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Emissions from dry inland waters are a blind spot in the global carbon cycle

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ABSTRACT

A large part of the world's inland waters, including streams, rivers, ponds, lakes and reservoirs is subject to occasional, recurrent or even permanent drying. Moreover, the occurrence and intensity of drying events are increasing in many areas of the world because of climate change, water abstraction, and land use alteration. Yet, information on the gaseous carbon (C) fluxes from dry inland waters is scarce, thus precluding a comprehensive assessment of C emissions including all, also intermittently dry, inland waters. Here, we review current knowledge on gaseous C fluxes from lotic (streams and rivers) and lentic (ponds, lakes, and reservoirs) inland waters during dry phases and the response to rewetting, considering controls and sources as well as implications of including 'dry' fluxes for local and global scale estimates. Moreover, knowledge gaps and research needs are discussed. Our conservative estimates indicate that adding emissions from dry inland waters to current global estimates of CO₂ emissions from inland waters could result in an increase of 0.22 Pg C year⁻¹, or ~10% of total fluxes. We outline the necessary conceptual understanding to successfully include dry phases in a more complete picture of inland water C emissions and identify potential implications for global C cycle feedbacks.

1. Introduction

The role of inland waters as active and significant players in the global carbon (C) cycle is now indisputable (Regnier et al., 2013). After decades of research, the current paradigm defines inland waters as a reactive Earth compartment, which strongly regulates how much continental C finally reaches the oceans (Tranvik et al., 2009). Inland waters fix inorganic C by photosynthesis, but overall, they have emerged as net mineralizers of organic C, most of which originates from terrestrial or wetland sources in their catchments (Tranvik et al., 2009; Abril et al., 2014). Inland waters also accumulate large quantities of C in their sediments (Heathcote et al., 2015), and emit carbon dioxide (CO₂) and methane (CH₄) to the atmosphere (Raymond et al., 2013; Stanley et al., 2016).

Recent estimates indicate that inland waters outgas over 2 Pg C year⁻¹ in the form of CO₂, of which 1.8 Pg C year⁻¹ are emitted from streams and rivers (Raymond et al., 2013) and from 0.32 to 0.50 Pg C year⁻¹ from lakes and reservoirs (Raymond et al., 2013; Delsontro et al., 2018). In addition, inland waters outgas 0.13 Pg C year⁻¹ in the

form of CH₄ (4.85 Pg C-CO₂e year⁻¹; CO₂e = CO₂-equivalents; 1 g CH₄ = 28 g CO₂e), of which 0.02 Pg C year⁻¹ (0.75 Pg C-CO₂e year⁻¹) are emitted from streams and rivers (Stanley et al., 2016) and 0.11 Pg C year⁻¹ (4.10 Pg C-CO₂e year⁻¹) from lakes and reservoirs (Delsontro et al., 2018). These flux estimates are of impressively high magnitude, yet several studies highlighted fundamental knowledge gaps that still preclude a reasonably precise, spatially and temporally unbiased estimation of global gaseous C fluxes from inland waters (Wehrli, 2013).

Recently, von Schiller et al. (2014) identified a new potential knowledge gap: CO₂ emissions from dry streams and rivers. Although this work could not offer a robust global estimation of C emissions from these dry watercourses due to data scarcity, it clearly showed the potential relevance considering the high CO₂ emission rates measured in these systems and the large area they cover globally. High CO₂ (and low CH₄) emission rates have been measured in the dry sediments of other types of inland waters, including ponds (Catalán et al., 2014; Fromin et al., 2010; Obrador et al., 2018), reservoirs (Gómez-Gener et al., 2015; Jin et al., 2016) and lakes (Koschorreck, 2000).

Here, we define dry inland waters as the sections of lotic (streams

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Fig. 1. Photographs of representative dry inland waters. (a) Fuirosos stream (Catalonia, Spain) showing its dry stream bed; (b) Collada pond (Catalonia, Spain); (c) Königshütte reservoir (Saxony-Anhalt, Germany); (d) Lake Waiiau (Hawaii, USA). All photographs by the authors, except (d) by Rebecca Rossi (U.S. Geological Survey).

and rivers) and lentic (ponds, lakes, and reservoirs) ecosystems in which surface water is absent, and sediments become temporarily or even permanently exposed to the atmosphere (see some examples in Fig. 1). A large part of the global river and stream network shows ephemeral or intermittent flow regimes, i.e. their flow ceases with varying frequency and duration, exposing the sediments of the riverbed to direct contact with the atmosphere (Fig. 1A). Most small ponds seasonally dry at least partially (Fig. 1B), and man-made reservoirs experience recurrent water level fluctuations that expose large areas of sediments to the atmosphere, particularly in the inflow sections (Fig. 1C). Finally, lakes can also totally or partially dry due to changes in climate and water diversion, exposing bottom sediments (Fig. 1D). The dry sections of inland waters tend to be highly dynamic and contract and expand over space and time, thereby occupying a varying fraction of the aquatic network (Stanley et al., 1997). In addition, exposed sediments of inland waters may be subject to different drying intensities due to groundwater influence and rainfall, thus maintaining different levels of moisture after surface water loss (Steward et al., 2012).

The mapping of inland waters remains very challenging and is in its infancy (Lehner et al., 2011; Verpoorter et al., 2014; Allen and Pavelsky, 2018). Available estimates indicate that a large part of the world's inland waters is subject to occasional or seasonal drying. Raymond et al. (2013) estimated that about two thirds of first-order streams below 60° latitude flow only temporarily, as do one third of larger, fifth-order rivers. In a more recent estimation, Schneider et al. (2017) indicate that 30% of the global river network below 60° latitude is intermittent, with much higher proportions in arid and semiarid regions. Similarly, some studies suggest that a large proportion of the world's small ponds and lakes may fall dry seasonally (Holgerson and Raymond, 2016), as do the shorelines and shallow parts of many lakes and reservoirs during periods of water drawdown (Jin et al., 2016). In addition, occurrence and intensity of drying events are increasing in many regions due to the combined effect of climate change, water abstraction, and land use alteration (Pekel et al., 2016). In extreme cases, inland waters dry out permanently, as has been reported for many endorheic lakes during the last decades (Wurtsbaugh et al., 2017). The Aral Sea in Central Asia constitutes a remarkable example (Micklin, 2016).

Emissions of C from some seasonally dry, semi-aquatic habitats have been traditionally studied by soil and wetland scientists; these include river floodplains (Batson et al., 2015), rice paddy fields (Lagomarsino et al., 2016) and peatlands (Moore and Knowles, 1989). In contrast, the dry phases (and sections) of streams, rivers, ponds, lakes, and reservoirs represent spatiotemporal discontinuities in aquatic networks that have been largely overlooked in terms of C emissions. This is probably because (i) they are conceptually located in a scientific “no man's land”, perceived to be outside the domain of aquatic as well as terrestrial ecology (Steward et al., 2012); (ii) despite recent advances, mapping the dry phases of inland waters is a complex issue, especially for small features such as headwater streams and small ponds (Pekel et al., 2016; Schneider et al., 2017); and (iii) the measurement of gas fluxes from these heterogeneous and dynamic habitats is still challenging (Lesmeister and Koschorreck, 2017). Collectively, this hinders an accurate assessment of the role of dry inland waters in the C cycle. There is, however, a growing interest in understanding the effects of drying on biogeochemical processing in inland waters (Datry et al., 2014; Datry et al., 2018).

Here, we put the spotlight on gaseous C fluxes from exposed sediments in dry inland waters, considering magnitude and patterns, sources and controls, as well as implications for C cycling at multiple scales. We provide a review of the current data situation and conceptual understanding and suggest a research agenda to constrain the currently large uncertainties and to cover knowledge gaps. We restrict our analysis to lotic (streams and rivers) and lentic (ponds, lakes and reservoirs) inland waters. We deliberately omitted those systems for which dry phases are already well covered in the literature, particularly peatlands, rice paddy fields, and river floodplains. However, we use knowledge from these systems as a convenient reference in some sections.

