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CO_2 and CH_4 fluxes from inundated floodplain ponds: role of diel variability and duration of inundation

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Small waterbodies like floodplain ponds are considered to be an important component of the global carbon budget. Although they are found in large numbers worldwide and their numbers are increasing every year due to the creation of new ponds, we do not have sufficient data on direct estimates of emission fluxes from these waterbodies yet. Herein, we present results from a set of 24 ponds located in the Morava River floodplain, Czech Republic. The ponds varied in their origin (man-made vs. natural), size, depth, sediment organic matter content, and macrophyte growth. Water chemistry parameters, concentrations, and exchange of CO_2 and CH_4 with the atmosphere were directly measured during the day and night from spring to summer 2020. The ponds emitted more CO_2 and CH_4 during nighttime, and both CO_2 and, in particular, CH_4 emissions tend to increase with the duration of pond inundation. Total diffusive fluxes of CO_2 and CH_4 into the atmosphere ranged from –37072.9 to 432683.3 μmol m^{-2} d^{-1}, and –11485.3 to 95,889.6 μmol m^{-2} day^{-1}, respectively. Generally, all ponds were found to be a net source of CO_2 and CH_4 to the atmosphere. In average, ponds emitted 7.64 g $CO_{2\text{-equivalent}}$ m^{-2} d^{-1}. Thus, our results indicate that floodplain ponds are an important source of both CO_2 and CH_4 to the atmosphere and they should not be omitted in a regional carbon budget.

KEYWORDS

floodplain ponds, carbon dioxide, methane, emission flux, carbon cycle

Introduction

Wetlands are not only among the world's most important but also most threatened ecosystems, offering many ecosystem services to humankind (Finlayson et al., 2018; Mitsch and Mander, 2018). Natural wetlands represent a long-term carbon sink and the potential for further carbon sequestration in the form of biomass accumulation, thus playing an important role in mitigating global climate change (Keller, 2011; Mitch et al., 2013; Nahlik and Fennessy, 2016; Villa and Bernal, 2018). Additionally, they comprise approximately 5%–8% of the terrestrial land surface, and 20%–30% of the earth's soil carbon (C) is stored in wetlands (Bridgham et al., 2006). However, these ecosystems are also considered to be natural sources of greenhouse gas (GHG) emissions, especially methane (Whalen, 2005; Mitsch and Mander, 2018; Dušek et al., 2020). Wetlands are the largest natural source of atmospheric methane (Bridgham et al., 2013), contributing 217 Tg of methane to the atmosphere per year (Ciais et al., 2013).

Wetlands globally vary in their capacity to store C and regulate GHG emissions (Bernal and Mitsch, 2012), with hydrology being a critical driver of river and floodplain wetland ecosystem functions (Bunn and Arthington, 2002; Altor and Mitsch, 2006; Kang and Jang, 2018; Zhao et al., 2019; dos Santos et al., 2020; Zou et al., 2022). Floodplain and depressional wetlands very often function as retention sites for organic matter and nutrients (Craft et al., 2017) and also significantly influence watershed hydrology (Evenson et al., 2018). The yearly inundation of floodplain wetlands increases the extent of aquatic habitat and creates and maintains a variety of small waterbodies. Ponds and pools, small standing waters that permanently or temporarily contain water, vary in size from 1 m^2 to approximately 2–5 ha in area, are shallow (<5 m), with <30% emergent vegetation by area (Søndergaard et al., 2005, Céréghino et al., 2008, 2017; Richardson et al., 2022). Being of man-made or natural origin, these waterbodies occur worldwide and represent approximately 30% of global standing water by surface area (Downing et al., 2006). Although they make up 0.46% of the global land surface (Premke et al., 2016), in some areas, they may be the most abundant surface waterbodies (Mullins and Doyle, 2019). As an integral part of wetlands, they have an irreplaceable ecological role in agricultural and urban landscapes and can be considered a key component of the wider landscape (Céréghino et al., 2014; Mullins and Doyle, 2019).

There is also substantial and increasing body of evidence that small ponds are critically important in diverse landscapes around the world by providing habitat, processing carbon, and mediating hydrological and nutrient fluxes to other larger surface waterbodies (Downing, 2010). While they are considered to be a biodiversity hot spot (Céréghino et al., 2014; Biggs et al., 2017) and are habitats for uncommon species of conservation importance (Duigan and Jones, 1997), ponds and pools also offer potential for studies in ecology, evolutionary biology, and conservation biology (De Meester et al., 2005). The small waterbodies (wetlands sensu lato) also play a very important role in the provision of various ecosystem services (Biggs et al., 2017) including the accumulation of organic matter, recycling of nutrients, trapping of sediments, and biomass production (Rulík and White, 2020). A largely unrecognized service, but potentially the most important of all those known, is their direct role in regulating water and air temperature—hence climate change—through evapotranspiration (ET). ET is an important part of the local water cycle and climate because it represents the combined loss of soil water from the earth's surface to the atmosphere by evaporation of water from the soil or plant surfaces and transpiration via plant stomates (Hatfield and Prueger, 2011). The transition of liquid into gas consumes energy and thus is accompanied by local cooling. Hence, ET from small waterbodies is a powerful cooling process, significantly affecting the climate of surrounding landscapes (Pokorný, 2001; Pokorný et al., 2010; Huryna et al., 2014). Generally, the cooling effect of wetlands is regarded as an important wetland ecosystem service (Costanza et al., 1997; Sun et al., 2012).

However, wetlands, including small waterbodies, are facing constant anthropogenic pressure and are gradually disappearing from the landscape (Zacharias et al., 2007; Zacharias and Zamparas. 2010; Bagella et al., 2016; Reis et al., 2017). It is estimated that since the Industrial Revolution, as much as half of the original wetlands have disappeared, mainly as a result of agricultural development. Many lowland ponds have been degraded or lost, mainly due to the conversion of wetlands to agricultural land and due to changes in agricultural activities (Joniak et al., 2017), large-scale and local drainage, expansion of urban areas, and pollution (Biggs et al., 2000). Landscape fragmentation, urbanisation, and unsustainable tourism development are also significant problems. For instance, in Czech Republic, the natural character of wetlands and streams has been modified to a large extent. As an example, more than a million hectares of field were drained by subsurface pipe drainage (Pokorný, 2017). When considering the total area of the Czech Republic (78,866 km^2), 1/7 of this area was drained by melioration. In the 1950s, approximately 1,300,000 ha of wetlands were recorded, and in 1995, only 350,000 ha remained (Rulík and White, 2020). From a total of 10,952 historical ponds that were larger than 0.5 ha, 7,536 still exist, with a total area of −44,000 ha. Most of these ponds have an area <5 ha. The majority of former ponds was turned into agricultural land, permanent grassland, and forest (Pavelková et al., 2014). As a consequence, degradation of freshwater wetlands occurred either through drainage or desiccation, and their conversion to agricultural use has often led to increased carbon emissions (Nieveen et al., 2005; Brigham et al., 2006; Watkins et al., 2017; Tan et al., 2020).

Recently, many new wetlands including small ponds were created across Europe (Thiere et al., 2009; Boix et al., 2012; Casas et al., 2011; Casas et al., 2012) and the Czech Republic. For instance, many new pools and ponds were created within the Operational Programme Environment 2007–2013 and 2014–2020 aimed at increasing the water retention capacity of the landscape, specifically in relation to adaptation strategies proposed to deal with changing climate and associated increase frequency and severity of drought in the Czech landscape. These new aquatic habitats often represent biodiversity's centres in an otherwise relatively homogeneous and predominantly agricultural landscape. However, these aquatic habitats may also greatly increase the regional relevance of the landscape as potential sources of greenhouse gases because they play an active role in carbon cycling and might be net emitters of CO_2, CH_4, and N_2O to the atmosphere (Torgersen and Branco, 2008; Premke et al., 2016; Grinham et al., 2018; Peacock et al., 2021a). These new, man-made waterbodies vary in size, depth, age, physicochemical parameters, and last but not the least, the purpose for which they were built. Their management can then fundamentally affect water residence time, nutrient levels, and ultimately carbon dynamics (Beaulieu et al., 2019). For example, several publications documented CH_4 flux from created and restored wetlands (Tuitilla et al., 2000; Mander et al., 2014). Hence, minimizing its emission from created and restored wetlands should be a desirable goal (Altor and Mitsch, 2006).

