*0.9 ± 6.9 (Drawdown)*	Amorim et al. 2019
Reservoir (China)	*7 ± 8.9 (Drawdown)*	Chen et al. 2011
Reservoir (China)	*4 ± 1.5 (Drawdown)*	Yang et al. 2012
Reservoir (China)	*7.7 ± 5 (Drawdown)*	Hao et al. 2019
Reservoir (Laos)	*27 ± 36 (Drawdown)*	Serça et al. 2016
Reservoir (Germany)	*4.1[a] (Drawdown)*	Marcé et al. 2019
Reservoir (Germany)	*7.2[a] (Drawdown)*	Marcé et al. 2019
Reservoir (Spain)	*0 (Drawdown)*	Marcé et al. 2019
Reservoir (Spain)	*4.1[a] (Drawdown)*	Marcé et al. 2019
Reservoir (Spain)	*0.3[a] (Drawdown)*	Marcé et al. 2019
Streams (United States)	*0.4 ± 0.5 (Dry river bed)*	Gallo et al. 2014
Streams (Spain)	*3.2 ± 0.9 (Dry river and impoundment beds)*	Gómez-Gener et al. 2015
Global CH_4 flux rates from surface waters (mg CH_4 m^{-2} d^{-1})		
Lakes	153 ± 293	Rosentreter et al. 2021
Ponds	12 ± 30	Holgerson and Raymond 2016
Reservoirs	165 ± 369	Rosentreter et al. 2021
Streams	112 ± 425	Rosentreter et al. 2021

[a] *Mean values*

Input variable	CH_4 flux			
	β	*SE*	*t-value*	*CI*
(Intercept)	3.53	0.30	11.64	2.93 – 4.12
Interaction (Organic matter:Sediment temperature)	0.39	0.10	3.69	0.18 – 0.59
Organic matter	-0.54	0.15	-3.55	-0.85 – -0.24
Moisture	0.49	0.15	3.20	0.19 – 0.79
Conductivity	0.37	0.12	3.01	0.12 – 0.61
Elevation	0.35	0.17	1.98	0.004 – 0.7
Interaction (Moisture:Organic matter)	-0.20	0.10	-2.01	-0.41 – -0.006
R^2m	0.23			
R^2c	0.57			

System type	Area of exposed aquatic sediments during one year [a] (km^2)	CH_4 emission rate (mg CH_4 m^{-2} d^{-1})	Cross-continental CH_4 emission (Tg CH_4 y^{-1})	Cross-continental CH_4 emission in CO_2 equivalents (Pg CO_2-eq y^{-1})	Cross-continental CH_4 emission as C emission (Tg C y^{-1})
Lakes and reservoirs	187,542 (Marcé et al., 2019)	44 ± 10.9	3.1 ± 0.7	0.1 ± 0.02	2.3 ± 0.5
Ponds	18,390 (Marcé et al., 2019)	38 ± 15.7	0.26 ± 0.1	0.009 ± 0.003	0.2 ± 0.08
Streams and rivers	84,461 (Raymond et al., 2013)	7 ± 5.6	0.21 ± 0.1	0.007 ± 0.006	0.16 ± 0.13
Total	290,393		3.6 ± 0.4	0.11 ± 0.01	2.7 ± 0.3