2. CO₂ and CH₄ emissions from dry inland waters

2.1. Magnitude and patterns

Measurements of CO₂ and CH₄ fluxes from dry inland waters are scarce in the literature. Reported CO₂ fluxes from exposed sediments are generally high and frequently above 100 mmol m⁻² day⁻¹ (range

Table 1

Gaseous C fluxes from dry inland waters reported from the literature. The mean \pm standard deviation and the range (in brackets) is shown for those studies reporting directly measured fluxes in the field.

System, condition and location	CO ₂ flux (mmol m ⁻² day ⁻¹)	CH ₄ flux (mmol m ⁻² day ⁻¹)	Reference
Reservoirs, lakes and ponds			
Dry areas of Soyang reservoir, extreme drought, South Korea	515 \pm 377 (208;1000)	N.D.	Jin et al. (2016)
Dry areas of Boadella reservoir, summer, Spain	216 \pm 177 (19–517)	1.2 \pm 2.3 (0–5.8)	Gómez-Gener et al. (2015)
Intermittent ponds, annual cycle, Spain	48 \pm 36 (4–131) ^{bare}	N.D.	Catalán et al. (2014); Obrador et al. (2018)
	149 \pm 111 (23–492) ^{veg}		
Intermittent pond, summer, France	(10–600)	N.D.	Fromin et al. (2010)
Intermittent kettle holes, dry phase, Germany	89 \pm 20 (66–102)	0.03 \pm 0.02 (0.006–0.05)	Reverey et al. (2018)
Supralittoral zone of lake Taihu, annual cycle, China	N.D.	0.15 \pm 0.75	Wang et al. (2006)
Drawdown areas of Three Gorges reservoir, China	N.D.	0.6 \pm 1.9 (–0.1–5.9)	Yang et al. (2013a)
Drawdown area of Miyun reservoir, China	N.D.	0.013 \pm 0.013 ^{veg}	Yang et al. (2014)
Drawdown area of Nam Theun 2 reservoir, Laos	279 \pm 27 (34–699)	1.67 \pm 2.23	Deshmukh et al. (2018); Serça et al. (2016)
Amazon floodplain lake, dry phase, Brazil	272 \pm 113 (72–360)	< 0.1	Koschorreck (2000); Koschorreck and Darwich (2003)
Streams and rivers			
Intermittent streams, summer, USA	44 \pm 23 (20–65)	< 0.1	Gallo et al. (2013)
Intermittent streams, after rain event, USA	569 \pm 530 (91–1532)	< 0.1	Gallo et al. (2013)
Intermittent streams, summer, Spain	205 \pm 21 (190–220)	< 0.1	Gómez-Gener et al. (2015)
Intermittent streams, summer, Spain	781 \pm 390 (342–1533)	N.D.	Gómez-Gener et al. (2016)
Intermittent stream, summer dry-wet cycles, Australia	72 \pm 27 (27–115)	N.D.	Looman et al. (2017)

N.D.: not determined; ^{bare}: flux from bare sediments; ^{veg}: includes flux from areas covered by microphytobenthos.

4–1533 mmol m⁻² day⁻¹; Table 1). These fluxes are typically higher than average literature values for ponds, lakes and reservoirs (18–55 mmol m⁻² day⁻¹; Raymond et al., 2013; Deemer et al., 2016; Holgerson and Raymond, 2016), and similar to fluxes reported from flowing streams and rivers (up to 600 mmol m⁻² day⁻¹; Raymond et al., 2013), dry peatlands (150–213.6 mmol m⁻² day⁻¹; Moore and Knowles, 1989), and soils (–45.6–5262 mmol m⁻² day⁻¹; Bond-Lamberty and Thomson, 2012). Similarly, results from the few studies that have compared C fluxes over dry and wet phases within the same ecosystems (i.e., seasonal assessments) highlight the importance of dry-phase fluxes (Gómez-Gener et al., 2016; Looman et al., 2017; Obrador et al., 2018). For instance, Gómez-Gener et al. (2016) found that the CO₂ flux from intermittent streams during dry conditions (781 \pm 390 mmol m⁻² day⁻¹) was twice the rate than during flowing conditions (306 \pm 206 mmol m⁻² day⁻¹). Experiments in soils and reservoir sediments suggest that CO₂ emissions tend to be higher at intermediate stages of drying (Sponseller, 2007; Kosten et al., 2018), but more studies with sediments of dry inland waters are needed.

Contrary to CO₂, CH₄ fluxes from exposed sediments of dry inland waters are low, typically falling below 0.1–1 mmol m⁻² day⁻¹ (Table 1). This contrasts with the generally higher CH₄ fluxes measured in flowing streams and rivers (4.2 \pm 8.4 mmol m⁻² day⁻¹, Stanley et al., 2016) as well as in lakes and reservoirs (3–10 mmol m⁻² day⁻¹, Deemer et al., 2016), suggesting a negative effect of drying on CH₄ emissions. Dry systems lack ebullition as a pathway of CH₄ emission, and most of the CH₄ produced in the exposed sediments is actually oxidized prior to evasion to the atmosphere (Koschorreck, 2000; Wang et al., 2006). CH₄ fluxes from exposed sediments are therefore only likely to be relevant during the first hours or days after surface water loss (Jin et al., 2016; Koschorreck, 2000; Kosten et al., 2018).

2.2. Microbial and geological sources

Identification of the ultimate sources of and the relevant processes behind the C emitted from inland waters is a complex, albeit necessary step for a complete understanding of the role of inland waters in the global C cycle. This is also critical for modeling, predicting and up-scaling, and it serves to identify which share of the emitted C corresponds to a global anthropogenic perturbation (Regnier et al., 2013). As in any ecosystem, C emissions derive from a set of abiotic and biotic sources, whose relative importance is tied to intrinsic features such as

geology, microbial communities and available organic substrates, and environmental controls such as moisture and nutrient availability. In contrast to headwater streams, where a substantial part of CO₂ emissions is a legacy of respiration in soils (Marx et al., 2017), C emissions from dry inland waters are more likely to originate from in-situ processes (a potential exception being CO₂ from underground water flow).

Changes in sediment moisture are widely recognized to modulate microbial activity in water-stressed ecosystems (Sponseller, 2007). Any change in moisture is expected to be translated to changes in C emissions from microbial compartments and in their relative contribution of CO₂ vs. CH₄. To mechanistically understand how these microbial gaseous C fluxes are shaped, it is key to consider effects of drying on the viability and activity of the microbial communities, including selection effects imposed by drought at various time scales.

Sediment desiccation impacts microbial viability and activity (Sabater et al., 2016), induces microbial dormancy or mortality, and reduces the activity of extracellular enzymes, the latter a critical component in organic matter degradation (Zoppini and Marxsen, 2011). It can be a long way from wet to dry, however, and at the onset of drying the increased oxygen availability can stimulate enzymatic activities (e.g. phenol oxidase) and overall microbial growth. This leads to an increased breakdown of organic matter and the subsequent release of CO₂, as seen in desiccated ponds (Fromin et al., 2010) and peatlands (Fenner and Freeman, 2011; Moore and Knowles, 1989). With continued drying, the various grades of desiccation differentially affect microbial species and ultimately select for a viable microbial community that can maintain activity down to low moisture levels (Sabater et al., 2016). In exposed sediments of dry streams, bacterial communities are mostly subsets of the community inhabiting the stream under established water flow, containing generally more stress-tolerant species but also immigrants from the terrestrial surrounding (Timoner et al., 2014). Light-dependent algae that grow on exposed surfaces suffer more from drying than bacteria, which can find refuges in interstitial microhabitats (Timoner et al., 2012).

Accordingly, at ecosystem scale, respiration has been reported to be more resistant to flow intermittence than primary production (Acuña et al., 2015). There may be concomitant shifts of multiple heterotrophic processes. For instance, restricted diffusion of oxygen in water supports the formation of anoxic sites, where methanogenesis can become important, while aerobic respiration and methanotrophy benefit from oxic conditions when a system falls dry. Anoxic rice paddy fields typically

produce CH₄, while this greenhouse gas is prone to oxidation during the drainage phases (Jäckel et al., 2001). Strongly increased oxygen diffusion in desiccated areas of rivers and floodplains (Baldwin and Mitchell, 2000), seasonal ponds (Fromin et al., 2010) and reservoirs (Mitchell and Baldwin, 1999) supports little methanogenesis but high aerobic respiration and thus production of CO₂.