Carbon exchange between wetlands and the atmosphere can be represented as the sum of two separate processes. First, aerobic ecosystem respiration, as well as autotrophic and heterotrophic respiration, produces carbon dioxide through the decomposition of organic matter and represents the emission of carbon dioxide to the atmosphere. Second, anaerobic respiration emits other chemical products, mainly methane (Sulman et al., 2009). Both processes are influenced primarily by water depth, and the amount of time the soil is submerged through inundation, which are affected by variable environmental factors (Tangen et al., 2015; Zhao et al., 2019).

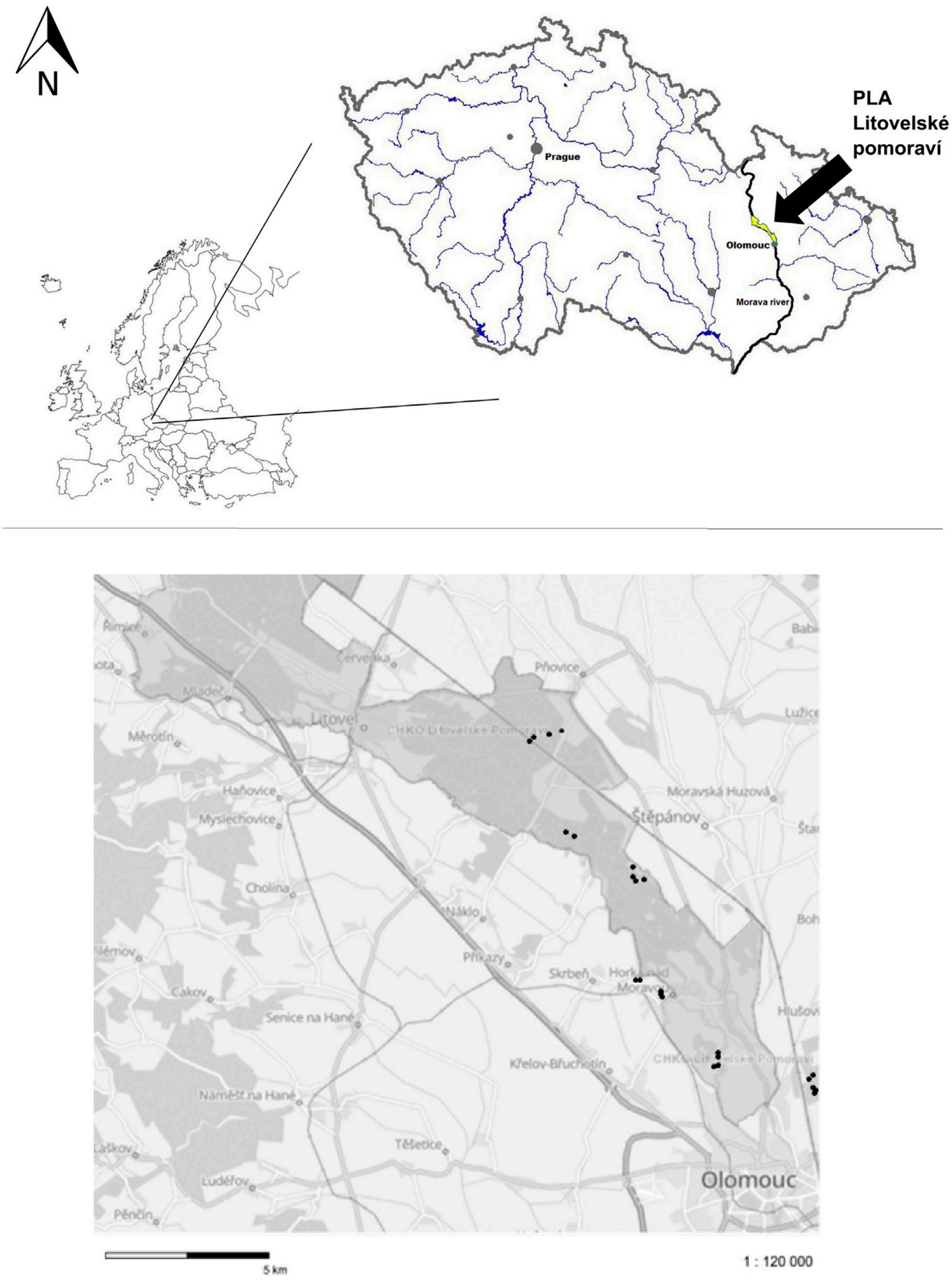

FIGURE 1
Map of Europe and Czech Republic with indications to the Morava River (black arrow in the cut-out) and the Litovelské Pomoraví Protected Landscape Area. Black dots in the lower figure represent the study sites.

Maximum emission of CH_4 occur when flooded wetlands have water levels well above the soil surface, while emissions of CO_2 may exhibit relative extremes for both high water level and low water table conditions (Zou et al., 2022). In addition to the position of the water table, temperature, redox conditions, and plant community composition are important ecosystem level controls on wetland GHG emissions (Turetsky et al., 2014). Changes in temperature, particularly the rise in water temperature, stimulates microbial activity, which increases decomposition rates and increases CO_2 and CH_4 emissions through ecosystem respiration (Davidson and Janssens, 2006; McNicol et al., 2017). Generally, wetland plant communities are shaped by the duration, timing, and frequency of inundation (Casanova and Brock, 2000), whereas sediment dynamics and associated biogeochemical processes change with flooding (Wilson et al., 2011). Wetlands can be both sources and sinks of carbon, depending on their age (Zemanová et al., 2010), operation, and the environmental boundary conditions, such as location and climate (Kayranli et al., 2010).

Compared to lakes or reservoirs (Tranvik et al., 2009), the role of small alluvial waterbodies in the carbon cycle and especially in

TABLE 1 Water physicochemical variables and sediment properties from sampled ponds summarized from sampling campaigns conducted in April, May, and August 2020.

Parameter	Artificial ponds, *n* = 13	Natural ponds, *n* = 11	*t*-test	All ponds, *n* = 24		
	Mean ± SD	Mean ± SD	P	Mean ± SD	Min	Max
Area (m^2)	1287 ± 2273	2766 ± 7557	0.31	1965 ± 5300	25	25,494
Water depth (m)	0.4 ± 0.3	0.2 ± 0.1	**0.04**	0.3 ± 0.3	0.07	0.9
Macrophyte cover (%)	42.3 ± 35.5	40.9 ± 44.6	0.47	41.7 ± 39.6	0	100
Water temperature (°C)	18.7 ± 3.9	16.5. ± 1.7	0.17	17.7 ± 3.3	26.2	26.2
pH	8.0 ± 0.7	7.5 ± 0.3	0.21	7.8 ± 0.6	7.00	10.1
Conductivity ($\mu S\ cm^{-1}$)	561 ± 133	525 ± 219	0.24	545 ± 174	246	931
Dissolved oxygen ($mg\ L^{-1}$)	9.2 ± 5.3	5.2 ± 1.3	**0.03**	7.4 ± 4.4	2.5	21.2
DOC ($mg\ L^{-1}$)	18.5 ± 17.9	16.5 ± 6.4	0.77	17.6 ± 13.6	5.8	71.5
Sediment POC (% C)	14.3 ± 11.0	14.0 ± 12.6	0.89	14.2 ± 11.5	2	39
Methanogenic potential ($\mu mol\ gDW^{-1}\ d^{-1}$)	36.5 ± 53.2	52.4 ± 68.5	0.29	43.3 ± 59.2	1.7	172.3
Concentration CO_2 ($\mu mol\ L^{-1}$)	734. 9 ± 566.2	701.7 ± 892.4	0.34	720 ± 576.9	1.7	3,352.8
Saturation ratio “R” CO_2	41.9 ± 29.8	33.0 ± 22.2	**0.008**	37.5 ± 17.8	8.64	110.9
Concentration CH_4 ($\mu mol\ L^{-1}$)	2.2 ± 4.02	2.1 ± 3.42	0.47	2.1 ± 3.8	0.001	20.7
Saturation ratio “R” CH_4	442.7 ± 1132.9	314.5 ± 428.9	0.16	380.5 ± 662.7	15.2	3,715

n is the sample size. The table also helps distinguish between natural and artificial ponds. Statistically significant p-values ($p < 0.05$ or $p < 0.01$ level) by the T-test are displayed in bold.

greenhouse gas production has so far been overlooked, although their global abundance (Downing et al., 2006; Verpoorter et al., 2014) and high potential for biogeochemical cycling indicate that they could be an important component of the global carbon budget (Downing, 2010). Due to their shallow depth and relatively larger perimeter, these small habitats retain large amounts of carbon (Downing et al., 2008) and produce more CO_2 and CH_4 compared to large lakes and reservoirs. Although very small ponds comprise only 8.6% of the area represented by ponds and lakes, they account for 15.1% of CO_2 and 40.6% of CH_4 emissions from these sources (Holgerson and Raymond, 2016). This inverse lake size-GHG flux relationship was also confirmed in a new synthesis, where the authors found that 37% of total lentic CH_4 emissions come from waterbodies <0.001 km^2 in size (Rosentretter et al., 2021).