[a] ***Seasonal and permanent exposure***

Figure 1

Click here to access/download;Figure;Fig1.tif

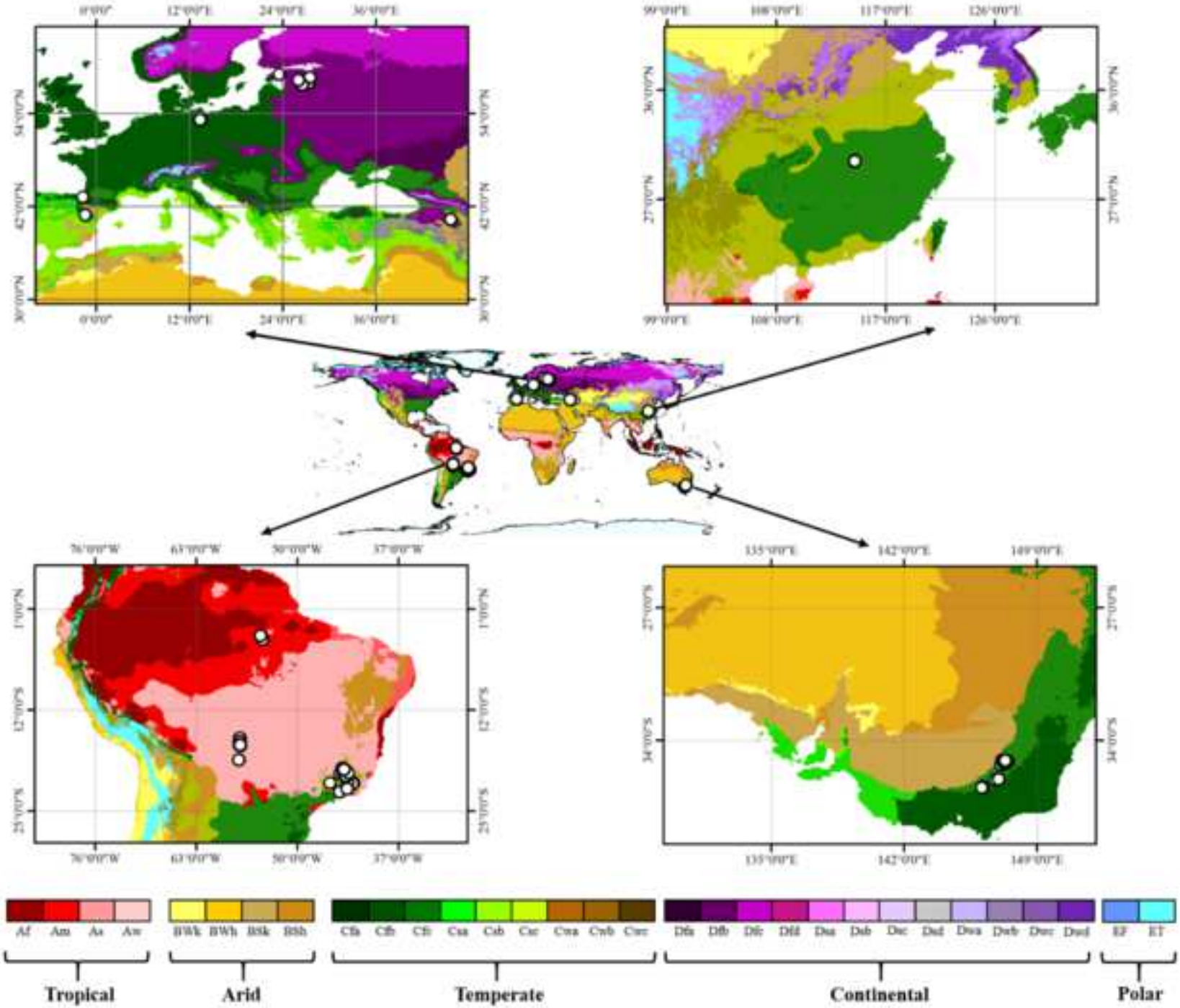

Figure 2