Besides microbial respiration, geologic C can be a relevant source for C emissions, particularly in carbonate-rich regions. This is because carbonate precipitation/dissolution reactions may continue upon drying, with potential implications for CO₂ emissions (Marcé et al., 2015). In this line, recent research has shown that abiotic CO₂ emissions in arid soils can be a relevant share of total C emissions (Rey, 2015). In addition, photodegradation of organic matter on dry light-exposed sediments could also lead to increased CO₂ losses (Rutledge et al., 2010), whereas CO₂ uptake in some desert soils has been related to dissolution of CO₂ in the soil solution and carbonate weathering (Ma et al., 2013). Currently, however, there is no direct evidence from dry inland waters supporting these mechanisms described for soils.

2.3. Environmental controls

Several environmental factors have been identified as drivers of gaseous C fluxes from dry inland waters. As already pointed out above, sediment moisture is one of the main drivers (Gallo et al., 2013; Gómez-Gener et al., 2015; Jin et al., 2016; Muñoz et al., 2018), both in the form of residual water during the drying process or of water delivered in short rewetting episodes by rain or episodic flows.

The mechanism by which moisture controls gaseous C fluxes is complex, as it results from a trade-off between stimulation of microbial respiration and limitation of gas diffusivity (Gómez-Gener et al., 2015). Noteworthy, exposed sediments may maintain certain levels of moisture after surface water loss. Moisture levels are maximized in rainy regions and in fine textured sediments covered with decaying vegetation, where even reduced redox conditions suitable for anaerobic metabolism and CH₄ production may be maintained (Koschorreck and Darwich, 2003).

Short rewetting episodes can trigger microbial respiration and CO₂ release from exposed sediments, a phenomenon well described in soils and known as the Birch effect (Birch, 1958; Jenerette et al., 2008). Although the Birch effect has not been assessed as such in exposed sediments of dry inland waters, increased CO₂ fluxes in response to rewetting have been reported from exposed sediments of intermittent streams (Gallo et al., 2013), ponds (Fromin et al., 2010), and river and reservoir mesocosms (Muñoz et al., 2018; Kosten et al., 2018). Therefore, marked punctual increases in the CO₂ flux from dry sediments are to be expected during rewetting after a dry period (e.g., rainfall event). Immediately after rewetting, gases in the pore-spaces are displaced by water potentially causing a significant efflux of CO₂ (Kim et al., 2012). In soils increases in the CO₂ flux of up to 5-fold during several days have been reported (Kim et al., 2012), significantly impacting the overall annual CO₂ flux.

Rewetting events can also cause the remobilization of organic matter and nutrients (Wilson and Baldwin, 2008). At the micro-scale, pore-filling will increase the dissemination of water-soluble substrates and mobilize labile substances from dead biomass. Aggregate disruption and the destabilization of organo-mineral complexes will also liberate C otherwise protected from microbial action (Borken and Matzner, 2009; Kim et al., 2012). Although the first and most direct impact of rewetting on the dry sediment community is an osmotic shock, the concomitantly lysing cells provide labile substrates for the community of survivors. Also, as a response to rewetting, organisms in dormant states are rapidly activated (Kim et al., 2012). In dry inland waters, there are often poor correlations between cell numbers and activities (Koschorreck and Darwich, 2003), pinpointing dormancy as a potentially relevant mechanism.

Other major drivers of CO₂ fluxes from dry inland waters include

the presence or absence of vegetation or microphytobenthos in the exposed sediments (Bolpagni et al., 2017; Catalán et al., 2014; Obrador et al., 2018), sediment texture (Gallo et al., 2013; Gómez-Gener et al., 2016), sediment temperature (Gómez-Gener et al., 2016) and sediment organic matter (Bolpagni et al., 2017; Gallo et al., 2013; Gómez-Gener et al., 2016; Deshmukh et al., 2018). Studies in intermittent streams indicate that organic matter quantity may be more important than quality in controlling the magnitude of CO₂ fluxes from exposed sediments (Gallo et al., 2013; Gómez-Gener et al., 2016); however, the few data available preclude reaching a solid conclusion. It has been shown that processes creating heterogeneous redox conditions in exposed sediments (e.g., bioturbation by small invertebrates) accelerate N₂O emissions (Koschorreck, 2005), but nothing is known about the effect of bioturbation on CO₂ and CH₄ emissions. In soils, other abiotic factors like pressure-pumping due to diurnal changes in temperature or synoptic weather patterns have been identified as controls of CO₂ emissions (Rey, 2015), but there is no direct evidence for such processes from dry inland waters.

As in soils (Lorenz and Lal, 2009), human activities altering emerged sediments are expected to directly alter the gaseous C fluxes from dry inland waters. For instance, in water-scarce regions, surface impermeabilization of intermittent streams is common in some sections along their course to optimize water resource use or to use streambeds as roads (Steward et al., 2012). The surface compaction and coverage by impervious materials will likely prevent gas diffusion and most of the microbial functions producing these gases. In the same line, simultaneous changes in nutrient status and sediment texture because of altered land use in the catchment can directly and indirectly impact sediment biogeochemistry and C emissions, as has been highlighted in ephemeral urban streams (Gallo et al., 2013).

3. Implications at the local, regional, and global scales

3.1. Drawdown areas in reservoirs: consequences for C balances and the hydropower footprint

Water level fluctuations are a typical feature of reservoirs. The dry area during low water level (i.e. the drawdown area) can cover a significant part of the total reservoir area. The drawdown area shows two characteristic habitats: (i) the banks of the main body of the reservoir, which are often steep and stony, and (ii) inflow areas, which are typically shallow with vegetation growing on exposed organic-rich mudflats (Fig. 1C).

Reservoirs are a relevant source of greenhouse gases on a global scale (Deemer et al., 2016; Delsontro et al., 2018). However, C emissions from drawdown areas are typically not considered in reservoir studies and only few data are available. Recent measurements suggest that the drawdown area, despite typically covering < 30% of the reservoir surface, has the potential to dominate CO₂ emissions from reservoirs (Table 2, Deshmukh et al., 2018). Ignoring CO₂ emissions from the drawdown area can result in a > 200% underestimation of CO₂ emissions. Thus, considering CO₂ emissions from drawdown areas has the potential to significantly increase our current estimate of global C emissions from reservoirs. Notably, not considering these C emissions could also considerably affect estimations of the hydropower footprint (Hertwich, 2013). CH₄ emissions from the drawdown area, on the other hand, seem to be low (Table 2). For instance, a study in the Chinese Miyun Reservoir showed that CH₄ emission from flooded sites was about 1000 times higher than from non-flooded sites (Yang et al., 2014).

There is little information about the effect of terrestrial vegetation in the drawdown area on gas emissions. By applying flux rates obtained in rice paddies, marshes, and temperate wetlands forming the drawdown area of the Three Gorges Reservoir (China), it was estimated that these drawdown zones contribute 17% and 74% to the annual emissions of CO₂ and CH₄, respectively (Yang et al., 2012). The high

Table 2

Gaseous C fluxes in drawdown areas of reservoirs. Areas are long term means calculated from water level recordings. Fluxes were integrated from transect measurements. Unpublished data from the authors. The methods used to obtain these data are explained in detail in the Supplemental Material.

Reservoir	Date (day/month/year)	Drawdown area (% of reservoir)	CO ₂ flux (mmol m ⁻² day ⁻¹)		Flux from drawdown area (% of total flux)	
			CO ₂	CH ₄	CO ₂	CH ₄
Sau (Spain)	14/10/2015	17 ± 14	13.9	0	3	0
Boadella (Spain)	28/8/2013	28 ± 15	170	0.26	78	14
Rappbode (Germany)	20/6/2017	11 ± 10	232	0.26	30	1
Königshütte (Germany)	29/5/2015	14 ± 7	193	0.45	27	3
Undurraga (Spain)	15/6/2016	10 ± 7	134	0.02	30	< 1

contribution of CH₄ originates from extremely high emissions by rice fields. CO₂ uptake by terrestrial vegetation also has the potential to lower net CO₂ emissions during low water level (Yang et al., 2013b).