Recent studies dedicated to measuring CO_2 and CH_4 emissions from various small waterbodies, e.g., small natural ponds like vernal pools (Catalán et al., 2014, Holgerson, 2015; Kifner et al., 2018) or various artificial waterbodies such as ponds, farming ponds, small dams, or ditches (Gilbert et al., 2017; Grinham et al., 2018; Ollivier et al., 2019a; Ollivier et al., 2019b; Peacock et al., 2021b) have provided evidence for the importance of small waterbodies in the global carbon cycle. Nevertheless, these studies are often limited by the fact that most measurements are rarey based on direct flux measurements and usually do not account for nighttime emissions. Indeed, GHG emissions can strongly be influenced by the diurnal cycle, which affects the temperature and especially photosynthetic activities. At night, the uptake of dissolved carbon is reduced, which, together with community respiration, increases the partial pressure of carbon dioxide in the water and consequently its emissions to the atmosphere (Rocher-Ros et al., 2020; Rudberg et al., 2021). In addition, the absence of oxygen during the nocturnal period can lead to the development of anaerobic conditions in the water column and sediment, resulting in increased rates of CH_4 production (Podgrajsek et al., 2014). In addition, methane fluxes can be affected in different ways by wetland vegetation. On the one hand, plants provide a substrate for methanogenesis, and on the other hand, oxygen released by roots facilitates methanotrophy (Whalen, 2005). While emergent vegetation can act as a conduit for methane (Laanbroek, 2010), the role of submersed and floating macrophytes in the flow of gases from sediments to the atmosphere is less clear (Heilmann and Carlton, 2001; Yoshida et al., 2014). Diurnal differences in methane flux rates are therefore evident, where pressurized convection (ventilation) driving the flow of gases through aerenchyma (Vretare Strand, 2002) and diffusive transport through plant tissue (Altor and Mitsch, 2008) occur simultaneously. Because maximum rates of pressurized convection and diffusion can vary throughout the day depending on the gas concentration gradient between sediments, plants, and the atmosphere, as well as between different wetland plant types, the diurnal dynamics of CH_4 compared to CO_2 are less straightforward. Although increased attention has been paid to the diurnal pattern of CO_2 and CH_4 emissions in lakes and rivers (Sieczko et al., 2020; Attermeyer et al., 2021; Rudberg et al., 2021), changes in production and especially CO_2 and CH_4 emissions are currently still unknown in the ponds. Another shortcoming is that previous studies have either measured CO_2 or CH_4 emissions only and have not been conducted together. Carbon fixation by primary production in flooded wetlands (sink for CO_2) is strongly coupled to CH_4 production and emission to the atmosphere (source of CH_4). Assuming that flooded wetlands

TABLE 2 **Changes in selected physicochemical parameters of the water from the studied ponds along different seasons.**

Parameter	Spring	Summer	*t*-test
	Mean ± SD	Mean ± SD	
pH	7.60 ± 0.49	7.76 ± 0.64	**0.0007**
Conductivity (μS cm^{-1})	596 ± 241	558 ± 147	**0.0018**
Dissolved oxygen (mg L^{-1})	6.98 ± 3.61	5.17 ± 13.09	0.228
Water temperature (°C)	14.30 ± 3.52	22.1 ± 4.09	**0.000001**

Statistically significant p-values ($p < 0.05$ or $p < 0.01$ level) by the T-test are displayed in bold.

generally act as sequesters of CO_2 from the atmosphere and release CH_4 to the atmosphere at the same time, the combination of these two factors then determines whether these offsetting processes make wetland ecosystems general contributors to the greenhouse effect (Whiting and Chanton, 2001).

Herein, we address these knowledge gaps by measuring diffusive CO_2 and CH_4 emissions from small ponds across Litovelské Pomoraví Protected Landscape Area near the city of Olomouc, Czech Republic, during the daytime and nighttime, and in spring and summer. A total of 24 small ponds varying in their nature (man-made vs. natural) were sampled during the flooding phase of the ponds when sufficient water level was present for diffusive CO_2 and CH_4 fluxes across the air–water interface along with basic physicochemical parameters, surface area, water depth, sediment carbon, and sediment methane potential production. The objective was to compare fluxes of CO_2 and CH_4 during the day and night. The second objective was to try to clarify which factors might be responsible for these fluxes. Our hypotheses for this study were as follows: 1) during the night, CO_2 concentrations and fluxes will be higher than during the day, while methane emissions will be more dependent on local site conditions; 2) methane concentrations and fluxes will be closely correlated with the organic carbon content and methanogenic potential of pond sediments; 3) fluxes of both gases will be higher during the summer period, when temperatures are generally higher and the long flooding time creates an anaerobic environment that supports both CH_4 and CO_2 fluxes.

Materials and methods

Study sites

In order to encompass the diversity of standing water systems present in Litovelské Pomoraví Protected Landscape Area (the Morava River floodplain, Czech Republic, Central Europe—49.7047072N–49.6187033N and 17.1557522E–17.2681906E), 24 small waterbodies were chosen for our study (Figure 1). The ecological backbone of the protected landscape area is the naturally meandering Morava River, in floodplain forests branching out and forming a complex system of permanent and temporary river arms, a so-called anastomosing river system. The ponds varied in their origin (man-made vs. natural), size, depth, sediment organic matter content, and macrophyte growth (Table 1). Artificial ponds comprised those depressions made during railway construction, various pits created during fen/bog mining, or ponds newly created or restored by nature's conservation activities. Most of the natural ponds were temporary pools found in former (abandoned) meanders of the Morava River, small alluvial depressions, and seasonally flooded grasslands. With the exception of water depth, dissolved oxygen concentration, and saturation ratio for CO_2, the two groups of pools (man-made vs. natural) were not significantly different from each other (Table 1). Sampling was conducted during the flooding phase of the ponds when sufficient water level was present due to extraordinary long and heavy rain period, where many temporary pools having usually short water duration period (February–May) persisted until the end of September 2020, hence allowing to carry out sampling on foot four times from spring (April–May) 2020 to summer (July–August) 2020.

Field and laboratory analyses

On each of the four sampling days, three replicated measurements of physicochemical parameters and the exchange of CO_2/CH_4 with the atmosphere (FCO_2 and FCH_4) were performed at all the localities between 10:00 and 16:00 for daytime hours and 22:00 and 04:00 for nighttime measurements (British Summer Time +01:00).

The surface area of each pond was measured *in situ* both manually (in the case of very small pools) and using a GPS and with the help of aerial photography in the MapoMat program version 2.0.0.8 (AOPK CR 2022). Water depth was measured at each waterbody during spring and summer season. The organic content of inundated sediments was determined by oven-drying at 105°C to a constant weight and subsequent combustion at 550°C for 5 h to obtain ash-free dry weight (AFDW). Organic matter values were then converted to carbon equivalents assuming a 45% carbon content of organic matter (Meyer et al., 1981).