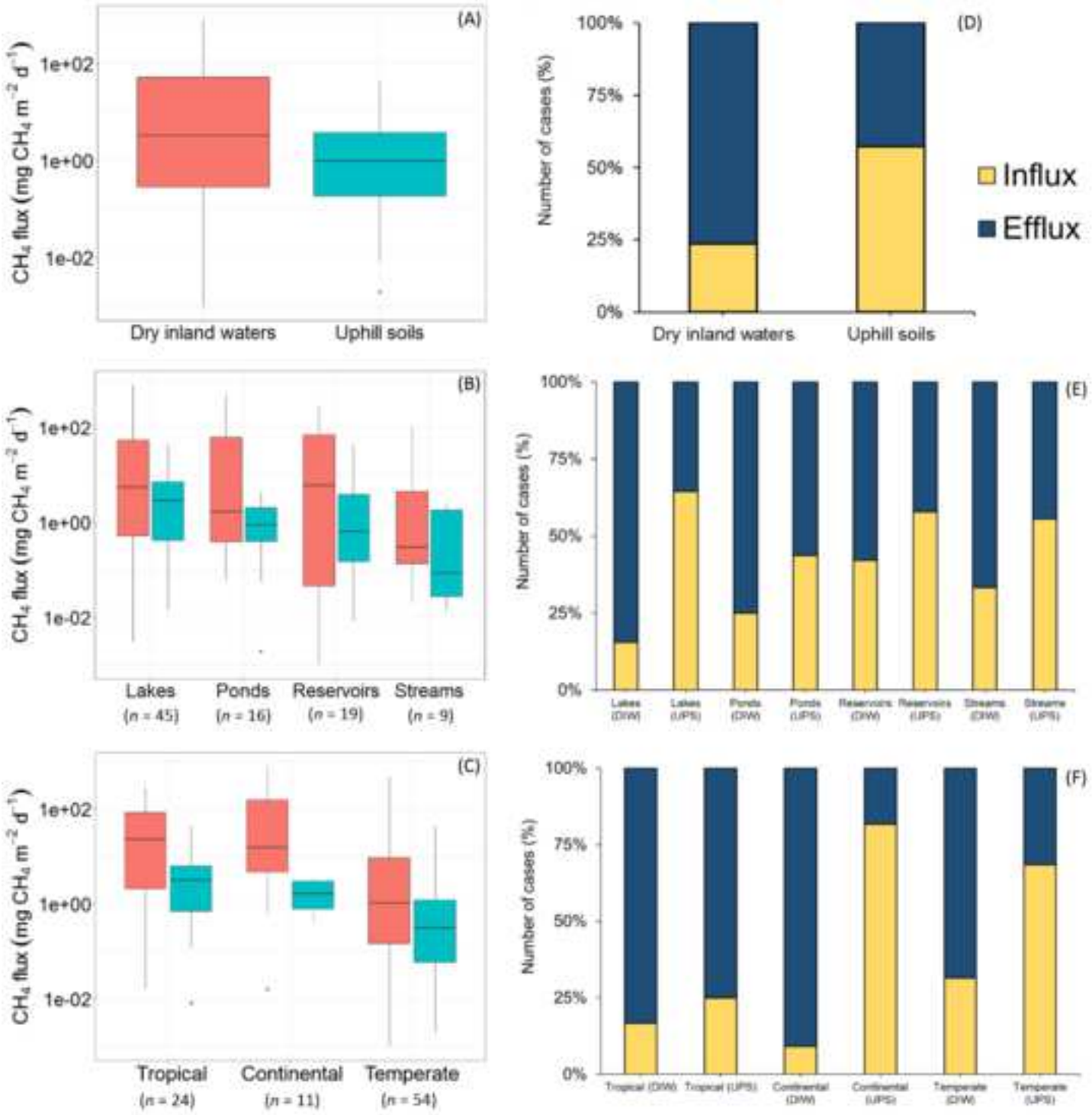

Figure 3

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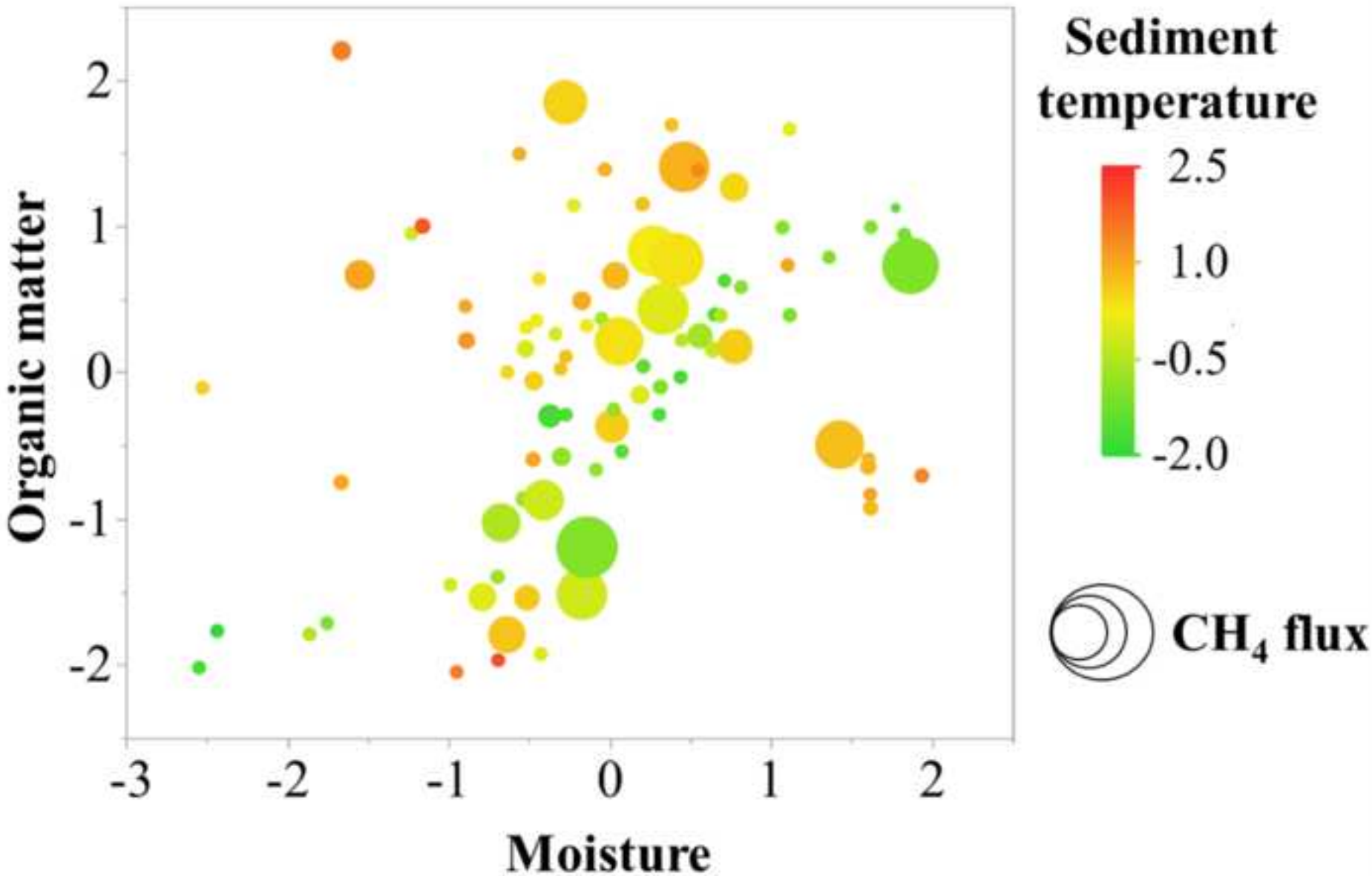

Figure 4