In the drawdown area of the shallow tropical Nam Theun 2 Reservoir, the CO₂ flux was not correlated with moisture, temperature, soil type, or topography, but weakly correlated with sediment C content (Deshmukh et al., 2018). The observed high variability calls for more data covering different reservoirs, climate zones, land uses, and seasons. Typically, there are spatial gradients with highest emissions of CH₄ found near the water line (Wang et al., 2006; Yang et al., 2014), while CO₂ emissions can show different patterns along this gradient (Gómez-Gener et al., 2015; Jin et al., 2016). These spatial gradients are probably the result of temporal changes, with higher areas being dry for longer periods. Thus, the temporal pattern of water level fluctuations, which results both from runoff dynamics and reservoir management, can strongly affect the annual C budget. Extreme drawdown events can lead to very high CO₂ emissions and have the potential to offset long term C accumulation in reservoir sediments (Jin et al., 2016; Kosten et al., 2018).

3.2. Permanent drying, increased seasonality, and the fate of lacustrine C sinks

Lake sediments have accumulated large quantities of organic C derived from terrestrial ecosystems and internal production during the Holocene (Tranvik et al., 2009). The total mass of stored C is estimated at ~820 Pg C (Einsle et al., 2001), an amount comparable to C stored in other Earth compartments, like the atmosphere (~829 Pg C), the surface ocean (~900 Pg C), terrestrial vegetation (~550 Pg C), non-frozen soils (~2000 Pg C), and permafrost (~1300 Pg C) (IPCC, 2013). The current paradigm defines lake sediments as C sinks (Heathcote et al., 2015), burying 0.15 Pg C every year globally (Mendonça et al., 2017).

Many lakes and reservoirs are currently shrinking and falling dry due to diversion of water for human uses and recent changes in climate. Up to ~90,000 km² of water surface have already vanished in the last 30 years, whereas ~800,000 km² of inland water area are currently seasonally drying (Pekel et al., 2016). Exposure of lake sediments to atmospheric oxygen and higher air temperatures reactivates decomposition of buried organic C of different ages (Tesi et al., 2016), which is eventually released to the atmosphere, compromising this millennial C sink. Remobilization of C stocks previously locked in lake sediments constitutes a C redistribution process potentially relevant as a climate change feedback. However, current global C budgets ignore this process by considering sediments as mere C traps (Regnier et al., 2013). Much is at stake, because appropriate mitigation and adaptation measures against climate change must be based on accurate accounting of current and future C redistribution between land and atmosphere.

To approach this question, we produced a first rough, conservative estimate of C released from dry lake sediments globally, including both systems that dried out permanently during the last 30 years and the dry sediments that emerge in current seasonally dry systems (Pekel et al., 2016). For this, we considered the average CO₂ emission estimate from

dry lake and reservoir sediments from Table 2 (320 mmol C m⁻² day⁻¹), as well as the maximum and minimum average estimates available (216 and 515 mmol C m⁻² day⁻¹, respectively) to give a first assessment of the uncertainty of the global estimate. We calculated the area of permanent and seasonally dry lakes and reservoirs from the water area vanished during the last 30 years (89,597 km²) and the current extension of seasonal water area (806,321 km²) as reported in Pekel et al. (2016). However, this analysis did not differentiate between lakes, reservoirs and the rest of inland waters, including wetlands. To obtain the percent of the above areas that correspond exclusively to lakes and reservoirs, we used the fraction of inland water bodies that correspond to lakes and reservoirs (i.e., excluding rivers and other inland wetlands) in the GLWD database (Lehner and Döll, 2004). Only 21% of the inland water area in this database is attributed to lakes and reservoirs, and consequently we revised our estimates for permanently dried systems to 18,755 km², and the area of seasonally dry lakes to 168,787 km². To calculate annual emissions from seasonally dry lakes we multiplied the aforementioned C emissions rates from dry systems times the area occupied by seasonally dry lakes, considering that those lakes will be dry only 3 months a year. For permanently dry lakes, we assumed 1) that the area of dry lakes linearly increased during the last 30 years from zero to the current 18,755 km²; and 2) that the C emissions from permanently dry systems is a transient phenomenon, due to an eventual limitation by the available amount and quality of organic C in the dry sediments. We applied a conservative criterion and assumed that C emissions will decrease to zero in 30 years, declining exponentially at annual steps from the emission rates detailed above, although circumstantial evidence is not conclusive at this respect (we have non-published data showing zero emissions in sediments exposed ~35 years ago in an endorheic lake in Spain, but exposed sediments from an Alaskan lake drained ~30 years ago emitted ~150 mmol C m⁻² day⁻¹ (Wickland et al., 2009)). These exponentially decaying emissions during 30 years imply that the remobilization of C to the atmosphere upon lake drying would account for ~65% of the total organic C pool in the dry lake sediments, assuming a conservative estimate of the average C stock in surface lake sediments (20 kg C m⁻², Kortelainen et al., 2004). Therefore, the calculated emissions are plausible from a mass balance perspective.

Results from this exercise show that 0.080 Pg C year⁻¹ of formerly buried C are released to the atmosphere, with uncertainty bounds going from 0.054 to 0.128 Pg C year⁻¹. This overlooked flux represents ~53% of the global C burial in lakes and reservoirs (0.15 (range 0.06–0.25) Pg C year⁻¹; Mendonça et al., 2017), and ~20% of the current estimates of the global annual CO₂ emissions from lakes and reservoirs (0.41 (range 0.06–0.84) Pg C year⁻¹; Raymond et al., 2013; Delsontro et al., 2018). These numbers are of the same order of magnitude than the global CH₄ emissions from inland waters which are now in the spotlight (0.13 (range 0.09–0.22) Pg C year⁻¹; Deemer et al., 2016). This annual C flux would imply between 1.87 and 4.50 Pg C released to the atmosphere between 2015 and 2050, which is not negligible considering that the upper soil horizons will emit ~30 Pg C during the same period (Crowther et al., 2016). Unfortunately, we do not have estimates of the share of new permanent and seasonal dry lake

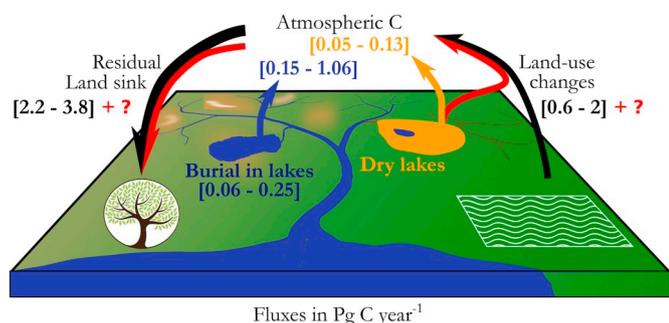


Fig. 2. Potential C redistribution from permanent and seasonally dry lakes (orange) compared with C burial in sediments (blue; Mendonça et al., 2017) and emissions from flooded lakes (blue arrow; Raymond et al., 2013; Delsontro et al., 2018). The potential impacts (red) on current estimates of anthropogenic fluxes between land and atmosphere (Le Quére et al., 2018) are also depicted. Values for dry lakes are first estimates produced for this work (see text). (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

area that must be attributed to anthropogenic influences on climate and land use change (e.g., water diversion). However, the potential flux from permanent and seasonally dry lakes and reservoirs suggests a sizeable impact of lake drying and increased seasonality on the global anthropogenic C cycle (Fig. 2).