Physicochemical variables

Dissolved oxygen, pH, conductivity, and temperature of surface water were measured with portable probes (HQ 40 days HACH, DiST® 3 EC/TDS conductometer, pH metre pHep®+ Hanna Instruments). Samples for the analysis of dissolved CO_2 and CH_4 were obtained using the headspace extraction technique (Drozd and Novák, 1979). Water samples (45 mL) were collected from the depth of 5–10 cm in glass vials equipped with septa, and the vials were immediately closed and kept gastight without a headspace in a portable fridge (10°C). Later, upon arrival to the laboratory, a 15 mL headspace was created by replacing 33.3% of the bottle with nitrogen gas, the vials were vigorously shaken for 60 s to equilibrate the gas between the headspace and the water, and 1 mL of gas sample was then collected from the headspace with a gastight syringe and manually injected into a closed loop between the gas inlet and the outlet of a Los Gatos ultraportable GHG analyser GGA-30p (Los Gatos Research Inc., CA, United States) to measure CO_2 and CH_4 contents (Baird et al., 2010; Mbaka et al., 2014). The effective volume

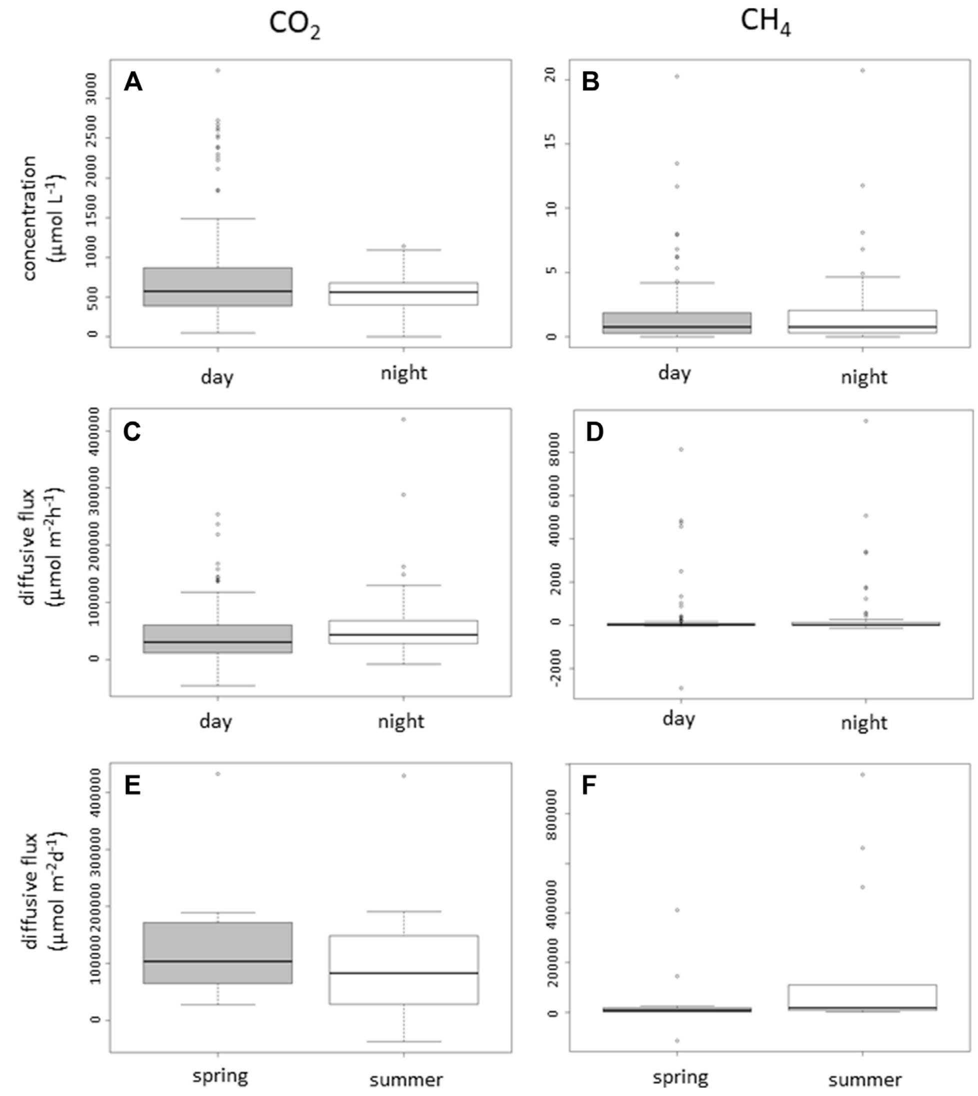

FIGURE 2
Concentrations (µmol L^{-1}) and diffusive fluxes (µmol m^{-2} h^{-1} and µmol m^{-2} d^{-1}, respectively) of CO_2 **(A)** and CH_4 **(B)** measured in the water from all ponds surveyed during the campaign showing differences between day and night. Diffusive fluxes of CO_2 **(C)** and CH_4 **(D)** measured in ponds surveyed during the campaign showing differences between day and night. **(E)** Total diffusive fluxes of CO_2 and **(F)** CH_4 **(D)** measured in ponds surveyed along different seasons (spring vs. summer). Box plots represent the minimum, lower quartile, median, upper quartile, and maximum values. Positive values represent an emission of CO_2 or CH_4 from the ponds to the atmosphere, while negative values represent an intake.

of the loop was calculated according to the LI-COR guide (LI-COR, Inc. 2020) using calibration gas and was 111 ± 4.7 mL, and the precision of measurements amounted to 3%–5%. The partial pressures of the gases were converted into concentrations in water (expressed as µmol L^{-1}) by using Henry's constant, the water temperature, and the measured gas partial pressures in the air (while accounting for the water volume and the headspace inside the bottle). Overall, 281 surface samples were collected at random locations across each pond over four sampling campaigns in April–August 2020 and used to measure the concentrations of CO_2 and CH_4. The CO_2 and CH_4 saturation ratio was calculated as follows:

$$CO_2/CH_4 \text{ saturation ratio} = Cm/Ceq, \tag{1}$$

where Cm represents the measured CO_2/CH_4 concentration (µmol L^{-1}) using the Los Gatos ultraportable GHG analyser GGA-30p, Ceq (µmol L^{-1}), which is the concentration of dissolved gases in equilibrium with the atmosphere related to partial pressure in the gas phase via Henry's law, using the solubility data of Wiesenburg and Guinasso (1979); Weiss (1974),; Weiss (1974). The degree of supersaturation was expressed in terms of a saturation ratio, defined as the measured concentration of gas divided by the concentration in equilibrium with the atmosphere at the environmental conditions of temperature and salinity (De Angelis and Scranton, 1993). A gas saturation ratio >1 means that CO_2/CH_4 is supersaturated in water, while a gas saturation ratio <1 represents undersaturation of CO_2/CH_4.

TABLE 3 Water–atmosphere fluxes (*F*) of CO_2 (FCO_2) and CH_4 (FCH_4) from the studied ponds along different seasons.

Parameter	Spring	Summer	*t*-test
	Mean ± SD	Mean ± SD	
FCO_2 daytime (μmol m^{-2} h^{-1})	5000 ± 3000	3000 ± 5000	0.09
FCO_2 nighttime (μmol m^{-2} h^{-1})	6000 ± 8000	6000 ± 5000	0.47
FCH_4 daytime (μmol m^{-2} h^{-1})	100 ± 500	500 ± 1000	0.07
FCH_4 nighttime (μmol m^{-2} h^{-1})	200 ± 400	700 ± 1000	0.10

The analysis of DOC from the surface water (~10 cm depth) was performed using a TOC analyser (Shimadzu TOC-LCPH, Japan) with a detection limit of ~ 0.05 mgL^{-1}.

Incubation experiments

Sediments intended for incubation experiments were sieved through a 1-mm sieve to remove coarse detritus, stones, or invertebrates and stored at 4°C until subsequent analyses, and laboratory experiments were carried out. For the determination of CH_4 production potential, approximately 5 g (wet weight) of the sediments were transferred into 60-mL sterile serum bottles in triplicates, flushed with N_2, closed with butyl rubber stoppers, and incubated at 25°C in a dark room. Gas samples (200 μL) were taken repeatedly (twice a week) during the course of incubation (4–6 weeks) and analysed for concentrations of CH_4 and CO_2. The concentration of both CO_2 and CH_4 was analysed using the Los Gatos ultraportable GHG analyser GGA-30p. CH_4 production potential was calculated from the slope of CH_4 concentration change over time (Bednařík et al., 2019).

Greenhouse gas flux measurements

Gas fluxes across the air–water interface were determined by the floating chamber method from spring 2020 to summer 2020 (April 21–22 and 26–27, May 9–10 and 17–18, July 19–20 and 28–29, and August 5–6 and 8–9). In total, 288 chamber measurements were performed at different ponds on 16 different days during the whole sampling campaign. Due to the high diel variability of CO_2 and CH_4 fluxes (Min and Rulík, 2020; Sieczko et al., 2020; Rudberg et al., 2021), FCO_2 and FCH_4 were consistently measured between 10:00 and 16:00 for daytime hours and 22:00 and 04:00 for nighttime measurements. On each sampling date, three replicated measurements were performed at all the ponds. The floating chamber was gently deployed from land onto the water surface in each pool in open water areas or between water plants to minimize any disturbances. The chamber was constructed from an inverted non-transparent plastic bucket (internal diameter 17.5 cm, total volume of 3,050 mL, and an area of 0.02 m^2) with

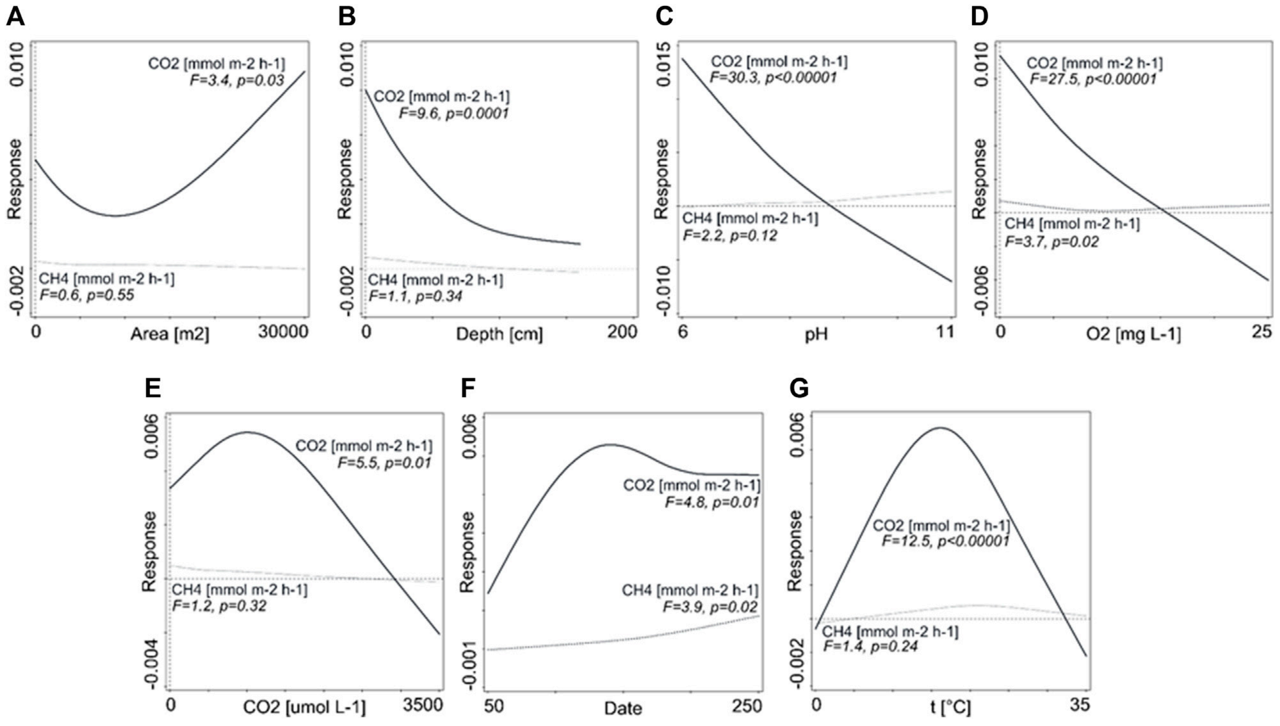

FIGURE 3
Generalised additive models for selected parameters showing a prediction of relationship between the response [diffusive fluxes of CO_2 and CH_4 (mol m^{-2} h^{-1}))] and predictors: **(A)** pond area (m^2); **(B)** water depth (cm); **(C)** pH of water; **(D)** content of dissolved oxygen (mg L^{-1}); **(E)** concentration of CO_2 (μmol L^{-1}); **(F)** duration of inundation (days); and **(G)** water temperature (°C). Solid bold line indicates significant prediction.

an attached floatation device around the base of the chamber, which assured that the volume of the chamber was above the water's surface. The 10-m long gastight inflow and outflow tubes (Tygon) connected the chamber to the Los Gatos ultraportable GHG analyser and fixed the chamber in position. The internal pump circulated the air in the gas chamber through the GHG analyser. A relatively small area of the pools combined with water levels considerably below the top of the pools' edges created a sheltered environment avoiding turbulence or disturbances caused by wind. The chamber was allowed to float on the water surface for 250 s, and the concentrations of CO_2 and CH_4 within the chamber were measured every second, which allowed the changes in CO_2/CH_4 to be tracked *in situ*. The concentrations of CH_4 and CO_2 inside the atmosphere of the chamber increased linearly over time under diffusional conditions, whereas CH_4 concentrations increased abruptly when bubbling occurred. Although our experimental approach was designed to measure diffusive fluxes, ebullition events were frequently observed, particularly during spring, more often due to frog activities. If ebullition events were captured by the chamber, the chamber was ventilated and replaced on the waterbody to measure a diffusive flux as we consider diffusive fluxes only in our study.

Wind speed was not measured during our measurements because most of the pools were very small in area or located in floodplain forests, and thus any effect of wind on CO_2 and CH_4 emissions was considered quite marginal.

The water–atmosphere fluxes (F) of CO_2 (FCO_2) and CH_4 (FCH_4) (mol $m^{-2}\,h^{-1}$) were calculated from the slopes of linear regressions of the concentrations in the chamber *versus* time as follows:

$$F = [s\,.\,(V_{ch}/\,RTA_{ch})]t, \qquad (2)$$

where F represents the diffusive gas flux from the water surface to the atmosphere, s represents the slope of change in chamber gas concentrations over time (ppm/s), V_{ch} is the chamber volume (m^3), R is the universal gas constant ($8.2 \times 10^{-5}\,m^3\,atm\,K^{-1}\,mol^{-1}$), T is the temperature in the chamber (K), A_{ch} is the chamber area (m^2), and t is the conversion from seconds to hour and μmol to mol $m^{-2}\,h^{-1}$, respectively (Attermeyer et al., 2016, Ollivier et al., 2019b). The volume of tubing was also accounted for in calculations of headspace volume and changes in CO_2 and CH_4 concentrations.

The total gas flux for each pond (T-FCO_2 and T-FCH_4) was expressed in mmol $m^{-2}\,d^{-1}$, with the convention that positive fluxes correspond to CO_2/CH_4 effluxes to the atmosphere. Day and night, FCO_2 and FCH_4 were calculated as measured emissions per hour multiplied by the length of the day and night. Day–night differences in FCO_2 and FCH_4 (night-time FCO_2 minus daytime FCO_2 and night-time FCH_4 minus daytime FCH_4) were calculated for each 24 h period, respectively. The length of the days and nights were defined according to the sunrise and sunset times (Czech Hydrometeorological Institute 2020) at each location and each month separately. Each day–night cycle started with a sunrise and ended with a sunrise on the consecutive day, thus the length of each light vs. dark period was dependent on the season.

Data analysis

To test for significant differences between respective data groups (day *versus* night, natural *versus* artificial ponds, and spring *versus* summer), one sample *t*-test was applied. Prior to the analysis, we visually checked data for normality. Possible interactions between measured parameters, CO_2 and CH_4 concentrations, and their gaseous emissions to the atmosphere were revealed by redundancy analysis (RDA). The forward selection procedure was used to select significant explanatory variables out of nine parameters. The response variables were CO_2 and CH_4 fluxes to the atmosphere. Among all measured factors, interactive forward selection selected four parameters in the RDA model that contribute the most to explain the variability of CO_2 and CH_4 fluxes in monitored ponds. The RDA analysis was conducted using Canoco 5.10 (Ter Braak and Šmilauer, 2012). Generalised additive models (GAMs) were also created for all tested parameters to predict the relationship between the response and predictors. Seasonal fluxes of CH_4 were converted to $CO_{2\ \text{equivalents}}$ assuming a 100-year global warming potential of 25 (IPCC 2007).

Results

Pond characteristics (physicochemical variables)

The studied ponds exhibited great variability in physical and chemical parameters, notably, the size area ranged from 25 to 25,484 m^2, conductivity ranged from 247 to 931 μS cm^{-1}, and dissolved oxygen ranged from 2.5 to 21.2 mg L^{-1}, while DOC varied among ponds with values ranging from 5.8 mg L^{-1} to 71.5 mg L^{-1} (Table 1). Artificial ponds differed significantly from natural ones in water depth ($p < 0.05$), dissolved oxygen ($p < 0.05$), and CO_2 saturation ratio "R" ($p < 0.01$) (Table 1). Within all monitored pools, temperatures in summer were significantly higher than those values measured in spring ($p < 0.01$). Water pH in pools also increased significantly in summer ($p < 0.01$), whereas conductivity decreased significantly during summer ($p < 0.01$) compared to values measured in spring. No significant change was observed in dissolved oxygen in pond water between spring and summer ($p = 0.2$) (Table 2).