It is worth mentioning that the fluxes calculated here cannot be directly translated into a net anthropogenic perturbation of the C cycle due to lake drying. The drying of a lake also implies the modification of fluxes present in the watershed-lake system before drying out, which must be taken into account for an overall assessment of the net perturbation of the C cycle. For such a calculation, it is not sufficient to subtract the CO_2 and CH_4 emissions and add the C burial present in the flooded lake to the emissions upon drying: most C emissions and burial in lakes originate from C imported from upstream ecosystems (terrestrial or aquatic), and for a complete assessment of the net impact of drying on the C cycle we must also track the fate of this C once the lake dries out. Clearly, this is a very complex exercise out of the scope of this review. Finally, these numbers must be put in context of the changes in water surface occurring on Earth, that also include an increasing water surface in many areas of the globe during the last decades (Pekel et al., 2016) despite others prone to desiccation. However, while we have a considerable amount of works supporting an increasing burial due to the creation of new water bodies (Clow et al., 2015; Mendonça et al., 2017), there are no published studies on the effect of drying on locked C stocks, and thus, no evaluation of the potential of these fluxes to counterbalance an increased burial in new water bodies.

3.3. Potential significance of C emissions from dry inland waters for the global C cycle

A first rough global estimate of C emissions from exposed sediments

Table 3
Global estimate of CO_2 fluxes from dry inland waters.

Dry inland waters	Accumulated dry area during a year (including seasonal and permanent drying) (km^2)	CO_2 emission rate ($\text{mmol m}^{-2} \text{day}^{-1}$) ^a	Global C emission (Pg C year^{-1})
Streams and rivers (up to 5th order)	84,461 ^b	334 (44–781)	0.124 (0.016–0.289)
Lakes, reservoirs (> 900 m^2)	187,542 ^c	320 (216–515)	0.080 (0.054–0.128)
Small ponds (< 900 m^2)	18,390 ^d	148 (10–600)	0.012 (0.001–0.048)
TOTAL	290,393		0.216 (0.071–0.465)

^a This study. Average, minimum, and maximum of the mean values reported in Table 1. For permanently dry lakes, emissions decrease exponentially to zero after 30 years of drying (see text for details).

^b Raymond et al., 2013. Sum of the area of exposed sediments across intermittent and ephemeral streams and rivers during a year.

^c This study. Current permanent and seasonally dry area modified from Pekel et al. (2016), see text for details.

^d This study. Sum of the area of exposed sediments of small ponds modified from Holgerson and Raymond (2016), see text for details.

in intermittent streams and rivers was provided by von Schiller et al. (2014). Here, we revise this estimate, including new emission data from streams and rivers as well as C emissions from other dry inland waters. We would like to stress that the global estimates included in this section are far from being the robust, spatially and temporally unbiased calculations needed to incorporate C emissions from dry inland waters into global C balances. However, a back-of-the-envelope calculation using the best data available may help to understand the potential relevance of this flux for the inland water C cycle, and prompt further research on the topic. Global estimates in this paper should not be used in any other way.

For ephemeral and intermittent rivers and streams (up to 5th order), we considered the total area of seasonally exposed sediments during a year reported in Raymond et al. (2013). The seasonally dry area of small ponds was calculated considering the last estimate of the global area of small ponds (334,366 km^2 , Holgerson and Raymond, 2016) assuming that the accumulated dry area along a year will cover 5.5% of this area (i.e. the percent area of 1st order streams considered as dry in Raymond et al., 2013). For lakes and reservoirs, we used the estimates presented in the preceding section. We combined these area estimates with CO_2 emission rates available in the literature for the different inland waters considered, using the average, minimum, and maximum mean emissions reported in the different studies (Table 3). We did not consider CH_4 emissions nor CO_2 emissions during rewetting episodes due to the severe scarcity of data. The final estimate of global CO_2 emission from dry inland waters (0.22 (range 0.07–0.46) Pg C year^{-1}) would represent 10% (range 2.4–29.8) of the global CO_2 emissions from inland waters (2.1 (range 1.56–2.94) Pg C year^{-1} , Raymond et al., 2013), suggesting that emissions from dry inland waters play a substantial role in the inland water C cycle.

4. A research agenda

Emissions of C from exposed sediments in dry streams, rivers, ponds, lakes, and reservoirs to the atmosphere can be considered a recent topic in C biogeochemistry research. Although several lines of evidence suggest that they cannot be disregarded to draw an accurate picture of the role of inland waters in the global C cycle, the scarcity of available data precludes precise estimates of its magnitude and relative relevance. As a wrap-up, we suggest a research agenda to constrain the main sources of uncertainty involved in C emissions from dry inland waters, not only to produce precise regional or global estimates of C emissions, but also to understand the physical and biological mechanisms behind this flux. These are the main points we have identified:

- 1) There is a paucity of C emission data from dry inland waters. This contrasts with the abundance of data for C emissions from surface waters (Deemer et al., 2016; Raymond et al., 2013) and terrestrial soils (Bond-Lamberty and Thomson, 2012). Collecting data from dry inland waters should be a research priority over the next years. However, relying on the collection of data by individual teams

would imply that we would need several years, or even decades, to gather enough data to produce robust global and regional C emission estimates. To speed up this process, we suggest the establishment of global collaborative sampling initiatives, such as the GLEON initiative DryFlux (<http://www.ufz.de/dryflux/>) and the 1000 Intermittent Rivers Project (https://1000_intermittent_rivers_project.irstea.fr/; Datry et al., 2018). These initiatives engage a high number of research teams in a common research objective, covering hundreds of sampling locations in very short time periods.

- 2) Estimation of the current and future extension of permanent and seasonally dry inland waters is one of the main challenges we face, particularly for small systems (i.e. low order streams, small ponds) that are not easily captured by remote sensing. Although several global estimates exist on the spatial and temporal extent of intermittent streams (Raymond et al., 2013; Schneider et al., 2017), they can only be considered as a first rough estimate. This is because the statistical models used to extrapolate to continental scales lead to poor results outside the climatic regions for which the models were calibrated, grossly underestimating the extent of intermittent streams. Probably, the best alternative for estimating the extension of small to medium dry streams in most of the river network (e.g., under canopy covers that hide streams from direct view from space or airborne imagery) is hydrological modeling, although modeling intermittence at large scales has not been a research priority until very recently (Datry et al., 2017). To our knowledge, there is no available database on the extension and temporal dynamics of dry phases in small ponds, although their role on global C emissions should not be disregarded (Holgerson and Raymond, 2016). Finally, the situation for lakes, reservoirs, and large rivers is better because they can be reasonably well captured by recorded information on water level fluctuations and remote sensing (Keys and Scott, 2017). In addition, we already have estimations of the extension of dry inland waters (Pekel et al., 2016) that can potentially be combined with lake and reservoir databases (Verpoorter et al., 2014) to deliver more accurate estimates of the extension of permanent and seasonally dry lakes. All in all, mapping dry inland waters is a major bottleneck for assessing their role in the global C cycle.
- 3) Soil science already considers some semi-aquatic habitats that recurrently fall dry, particularly peatlands, rice paddy fields, river floodplains, and tidal wetlands. Research on C emissions from dry inland waters should take advantage of all technical and theoretical developments available from soil science (Arce et al., 2018). This includes not only the methodologies to measure gas emissions from dry surfaces (Lesmeister and Koschorreck, 2017), but also the controls of these emissions (e.g., Gómez-Gener et al., 2016). Therefore, developments from soils about organic matter degradation and persistence, impact of land use alterations, or rewetting effects, may shed light on C emissions from dry inland waters. Interfacing with terrestrial sciences may also help to consider the potential implications of establishment of ephemeral and permanent vegetation on the C balance of dry sediments of inland waters. Indeed, vegetation growth on dry sediments (i.e., terrestrialization) may offset C emissions by respiratory processes in the sediments (Bolpagni et al., 2017).
- 4) Estimating C fluxes from dry inland waters is just a first step in our understanding of the role of these ecosystems on global and regional C budgets. For a complete picture of their role at the global scale and potential feedbacks related to climate we also need an estimate of the C fluxes promoted by anthropogenic perturbations since the pre-industrial era (Regnier et al., 2013). This implies that we will need a deep understanding of the changes in extension and seasonality of dry inland waters, particularly those in response to climate oscillations, water diversions, and land use changes at decadal time-scales. Again, hydrological models accounting for drying dynamics in response to these factors (a challenge for current large-scale hydrological models) are the best option to move forward in this direction.

In conclusion, we provided evidence aimed to persuade the Earth-science community that dry phases in streams, rivers, ponds, lakes and reservoirs must be considered to draw a complete picture of the inland water C cycle. Dry inland waters will be increasingly frequent in our landscapes, and considering the C fluxes associated with them will surely improve our understanding of the role of inland waters in the current, past, and future global C cycle.

Data availability

We show all data used in this manuscript in text, figures and tables.

Competing interests statement

The authors have no competing interests to declare.

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Appendix A. Supplementary data

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References

- Abril, G., Martinez, J.M., Artigas, L.F., Moreira-Turcq, P., Benedetti, M.F., Vidal, L., Meziane, T., Kim, J.H., Bernardes, M.C., Savoye, N., Deborde, J., Albéric, P., Souza, M.F.L., Souza, E.L., Roland, F., 2014. Amazon River carbon dioxide outgassing fuelled by wetlands. *Nature* 505, 395–398.
- Acuña, V., Casellas, M., Corcoll, N., Timoner, X., Sabater, S., 2015. Increasing extent of periods of no flow in intermittent waterways promotes heterotrophy. *Freshw. Biol.* 60, 1810–1823.
- Allen, G.H., Pavelsky, T.M., 2018. Global extent of rivers and streams. *Science* 585–588.
- Arce, M.I., Mendoza-Lera, C., Almagro, M., Catalan, N., Mutz, M., Romani, A., Martí, E., Rosa, G., Foulquier, A., Marcé, R., Bernal, S., Zoppini, A., Gionchetta, G., Weigelhofer, G., del Campo, R., Robinson, C., Gilmer, A., Rulik, M., Obrador, B., Shumilova, O., Zlatanović, S., Arnon, S., Baldrian, P., Singer, G., Datry, T., Skoulikidis, N., Tietjen, B., von Schiller, D., 2018. A conceptual framework for understanding the biogeochemistry of dry riverbeds through the lens of soil science. *Earth-Science Rev* (in review).
- Baldwin, D.S., Mitchell, A.M., 2000. The effects of drying and re-flooding on the sediment and soil nutrient dynamics of lowland river-floodplain systems: a synthesis. *Regul. Rivers Res. Manag.* 16, 457–467.
- Batson, J., Noe, G.B., Hupp, C.R., Krauss, K.W., Rybicki, N.B., Schenk, E.R., 2015. Soil greenhouse gas emissions and carbon budgeting in a short-hydroperiod floodplain wetland. *J. Geophys. Res. Biogeosci.* 120, 77–95.
- Birch, H.F., 1958. The effect of soil drying on humus decomposition and nitrogen availability. *Plant Soil* 10, 9–31.
- Bolpagni, R., Folegot, S., Laini, A., Bartoli, M., 2017. Role of ephemeral vegetation of emerging river bottoms in modulating CO₂ exchanges across a temperate large