CO_2 concentrations

Carbon dioxide concentration was supersaturated across all ponds and all sampling dates, with an overall median of 569.1 (quartile 1 = 391.6 and quartile 3 = 850.8 μmol L^{-1}), equal to 37.5-fold supersaturation. The CO_2 saturation ratio "R" varied from 8.6 to 110.9 with an average ratio of 37.5 (±17.8 SD) (Table 1). There was also a highly significant difference ($p < 0.01$) between CO_2 concentration in water during daytime measurements (median = 573.1 μmol L^{-1}, Q1 = 387 μmol L^{-1}, and Q3 = 871.8 μmol L^{-1}) compared to the nighttime concentration (median = 562 μmol L^{-1}, Q1 = 403.4 μmol L^{-1}, and Q3 = 679.0 μmol L^{-1}) (Figure 2A). The CO_2 concentration did not differ with seasons as there was no significant difference between spring and summer measurements ($p = 0.08$).

CH_4 concentrations

Methane concentrations were supersaturated across all except three ponds, with an overall median of 0.75 (Q1 = 0.3 and Q3 = 2) μmol L^{-1}, equal to 380.5-fold supersaturation. The CH_4 saturation ratio ranged from 15.2 to 3, 715 with an average ratio of 380.5 (±662.7 SD) (Table 1). No significant difference between day (median = 0.8 μmol L^{-1}, Q1 = 0.3 μmol L^{-1}, and Q3 = 1.8 μmol L^{-1}) and night measurements (median = 0.8 μmol L^{-1}, Q1 = 0.3 μmol L^{-1}, and Q3 = 2.1 μmol L^{-1}) was found for the CH_4 concentration ($p = 0.3$) (Figure 2B). Methane concentrations showed no significant changes during the seasons, with spring CH_4 concentrations being similar to those found during the summer ($p > 0.05$).

Magnitude and variability of CO_2 and CH_4 fluxes

CO_2 flux

Flux rates of CO_2 (FCO_2) varied markedly among ponds and during the daytime over the sampling campaign. The median of FCO_2 was 3,600 (Q1 = 1800 and Q3 = 6,200) μmol $m^{-2}h^{-1}$, ranging from −4600 to 42,000 μmol $m^{-2}h^{-1}$. In average, the ponds emitted more CO_2 during nighttime (median = 4,000, Q1 = 3,000, and Q3 = 7,000 μmol $m^{-2}h^{-1}$) compared to daytime (median = 3,000, Q1 = 1,000, and Q3 = 6,000 μmol $m^{-2}h^{-1}$) ($p = 0.07$) (Figure 2C). Both daytime and nighttime FCO_2 were higher during spring measurements than those during summer measurements, but the differences were not significant (Table 3).

With the exception of one pond, all other ponds were net emitters of CO_2 to the atmosphere regardless of the season and pond type, with a median of total flux (T-FCO_2) of 100,000 (Q1 = 500,000 and Q3 = 160,000) μmol m^{-2} d^{-1} and a range −37072.9–432683.3 μmol m^{-2} d^{-1}. The median of total CO_2 flux during the spring (April–May) measurement 100,000 (Q1 = 50,000 and Q3 = 170,000) μmol m^{-2} d^{-1} was higher than that during summer (June–August) (median = 80,000, Q1 = 30,000, and Q3 = 140,000 μmol m^{-2} d^{-1}); however, the difference was not statistically significant ($p = 0.39$) (Figure 2E).

CH_4 flux

The flux rate of CH_4 (FCH_4) also varied among ponds and during the day (Figure 2D). The median of FCH_4 was 25 (Q1 = 4 and Q3 = 77 μmol $m^{-2}h^{-1}$), ranging from −2900 μmol $m^{-2}h^{-1}$ to 9400 μmol $m^{-2}h^{-1}$. In average, the ponds emit non-significantly more CH_4 during nighttime (median = 29, Q1 = 4.2, and Q3 = 130 μmol $m^{-2}h^{-1}$) compared to daytime (median = 21, Q1 = 4.5, and Q3 = 73 μmol $m^{-2}h^{-1}$) (Figure 2D). Summer FCH_4 were slightly non-significantly ($p = 0.07$) higher than those in spring CH_4 fluxes (Table 2).

Three ponds had very low CH_4 concentration, thus the saturation ratio is usually <1, based on direct day–night measurements, and one pond showed a negative flux. With the exception of one pond, all the other ponds were net emitters of CH_4 to the atmosphere irrespective of the season and pond type. A median of total flux (T-FCH_4) was 800 μmol m^{-2} d^{-1} (Q1 = 400 and Q3 = 6500 μmol m^{-2} d^{-1}) and ranged between −11485.3 to 95,889.6 μmol m^{-2} day^{-1}. The median of total CH_4 flux in summer was higher than that in spring (April–May), with the difference not statistically significant ($p = 0.06$) (Figure 2F).

Relationship with environmental variables

To unveil possible significant relationships between measured factors and net CO_2 and CH_4 fluxes, we conducted RDA(Supplementary Figure S1). Among all measured factors, interactive forward selection selected four parameters in the RDA model that contribute the most to explain the variability of CO_2 and CH_4 fluxes in monitored ponds. Dissolved oxygen content and pH together with the CH_4 concentration and total area of the ponds were the explanatory variables, which explained 37.9% of the variability in CO_2 and CH_4 fluxes (FCO_2 and FCH_4). Dissolved oxygen content was the most important of the explanatory variables (19.6%, $F = 28.6$, $p < 0.01$), and water pH explained 10.9% of the variability ($F = 19.9$, $p < 0.01$). According to the first axis of RDA, these explanatory variables mainly explained the variability in CO_2 fluxes (37.7%). CO_2 fluxes to the atmosphere significantly ($p < 0.05$) increased with an increasing pond area (Figure 3A), while decreasing significantly ($p < 0.01$) with increasing depth, pH, and dissolved oxygen content in the water (Figures 3B–D). CO_2 emissions from the water surface showed a non-linear relationship with CO_2 concentration in the water and water temperature (Figures 3E,G). Generally, FCO_2 tends to increase with the duration (length) of pond inundation, but in the late spring (around the middle of the time period), a downward trend in the FCO_2 rate was observed there (Figure 3F). CO_2 emissions increased with temperature up to approximately 20°C, and then further temperature increase caused fluxes to decrease. Similar to FCO_2, FCH_4 also decreased with increasing water depth (Figure 3B). CH_4 fluxes increased significantly ($p < 0.05$) with higher oxygen concentration in the water (Figure 3D). Generally, FCH_4 tend to increase with the duration of pond inundation (3F). Compared to FCO_2, the response of FCH_4 to temperature is less clear and non-significant (Figure 3G).

Discussion

Our results support previous observations that despite their small size, small waterbodies have relatively large contributions to CO_2 and CH_4 emissions (Abnizova et al., 2012; Raymond et al., 2013; Holgerson, 2015; Holgerson and Raymond, 2016; Onandia et al., 2018). During their flooding phase, the studied ponds were net emitters of CO_2 and CH_4 to the atmosphere. Total CO_2 and CH_4 emissions from our ponds were lower than those heavily impacted artificial waterbodies (*cf.* Ollivier et al., 2019a), but comparable to emissions from similar waterbodies.

CO_2 and CH_4 concentrations and drivers of CO_2 and CH_4 emissions

CO_2 and CH_4 concentrations and fluxes in this study are of similar magnitude to those observed on small, temporary pools (Catalán et al., 2014; Holgerson, 2015; Kifner et al., 2018) and other small waterbodies (Premke et al., 2016; Gilbert et al., 2017; Grinham et al., 2018; Obrador et al., 2018; Ollivier et al., 2019a; Peacock et al., 2021a). The ponds were supersaturated with respect to CO_2 across all surface samples and dates, indicating that all pools were emitting CO_2 to the atmosphere. To the best of our knowledge, CO_2 concentrations and saturation ratios in the studied ponds are some of the highest reported from small waterbodies and suggest high potential of these ponds for CO_2 emission flux. In the case of CH_4, three ponds were found to be undersaturated with respect to CH_4; however, total CH_4 fluxes (T-FCH_4) were positive for each pond, indicating that, on daily basis measurements, those ponds are also net emitters of CH_4 to the atmosphere. Similar to CO_2, comparison made with available data (*cf.* Holgerson, 2015; Holgerson and Raymond, 2016; Kifner et al., 2018) shows that CH_4 concentrations and especially the CH_4 saturation ratio in our ponds were also among the highest reported values. However, our data were obtained from waterbodies only minimally affected by anthropogenic activities. Moreover, nutrient inputs due to the direct management were also minimal or zero. The mean GHG emissions from our waterbodies amounted to 7.64 g $CO_{2\text{-equivalent}}$ m^{-2} d^{-1}, a value lower than those of Australian agricultural dam emissions, which were 11.1 g $CO_{2\text{-equivalent}}$ m^{-2} d^{-1} (Ollivier et al., 2019a). This is due, among other reasons, to the fact that methane and sometimes CO_2 emissions can be up to an order of magnitude higher in eutrophic systems than in oligotrophic waters (Huttunen et al., 2003). Thus, in direct comparison with other small waterbodies, it is necessary to keep in mind their use, the extent of anthropogenic influence, and land use of the surrounding landscape. In any case, the total fluxes of CO_2 and CH_4 from our ponds were significantly higher than those emissions from lakes and reservoirs (St. Louis et al., 2000; Deemer et al., 2016; DelSontro et al., 2016), confirming previous findings of an inverse relationship between waterbody size and CH_4 and CO_2 fluxes (Holgerson and Raymond, 2016; Rosentreter et al., 2021).

CH_4 atmospheric emissions in our study only considered diffusion across the water boundary layer even though ebullition can also be an important mechanism for its transport to the atmosphere. Due to their relatively shallow depth and relatively low hydrostatic pressure, small waterbodies can experience CH_4 ebullition (DelSontro et al., 2016; Grinham et al., 2018). Although we have observed the release of methane bubbles very often in ponds and pools with the occurrence of amphibians, namely, mating frogs dwelling close to the bottom (see methods for CH_4 flux measurements), the total CH_4 emissions presented here are underestimated because the study does not report ebullitive fluxes. Hence, estimated diffusive fluxes from investigated ponds into the atmosphere should represent minimum values, especially for CH_4. Since recent publications on methane dynamics in reservoirs reported significant changes in ebullition intensity as the water level decreased (Beaulieu et al., 2018; Hilgert et al., 2019), it is reasonable to expect that a decreasing water level could also stimulate deeper zones of ponds to begin bubbling or increase the intensity to bubbling. This could potentially offset the reduction on the surface available for diffusive emission, while total emissions would remain relatively constant (Grinham et al., 2018).

Carbon dioxide and methane fluxes were measured only during periods of inundation. Although there are some reports on methane fluxes from dry or wet phases of the ponds (Obrador et al., 2018), methanogenesis may only occur in saturated areas of the ponds (Kifner et al., 2018). Water table fluctuation in the floodplain area influences CO_2 and CH_4 production (Boon et al., 1997; Fromin et al., 2010). A higher water level generally leads to the prevalence of anoxic–anaerobic conditions and higher CH_4 emissions, whereas inundated habitats may act either as a source or a sink of atmospheric CO_2 along the year (Obrador et al., 2018). On the contrary, a lower water level leads to aerobic respiration and consequently to higher CO_2 emissions (Fromin et al., 2010; Obrador et al., 2018). Generally, such processes are well known from various inland waters that are subjected to wetting and drying cycles (von Schiller et al., 2014; Marcé et al., 2019), as well as from inundated freshwater wetlands ecosystems, where CO_2 exchange and carbon sink potential are mainly driven by hydrology (Altor and Mitsch, 2006; Huertas et al., 2017; Kang and Jang, 2018; Zou et al., 2022). In our study, both CO_2 and CH_4 emissions tend to increase significantly with the length of pond inundation. This was particularly true for methane, whose emission fluxes showed an increasing trend with increasing flooding duration. This suggests that permanent pools, which are filled with water throughout the year, are much more important in terms of methane production than periodic pools, which are characterised by relatively short flooding times (Figure 3F).

The variability of CO_2 fluxes (FCO_2) during the study across all measured pools was high, as determined by the standard deviation and the mean (0.006 ± 0.006 mol $m^{-2}h^{-1}$). This high variability indicates possible difficulty in making estimates of pond gas fluxes from limited number of measurements and is likely driven by multiple changing drivers of pond metabolisms (Torgersen and Branco, 2008). Although small waterbodies are expected to be highly dependent on external drivers, the differences in CO_2 fluxes between ponds were most likely related to intrinsic properties of the pond. For instance, Catalán et al. (2014) found that the CO_2 efflux was significantly correlated with the organic content of sediments; however, CO_2 fluxes from the inundated sections were independent of this. This finding is congruent with our observation, as we observed no relationships between sediment organic carbon and CO_2 and CH_4 fluxes. This lack of relationship might be influenced not only by a water column and presence of water plants but also due to the respiration of DOC in the water column. Hence, it is possible that fluxes of gases in flooded ponds would more likely be related to DOC in the water column than to the sediment's organic matter (Catalán et al., 2014). However, no relationship of CO_2 fluxes to DOC was found in this study.

The production and emission of greenhouse gases is usually closely related to temperature due to an increase in the microbial activity with increasing temperature (Yvon-Durocher et al., 2011; Yvon-Durocher et al. 2014; Yvon-Durocher et al. 2017; Kifner et al., 2018; Rodriguez et al., 2018). In this study, interestingly enough, CO_2 emissions increased with temperature up to 20°, and then further temperature increase caused fluxes to decrease. For methane, this response to temperature is less clear and non-significant (Figure 3G). A possible explanation regarding CO_2 would be an increased consumption of CO_2 by the primary producers during summer since longer hydroperiod favour the autochthonous C capture by phytoplankton (Morris et al., 2013). As we did not measure chlorophyll *a*, this consumption might be inferred from a significant decrease of CO_2 fluxes with increasing flooding time and increasing oxygen concentration (Figures 3D,F). A higher oxygen content of the water indicates the high photosynthetic activity of primary producers to be present, which although releasing CO_2 into the aquatic environment by respiration at night, substantially affects the diffusive CO_2 fluxes during the day. In general, pools that were completely shaded by free-floating vegetation had lower total CO_2 and CH_4 emissions than pools with free-floating or submersed macrophytes in the water column and at the bottom. Reduction in diffusive CO_2 fluxes due to fixation through photosynthesis from areas covered by floating water hyacinth (*Eichhornia crassipes*) was reported, for instance, by Attermeyer et al. (2016) from South India. Interestingly, the relationship between CO_2 concentration in water and emissions showed a clear non-linear trend, where emission fluxes increased with increasing CO_2 concentration, but then there was a steep decline. In general, we expected CO_2 fluxes to increase with increasing concentration, and we cannot explain this contradiction objectively yet.

Compared to CO_2, prediction of methane response to the tested parameters showed only few significant results, some of them being rather controversial. For instance, CH_4 fluxes increased with higher oxygen concentration in the water of the ponds (Figure 3D), suggesting that the predicted methane behaviour in these small aquatic habitats is rather difficult. Since higher oxidation in the water column can be expected with higher oxygen content, methane concentrations and emissions to the atmosphere should decrease. A possible explanation for the observed higher emissions could be the role of submerged vegetation, which on the one hand releases oxygen into the water column by photosynthesis, and on the other hand, may also transport and release methane at the water surface. Thus, methane escapes potential oxidation in the water column in this case. In general, there may be several reasons why predicting the behaviour of methane in the ponds is difficult; first, methane concentration in the water may be lowered by aerobic (Chowdhury and Dick, 2013) or anaerobic methane oxidation (AOM). For instance, AOM in freshwater wetlands may reduce their potential methane emissions by over 50% (Segarra et al., 2015). Second, the presence of vascular plants has been recognized as one of the key factors controlling the scale of methane fluxes because it affects processes coupled to transport, production, and consumption of methane (Sebacher et al., 1985; Segers, 1998; Joabsson et al., 1999; Whalen, 2005; Bergström et al., 2007; Carmichael et al., 2014). Most authors indicate that emergent vegetation is much more important in relation to methane emissions than free-floating and submerged macrophytes (Laanbroek, 2010). In both emersed and submerged plants, CH_4 diffuses into the roots and further into the lacunar systems of the plants. While CH_4 emissions from emersed plants to the atmosphere are well documented (Altor and Mitsch, 2008; Laanbroek, 2010; Carmichael et al., 2014), we do not know much about the fate of lacunar CH_4 within submersed macrophytes so far. Similar to emersed plants, O_2 transport into and out of the roots of submersed plants may support root-associated methanotrophs that reduce the diffusion of CH_4 from the sediment into the plants. In addition, submersed vegetation may support communities of epiphytic methane-oxidizing bacteria that are involved in methane oxidation, thus reducing the diffusive flux of CH_4 from plants into the surrounding water (Heilmann and Carlton, 2001; Yoshida et al., 2014). As free-floating plants can affect CH_4 emissions both positively and negatively, their general effect on CH_4 emissions will depend strongly on local conditions (Kosten et al., 2016). The dominant vegetation in our ponds was usually submerged vegetation (*Myriophyllum spicatum, Ceratophyllum demersum,* and *Hottonia palustris*) or floating *Lemna minor*. In general, pools that were completely shaded by free-floating vegetation had lower total CO_2 and CH_4 emissions than those with free-floating or submersed macrophytes in the water column and at the bottom.