- lowland river stretch. *Aquat. Sci.* 79, 149–158.
- Bond-Lamberty, B.P., Thomson, A.M., 2012. A global database of soil respiration data, Version 2.0. Data set. Oak Ridge National Laboratory Distributed Active Archive Center, Oak Ridge, Tennessee, U.S.A.
- Borken, W., Matzner, E., 2009. Reappraisal of drying and wetting effects on C and N mineralization and fluxes in soils. *Glob. Chang. Biol.* 15, 808–824.
- Catalán, N., Von Schiller, D., Marcé, R., Koschorreck, M., Gomez-Gener, L., Obrador, B., 2014. Carbon dioxide efflux during the flooding phase of temporary ponds. *Limnetica* 33, 349–360.
- Clow, D.W., Stackpoole, S.M., Verdin, K.L., Butman, D.E., Zhu, Z., Krabbenhoft, D.P., Striegl, R.G., 2015. Organic carbon burial in lakes and reservoirs of the conterminous United States. *Environ. Sci. Technol.* 49, 7614–7622.
- Crowther, T., Todd-Brown, K., Rowe, C., Wieder, W., Carey, J., Machmuller, M., Snoek, L., Fang, S., Zhou, G., Allison, S., Blair, J., Bridgman, S., Burton, A., Carrillo, Y., Reich, P., Clark, J., Classen, A., Dijkstra, F., Elberling, B., Emmett, B., Estiarte, M., Frey, S., Guo, J., Harte, J., Jiang, L., Johnson, B., Kröel-Dulay, G., Larsen, K., Landon, H., Lavallee, J., Luo, Y., Lupascu, M., Ma, L., Marhan, S., Michelsen, A., Mohan, J., Niu, S., Pendall, E., Penuelas, J., Pfeifer-Meister, L., Poll, C., Reinsch, S., Reynolds, L., Schmidh, I., Sistla, S., Sokol, N., Templer, P., Treseder, K., Welker, J., Bradford, M., 2016. Quantifying global soil C losses in response to warming. *Nature* 104, 104–108.
- Datry, T., Larned, S.T., Tockner, K., 2014. Intermittent rivers: a challenge for freshwater ecology. *Bioscience* 64, 229–235.
- Datry, T., Singer, G., Sauquet, E., Jorda-Capdevila, D., Von Schiller, D., Subbington, R., Magand, C., Pavril, P., Miliša, M., Acuña, V., 2017. Science and management of intermittent rivers and ephemeral streams (SMIRES). *Res. Ideas Outcomes* e21774, 3.
- Datry, T., Foulquier, A., Corti, R., von Schiller, D., Tockner, K., Mendoza-Lera, C., Clément, J.C., Gessner, M.O., Moleón, M., Stubbington, R., Gücker, B., 2018. A global analysis of terrestrial plant litter dynamics in non-perennial waterways. *Nat. Geosci.* 11, 497–503.
- Deemer, B.R., Harrison, J.A., Li, S., Beaulieu, J.J., Delsontro, T., Barros, N., Bezerra-Neto, J.F., Powers, S.M., Dos Santos, M.A., Vonk, J.A., 2016. Greenhouse gas emissions from reservoir water surfaces: a new global synthesis. *Bioscience* 66, 949–964.
- Delsontro, T., Beaulieu, J.J., Downing, J.A., 2018. Greenhouse gas emissions from lakes and impoundments: Upscaling in the face of global change. *Limnol. Oceanogr. Letters* 3, 64–75.
- Deshmukh, C., Guérin, F., Vongkhamsoo, A., Pighini, S., Oudone, P., Soprasedu, S., Godon, A., Rode, W., Guédant, P., Oliva, P., Audry, S., et al., 2018. Carbon dioxide emissions from the flat bottom and shallow Nam Theun 2 Reservoir: drawdown area as a neglected pathway to the atmosphere. *Biogeosciences* 15, 1775–1794.
- Einsele, G., Yan, J., Hinderer, M., 2001. Atmospheric carbon burial in modern lake basins and its significance for the global carbon budget. *Glob. Planet. Change* 30, 167–195.
- Fenner, N., Freeman, C., 2011. Drought-induced carbon loss in peatlands. *Nat. Geosci.* 4, 895–900.
- Fromin, N., Pinay, G., Montuelle, B., Landais, D., Ourcival, J.M., Joffre, R., Lensi, R., 2010. Impact of seasonal sediment desiccation and rewetting on microbial processes involved in greenhouse gas emissions. *Ecohydrology* 3, 339–348.
- Gallo, E.L., Lohse, K.A., Ferlin, C.M., Meixner, T., Brooks, P.D., 2013. Physical and biological controls on trace gas fluxes in semi-arid urban ephemeral waterways. *Biogeochemistry* 121, 189–207.
- Gómez-Gener, L., Obrador, B., von Schiller, D., Marcé, R., Casas-Ruiz, J.P., Proia, L., Acuña, V., Catalán, N., Muñoz, I., Koschorreck, M., 2015. Hot spots for carbon emissions from Mediterranean fluvial networks during summer drought. *Biogeochemistry* 125, 409–426.
- Gómez-Gener, L., Obrador, B., Marcé, R., Acuña, V., Catalán, N., Casas-Ruiz, J.P., Sabater, S., Muñoz, I., von Schiller, D., 2016. When water vanishes: magnitude and regulation of carbon dioxide emissions from dry temporary streams. *Ecosystems* 19, 710–723.
- Heathcote, A.J., Anderson, N.J., Prairie, Y.T., Engstrom, D.R., del Giorgio, P.A., 2015. Large increases in carbon burial in northern lakes during the Anthropocene. *Nat. Commun.* 6, 10016.
- Hertwich, E., 2013. Addressing biogenic greenhouse gas emissions from hydropower in LCA. *Environ. Sci. Technol.* 47, 9604–9611.
- Holgerson, M.A., Raymond, P.A., 2016. Large contribution to inland water CO₂ and CH₄ emissions from very small ponds. *Nat. Geosci.* 9, 222–226.
- IPCC, 2013. Climate Change 2013: The Physical Science Basis. Contribution of Working Group I to the Fifth Assessment Report of the Intergovernmental Panel on Climate Change, Working Group I Contribution to the Fifth Assessment Report of the Intergovernmental Panel on Climate Change. Summary for Policymakers, IPCC, Cambridge University Press, Cambridge, United Kingdom.
- Jäckel, U., Schnell, S., Conrad, R., 2001. Effect of moisture, texture and aggregate size of paddy soil on production and consumption of CH₄. *Soil Biol. Biochem.* 33, 965–971.
- Jenerette, G.D., Scott, R.L., Huxman, T.E., 2008. Whole ecosystem metabolic pulses following precipitation events. *Funct. Ecol.* 22, 924–930.
- Jin, H., Yoon, T.K., Lee, S.-H., Kang, H., Im, J., Park, J.-H., 2016. Enhanced greenhouse gas emission from exposed sediments along a hydroelectric reservoir during an extreme drought event. *Environ. Res. Lett.* 11, 124003.
- Keys, T.A., Scott, D.T., 2017. Monitoring volumetric fluctuations in tropical lakes and reservoirs using satellite remote sensing. *Lake Reserv. Manag.* 00, 1–13.
- Kim, D.G., Vargas, R., Bond-Lamberty, B., Turetsky, M.R., 2012. Effects of soil rewetting and thawing on soil gas fluxes: a review of current literature and suggestions for future research. *Biogeosciences* 9, 2459–2483.
- Kortelainen, P., Pajunen, H., Rantakari, M., Saarnisto, M., 2004. A large carbon pool and small sink in boreal Holocene lake sediments. *Glob. Chang. Biol.* 10, 1648–1653.
- Koschorreck, M., 2000. Methane turnover in exposed sediments of an Amazon floodplain lake. *Biogeochemistry* 50, 195–206.
- Koschorreck, M., 2005. Nitrogen turnover in drying sediments of an Amazon floodplain lake. *Microb. Ecol.* 49, 567–577.
- Koschorreck, M., Darwich, A., 2003. Nitrogen dynamics in seasonally flooded soils in the Amazon floodplain. *Wetl. Ecol. Manag.* 11, 317–330.
- Kosten, S., van den Berg, S., Mendonça, R., Paranaíba, J.R., Roland, F., Sobek, S., Van Den Hoek, J., Barros, N., 2018. Extreme drought boosts CO₂ and CH₄ emissions from reservoir drawdown areas. *Inland Waters* 8 (3), 329–340.
- Lagomarsino, A., Agnelli, A.E., Pastorelli, R., Pallara, G., Rasse, D.P., Silvennoinen, H., 2016. Past water management affected GHG production and microbial community pattern in Italian rice paddy soils. *Soil Biol. Biochem.* 93, 17–27.
- Le Quéré, C., Andrew, R.M., Friedlingstein, P., Sitch, S., Pongratz, J., Manning, A.C., Korsbakken, J.I., Peters, G.P., Canadell, J.G., Jackson, R.B., Boden, T.A., Tans, P.P., Andrews, O.D., Arora, V.K., Bakker, D.C.E., Barbero, B., Beck, M., Betts, R.A., Bopp, L., Chevallier, F., Chini, L.P., Ciais, P., Cosca, C.E., Cross, J., Currie, K., Gasser, T., Harris, I., Hauck, J., Haverd, V., Houghton, R.A., Hunt, C.W., Hurtt, G., Ilyina, T., Jain, A.K., Kato, E., Kautz, M., Keeling, R.F., Klein Goldewijk, K., Körtzinger, A., Landschützer, P., Lefèvre, N., Lenton, A., Lienert, S., Lima, I., Lombardozzi, D., Metz, N., Millero, F., Monteiro, P.M.S., Munro, D.R., Nabel, J.E.M.S., Nakaoka, S., Nojiri, Y., Padin, X.A., Peregon, A., Pfeil, B., Pierrot, D., Poulter, B., Rehdiger, G., Reimer, J., Rödenbeck, C., Schwinger, J., Séférian, R., Skjelvan, I., Stocker, B.D., Tian, H., Tilbrook, B., van der Laan-Luijkx, I.T., van der Werf, G.R., van Heuven, S., Viovy, N., Vuichard, N., Walker, A.P., Watson, A.J., Wiltshire, A.J., Zaehle, S., Zhu, D., 2018. Global carbon budget 2017. *Earth Syst. Sci. Data* 10, 405–448.
- Lehner, B., Döll, P., 2004. Development and validation of a global database of lakes, reservoirs and wetlands. *J. Hydrol.* 296, 1–22.
- Lehner, B., Liermann, C.R., Revenga, C., Vörösmarty, C., Fekete, B., Crouzet, P., Döll, P., Endejan, M., Frenken, K., Magome, J., 2011. High-resolution mapping of the world's reservoirs and dams for sustainable river-flow management. *Front. Ecol. Environ.* 9, 494–502.
- Lesmeister, L., Koschorreck, M., 2017. A closed chamber method to measure greenhouse gas fluxes from dry aquatic sediments. *Atmos. Meas. Tech.* 10, 2377–2382.
- Looman, A., Maher, D.T., Pendall, E., Bass, A., Santos, I.R., 2017. The carbon dioxide evasion cycle of an intermittent first-order stream: contrasting water-air and soil-air exchange. *Biogeochemistry* 132, 87–102.
- Lorenz, K., Lal, R., 2009. Biogeochemical C and N cycles in urban soils. *Environ. Int.* 35, 1–8.
- Ma, J., Wang, Z.Y., Stevenson, B.A., Zheng, X.J., Li, Y., 2013. An inorganic CO₂ diffusion and dissolution process explains negative CO₂ fluxes in saline/alkaline soils. *Sci. Rep.* 3, 2025.
- Marcé, R., Obrador, B., Morguá, J.A., Riera, J.L., López, P., Armengol, J., 2015. Carbonate weathering as a driver of CO₂ supersaturation in lakes. *Nat. Geosci.* 8, 107–111.
- Marx, A., Dusek, J., Jankovec, J., Sanda, M., Vogel, T., Geldern, R., Hartmann, J., Barth, J.A.C., 2017. A review of CO₂ and associated carbon dynamics in headwater streams: a global perspective. *Rev. Geophys.* 55, 560–585.
- Mendonça, R., Müller, R.A., Clow, D., Verpoorter, C., Raymond, P., Tranvik, L.J., Sobek, S., 2017. Organic carbon burial in global lakes and reservoirs. *Nat. Commun.* 8, 1694.
- Micklin, P., 2016. The future Aral Sea: hope and despair. *Environ. Earth Sci.* 75, 1–15.
- Mitchell, A.M., Baldwin, D.S., 1999. The effects of sediment desiccation on the potential for nitrification, denitrification, and methanogenesis in an Australian reservoir. *Hydrobiologia* 392, 3–11.
- Moore, T.R., Knowles, R., 1989. The influence of water table levels on methane and carbon dioxide emissions from peatland soils. *Can. J. Soil Sci.* 69, 33–38.
- Muñoz, I., Casas-Ruiz, J.P., Casellas, M., Gómez-Gener, L., Marcé, R., Menéndez, M., Obrador, B., Sabater, S., von Schiller, D., Acuña, V., 2018. Does the severity of non-flow periods influence ecosystem structure and function of temporary streams? A mesocosm study. *Freshw. Biol.* 63, 613–625.
- Obrador, B., von Schiller, D., Marcé, R., Gómez-Gener, L., Koschorreck, M., Borrego, C., Catalán, N., 2018. Dry habitats sustain high CO₂ emissions from temporary ponds across seasons. *Sci. Rep.* 8, 3015.
- Pekel, J.-F., Cottam, A., Gorelick, N., Belward, A.S., 2016. High-resolution mapping of global surface water and its long-term changes. *Nature* 540, 418–422.
- Raymond, P.A., Hartmann, J., Lauerwald, R., Sobek, S., McDonald, C., Hoover, M., Butman, D., Striegl, R., Mayorga, E., Humborg, C., Kortelainen, P., Durr, H., Meybeck, M., Ciais, P., Guth, P., 2013. Global carbon dioxide emissions from inland waters. *Nature* 503, 355–359.
- Regnier, P., Friedlingstein, P., Ciais, P., Mackenzie, F.T., Gruber, N., Janssens, I.A., Laruelle, G.G., Lauerwald, R., Luyssaert, S., Andersson, A.J., Arndt, S., Arnosti, C., Borges, A.V., Dale, A.W., Gallego-Sala, A., Goddérís, Y., Goossens, N., Hartmann, J., Heinze, C., Ilyina, T., Joos, F., Larowe, D.E., Leifeld, J., Meysman, F.J.R., Munhoven, G., Raymond, P.A., Spahni, R., Suntharalingam, P., Thullner, M., 2013. Anthropogenic perturbation of the carbon fluxes from land to ocean. *Nat. Geosci.* 6, 597–607.
- Rey, A., 2015. Mind the gap: non-biological processes contributing to soil CO₂ efflux. *Glob. Chang. Biol.* 21, 1752–1761.
- Rutledge, S., Campbell, D.I., Baldocchi, D., Schipper, L.A., 2010. Photodegradation leads to increased carbon dioxide losses from terrestrial organic matter. *Glob. Change Biol.* 16, 3065–3074.
- Sabater, S., Timoner, X., Borrego, C., Acuña, V., 2016. Stream biofilm responses to flow intermittency: from cells to ecosystems. *Front. Environ. Sci.* 4, 14.
- Schneider, A., Jost, A., Coulon, C., Silvestre, M., Théry, S., Ducharne, A., 2017. Global-scale river network extraction based on high-resolution topography and constrained by lithology, climate, slope, and observed drainage density. *Geophys. Res. Lett.* 44, 2773–2781.
- Serça, D., Deshmukh, C., Pighini, S., Oudone, P., Vongkhamsoo, A., Guédant, P., ... Guérin, F., 2016. Nam Theun 2 Reservoir four years after commissioning: significance of drawdown methane emissions and other pathways. *Hydroécologie Appliquée* 19, 119–146.
- Sponseller, R.A., 2007. Precipitation pulses and soil CO₂ flux in a Sonoran Desert

- ecosystem. *Glob. Chang. Biol.* 13, 426–436.
- Stanley, E.H., Fisher, S.G., Grimm, N.B., 1997. Ecosystem expansion and contraction in streams. *Bioscience* 47, 427–435.
- Stanley, E.H., Casson, N.J., Crawford, J.T., Loken, L.C., Oliver, S.K., 2016. The ecology of methane in streams and rivers: patterns, controls and global significance. *Ecol. Monogr.* 86, 146–171.
- Steward, A.L., von Schiller, D., Tockner, K., Marshall, J.C., Bunn, S.E., 2012. When the river runs dry: human and ecological values of dry riverbeds. *Front. Ecol. Environ.* 10, 202–209.
- Tesi, T., Muschitiello, F., Smittenberg, R.H., Jakobsson, M., Vonk, J.E., Hill, P., Andersson, A., Kirchner, N., Noormets, R., Dudarev, O.V., Semiletov, I.P., Gustafsson, Ö., 2016. Massive remobilization of permafrost carbon during post-glacial warming. *Nat. Commun.* 7, 13653.
- Timoner, X., Acuña, V., von Schiller, D., Sabater, S., 2012. Functional responses of stream biofilms to flow cessation, desiccation and rewetting. *Freshw. Biol.* 57, 1565–1578.
- Timoner, X., Borrego, C.M., Acuña, V., Sabater, S., 2014. The dynamics of biofilm bacterial communities is driven by flow wax and wane in a temporary stream. *Limnol. Oceanogr.* 59, 2057–2067.
- Tranvik, L.J., Downing, J.A., Cotner, J.B., Loiselle, S.A., S, R.G., Ballatore, T.J., Dillon, P.J., Finlay, K., Fortino, K., Knoll, L.B., Kortelainen, P.L., Kutser, T., Larsen, S., Laurion, I., Leech, D.M., McCallister, S.L., McKnight, D.M., Melack, J.M., Overholt, E., Porter, J.A., Prairie, Y., Renwick, W.H., Roland, F., Sherman, B.S., Schindler, D.W., Sobek, S., Tremblay, A., Vanni, M.J., Verschoor, A.M., Von Wachenfeldt, E., Weyhenmeyer, G.A., 2009. Lakes and reservoirs as regulators of carbon cycling and climate. *Limnol. Oceanogr.* 54, 2298–2314.
- Verpoorter, C., Kutser, T., Seekell, D.A., Tranvik, L.J., 2014. A global inventory of lakes based on high-resolution satellite imagery. *Geophys. Res. Lett.* 41, 6396–6402.
- von Schiller, D., Marcé, R., Obrador, B., Gómez, L., Casas, J.P., Acuña, V., Koschorreck, M., 2014. Carbon dioxide emissions from dry watercourses. *Inl. Waters* 4, 377–382.
- Wang, H., Lu, J., Wang, W., Yang, L., Yin, C., 2006. Methane fluxes from the littoral zone of hypereutrophic Taihu Lake, China. *J. Geophys. Res. Atmos.* 111, D17109.
- Wehrli, B., 2013. Biogeochemistry: conduits of the carbon cycle. *Nature* 503, 346–347.
- Wickland, K., O'Donnell, J.A., Koch, J.C., Jorgenson, M.T., Harden, J.W., Striegl, R.G., Anderson, L., 2009. Fate of Carbon in Sediments of a Drying High Latitude Lake, Interior Alaska. In: *Eos Trans. AGU*. p. 90(52), fall Meet. Suppl. In: Abstract U41C-0057.
- Wilson, J.S., Baldwin, D.S., 2008. Exploring the “Birch effect” in reservoir sediments: influence of inundation history on aerobic nutrient release. *Chem. Ecol.* 24, 379–386.
- Wurtsbaugh, W.A., Miller, C., Null, S.E., Justin De Rose, R., Wilcock, P., Hahnenberger, M., Howe, F., Moore, J., 2017. Decline of the world's saline lakes. *Nat. Geosci.* 10, 816–821.
- Yang, L., Lu, F., Wang, X., Duan, X., Song, W., Sun, B., Chen, S., Zhang, Q., Hou, P., Zheng, F., 2012. Surface methane emissions from different land use types during various water levels in three major drawdown areas of the three Gorges Reservoir. *J. Geophys. Res. Atmos.* 117, D10109.
- Yang, J., Liu, J., Hu, X., Li, X., Wang, Y., Li, H., 2013a. Effect of water table level on CO₂, CH₄ and N₂O emissions in a freshwater marsh of Northeast China. *Soil Biol. Biochem.* 61, 52–60.
- Yang, J., Liu, J., Hu, X., Li, X., Wang, Y., Li, H., 2013b. Effect of water table level on CO₂, CH₄ and N₂O emissions in a freshwater marsh of Northeast China. *Soil Biol. Biochem.* 61, 52–60.
- Yang, M., Geng, X., Grace, J., Lu, C., Zhu, Y., Zhou, Y., Lei, G., 2014. Spatial and Seasonal CH₄ Flux in the Littoral Zone of Miyun Reservoir near Beijing: the Effects of Water Level and its fluctuation. *PLoS One* 9, e94275.
- Zoppini, A., Marxsen, J., 2011. Importance of extracellular enzymes for biogeochemical processes in temporary river sediments during fluctuating dry–wet conditions. In: Shukla, G., Varma, A. (Eds.), *Soil Enzymology SE - 6, Soil Biology*. Springer, Berlin Heidelberg, pp. 103–117.