Diel variability in CO_2 and CH_4 emissions from small ponds

On an average, the ponds emitted more CO_2 and CH_4 at night. These findings are somewhat in contrast to previous studies which considered diel variability of both CO_2 and methane emissions and observed the highest CO_2 and CH_4 emission in the daytime than nighttime (Sieczko et al., 2020; Rudberg et al., 2021). However, their measurements come from large lakes where different environmental drivers might play a role in controlling diel CO_2 and CH_4 flux dynamics. In accordance with our results, higher nighttime CO_2 fluxes compared to daytime fluxes have been observed, for example, in rice paddies (Min and Rulík, 2020), in European and Arctic streams (Rocher-Ros et al., 2020; Attermeyer et al., 2021), and global rivers (Gómez-Gener et al., 2021). A recent study by Lhosmot et al. (2022) also showed a diel variability of CH_4 fluxes, with higher fluxes at night and lower during the day. The ecosystem is different (peatland) but is close to rice paddies as cited here. In their study, Lhosmot et al. hypothesised that the injection of oxygen during the day by the photosynthetic activity could be at the origin of reduced CH_4 fluxes compared to at night. This is also consistent with our hypothesis because we expected higher respiration in vegetated ponds and therefore higher CO_2 concentrations and emissions during the night. However, because a number of ponds were without vegetation due to shading, it was not entirely clear whether the diurnal pattern of emissions described previously would be valid for all pools examined. In the case of methane, we do not have an explanation for the higher nocturnal fluxes yet because maximum rates of pressurized convection and diffusion can vary throughout the day depending on the gas concentration gradient between sediment, plant, and atmosphere. Nevertheless, our data are among the first measurements to take the ponds' nighttime measurements into account and suggest that due to the existing diel variability, future research needs to include both daytime and nighttime measurements in total CO_2 and CH_4 emission estimates, as otherwise they may be significantly over- or under-estimated. In addition, direct daytime and nighttime measurements provided objective information on the net fluxes of CO_2 and CH_4 emissions from individual pools to the atmosphere and allowed an assessment of the role of these pools in the sink or source of GHG emissions.

Emissions of CO_2 and CH_4 from natural vs. artificial ponds

There are many reasons why artificial ponds differ from natural ponds (Clifford and Heffernan, 2018). In this study, natural pond emissions were usually higher when compared to the artificial waterbodies; however, the differences in CO_2 and CH_4 emissions were generally not significant. As natural ponds also showed to some degree similar values of the physicochemical parameters with artificial ones (Table 1), and with some cautions, it was possible to consider natural and anthropogenic waterbodies as one type and use the average emission values for possible regional extrapolation. This conclusion is somewhat at odds with the study proposed by Peacock et al. (2021a), where the authors claim that "emissions from artificial waterbodies are on average four times greater than emissions from analogous natural waterbodies" and therefore argue that emissions from natural systems cannot be used as a proxy for emissions from artificial waterbodies (Peacock et al., 2021a). An explanation for this discrepancy can be found in the fact that, under the term "artificial ponds," we can include various farm ponds used for irrigation (Casas et al., 2012; Fuentes-Rodríguez et al., 2013) and small agricultural dams used as a collection point for rainwater runoff from surrounding lands (Olivier et al. 2019a; Olivier et al. 2019b), fishponds (Adámek et al., 2012; Pokorný and Květ, 2018), and urban ponds (Peacock et al., 2019) to small pools created primarily to enhance the biodiversity. Moreover, the very definition of the term "pond," which is now widely used to refer to various small waterbodies, is problematic (Richardson et al., 2022). As mentioned previously, hydrology and the use of our waterbodies, both natural and artificial, have been only marginally affected by anthropogenic activities that may significantly affect biogeochemical cycling and consequently GHG emissions of the waterbodies (Altor and Mitsch, 2008). Artificial waterbodies are often subjected to an extensive hydrological management (e.g., regulated inflows and outflows or water abstraction), which affect retention times, in turn affecting pond biogeochemistry (Clifford and Hefferman, 2018). The use of ponds as breeding facilities for fish (i.e., fishponds), especially carp, is typical for the Czech Republic (Kořínek et al., 1987; Pokorný et al., 1994; Pokorný and Květ, 2018). Feeding and the associated introduction of huge amounts of nutrients lead to eutrophication of these ponds and consequently to higher GHG emissions (Rutegwa et al., 2019). Furthermore, the positive relationship between eutrophication and CH_4 emissions has already been sufficiently documented for aquatic ecosystems (Beaulieu et al., 2019). However, this situation does not apply to newly built ponds and small waterbodies studied here, which are primarily intended to support biodiversity in the landscape and increase the water retention capacity of the landscape or as climate-improving elements in urban areas. However, another question is whether we need to consider emissions from these ponds strictly as an anthropogenic source and include it in national emission reports (according to the Intergovernmental Panel on Climate Change guidelines) (IPPC 2019; Peacock et al., 2021a).

Conclusion

Our data showed that despite their importance for water retention and storage in the landscape and their value for nature conservation, small waterbodies can be a significant source of GHG to the atmosphere. The ponds, like many other wetland systems, provide a range of ecosystem services, and many of these systems may represent net carbon sinks in the long term; however, in the light of recent measurements and in line with recent publications, it must be stated that small waterbodies may also represent hot spots of GHG emissions in the landscape. Carbon exchange from small waterbodies may be highly variable in time and in ways that are not usually accounted for in emission estimates. In particular, the time of the day can greatly influence the concentration and thus affect the exchange of C between the pond and the atmosphere. Therefore, our results based on direct day–night measurements provide objective information on the net fluxes of CO_2 and CH_4 emissions from individual ponds to the atmosphere, allowing us to assess the role of these ponds in the sink or source of GHG emissions. This view is by no means short-sighted and does not impose on anyone the idea that new wetlands should not be created because they produce GHG emissions (Mitsch and Mander. 2013; Mitsch and Mander, 2018). On the other hand, with respect to the latest assessment that nearly half of global methane emissions come from aquatic ecosystems (Rosentreter et al., 2021), future regional emission estimates would be greatly improved with the inclusion of man-made ponds and other small waterbodies, as their proliferation in the Czech Republic is evident.

We also believe that the knowledge of the processes by which small waterbodies can influence carbon cycling in the landscape will contribute to the better management of these water systems (van den Bos, 2003; Abdalla et al., 2016) and will be the most precise and beneficial path forward to counteract human-induced climate change (Premke et al., 2016). An example is the influence of hydrology on the frequency of drying and rewetting cycles and their impact on both CO_2 and CH_4 fluxes among ponds in the landscape (Gilbert et al., 2017). Longer hydroperiods may also favour autochthonous carbon sequestration by phytoplankton. Both direct anthropogenic influences and climate change (unanticipated and locally lower precipitation and greater evapotranspiration) have shortened hydroperiods in many reservoirs, suggesting the potential for altered C sequestration (Morris et al., 2013).

Data availability statement

The raw data supporting the conclusion of this article will be made available by the authors, without undue reservation.

Author contributions

MR—wrote the manuscript, field measuring, conceptualization, and methodology. LW—analysed the data, field measuring, laboratory analyses, and original draft preparation. SM—field measuring and laboratory analyses. RŠ—field measuring and laboratory analyses. All authors contributed to the article and approved the submitted version.

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Conflict of interest

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

Publisher's note

Supplementary material

The Supplementary Material for this article can be found online at: https://www.frontiersin.org/articles/10.3389/fenvs.2023.1006988/full#supplementary-material

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